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An Army of One: Predaceous Diving Beetle Life History Stages Affect Interactions With Shared Mosquito Prey

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13 Short title: Complex life-history effects of predators on prey

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24 **Abstract**

25 Predators with complex life cycles often differ in their morphology, behavior, and trophic
26 position across their ontogeny, and may thus have variable effects on shared prey. We used the
27 predaceous diving beetle *Laccophilus fasciatus rufus* as our predator, whose larvae and adults
28 often co-occur in freshwater lentic systems. As a shared prey we used early and late instar *Culex*
29 *quinquefasciatus*, a common wetland mosquito. We found that single adult predators were more
30 likely to consume late instar prey compared to juvenile predators, who ate early and late instar
31 prey equally. A mixture of juvenile and adult predator stages led to higher consumption of prey
32 when compared to either predator type alone. Adult dytiscids consumed three times as many
33 dead prey compared to living ones, thus implying a role in scavenging for this life history stage.
34 Our work highlights that predators with complex life history stages may affect shared prey in
35 complicated and unpredictable ways.

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37 Keywords: complex life cycle, Culicidae, Dytiscidae, pond

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47 Temporary lentic aquatic systems are often dominated by animals that exhibit complex life
48 cycles, including anurans and many insects, however the interactions of these adult and juvenile
49 predators with other species are not well studied. A complex life cycle is a maturation cycle in
50 which different morphological changes occur during the growth of an organism (Wilbur 1980).
51 Examples of animals that have a complex life cycle amphibians (e.g., frogs), many marine
52 invertebrates, and many aquatic insects (e.g., Odonata, Coleoptera). Some insects exhibit indirect
53 metamorphosis, wherein adults and juveniles are morphologically distinct, as opposed to direct
54 metamorphosis where the emerging young are just smaller versions of the adults. Besides
55 morphological changes, some animals with complex life cycles have larval and adult stages that
56 occur in different habitats, have different diets, and are exposed to different interactions
57 (predation, mutualisms) (Wilbur 1980). Predators with complex life cycles may exert different
58 effects on a food web depending on their stage, and their effects may move beyond their current
59 niche (McCoy et al. 2009).

60 Although common in lentic habitats, predaceous diving beetles (Coleoptera: Dytiscidae),
61 have received little attention as predators. What is known is that they are important predators on
62 both invertebrate and vertebrate prey (Culler et al. 2014). This highly diverse family of predators
63 (~ 4,200 species worldwide) play a structurally important role in aquatic food webs (Thakare &
64 Zade 2011) and are potentially important predators of many taxa, including mosquito larvae, in
65 natural habitats (Larson et al. 2000), especially in fishless systems (Batzer & Wissinger 1996).
66 Adult dytiscids are often capable of flight and move among isolated bodies of freshwater, using
67 vision, chemoreception, and vibration to recognize and choose their prey (Hagen et al. 1976).
68 When comparing them to their juvenile counterparts, whom are obligate aquatic predators
69 requiring prey movement to elicit a response, adult dytiscids are not adept hunters (Johnson et al.

70 2003). Unlike adults, juveniles have also been seen to exhibit a variety of different predatory
71 behaviors including sit-and-pursue, sit-and-wait, and active hunting modes (Young 1967,
72 Formanowicz 1982, Yee 2010). Regarded as “clumsy”, the adults may select prey that is easy to
73 capture, including dead or dying individuals; scavenging on dead material that may be
74 energetically favorable (Bosi 2001). Adults and juvenile beetles often co-occur in the same
75 habitats (Larson et al. 2000), however it is unknown how the different stages within each species
76 differ with respect to predation.

77 Mosquito larvae are thought to be an important food item for many aquatic animals,
78 including many species of predaceous diving beetles (summarized in Culler et al. 2014, Shalan
79 & Canyon 2009). Since the 1990s, insecticides have become a widely acceptable method of
80 mosquito control, but resistance to these chemicals have been a challenge to effective control
81 measures (Brogdon & McAllister 1998). As a consequence of this resistance, aquatic ecologists
82 see the necessity to study the use of natural predators as a biocontrol on mosquito populations.
83 Research on larval mosquito population control via aquatic predators has become of recent
84 interest, however the focus on these investigations has been on factors like prey stage (Chandra
85 et al. 2008), habitat characteristics (Ohba & Ushio 2015), and prey type (Culler & Lamp 2009).
86 Currently, no studies have investigated the effects of different predator life-history stages on
87 consumption of mosquito prey.

88 We conducted a series of experiments to better understand the contribution of both the adults
89 and juveniles of the beetle *Laccophilus fasciatus rufus* on prey populations of the mosquito
90 *Culex quinquefasciatus*. *Laccophilus fasciatus rufus* is a common dytiscid in North America
91 (Larson et al. 2000) and has been shown to prey on mosquitoes (Pitcher & Yee 2014). *Culex*
92 *quinquefasciatus* (southern house mosquito) is a common open water mosquito that has a world-

93 wide distribution, and has been used as a prey species of dytiscid predation elsewhere (Aditya et
94 al. 2006, Chandra et al. 2008). Specifically, our objectives in this study were to 1) quantify
95 consumption rates of *L. f. rufus* adults and juveniles on different stages of mosquito larvae under
96 different prey and plant densities, 2) examine if combinations of predator life-history stages
97 affected predation rates compared to single predator stages, and 3) test adult dytiscid prey
98 preference between living and dead prey. We hypothesized that because of potential differences
99 in hunting behavior and other life-history differences (Yee 2010), adult and juvenile predators
100 will display different effects on prey populations. For instance, as adults are more likely to
101 exhibit searching behavior (Larson et al. 2010) and some juveniles are known to be sit-and-wait
102 hunters (Yee 2010), we may predict that adults would consume more prey given the potential for
103 higher encounter rates, and that these differences may also influence predation rates in single
104 versus multi-predator trials. Studying such interactions will improve the understanding of the
105 effect of the complex life history of predators on shared prey in general, and will lead
106 specifically to a better understanding of the bio-control abilities of dytiscids in natural
107 environments.

108

109 **Materials and Methods**

110 *Laccophilus fasciatus rufus*. No taxonomic keys exist to distinguish different species of
111 *Laccophilus* larvae (hereafter, juveniles, to distinguish from mosquito prey). Thus, to assure that
112 the correct species of *Laccophilus* was used, breeding of adults in a controlled setting was
113 necessary. Specifically, adult *L. f. rufus* were collected from aquatic habitats in and around
114 Hattiesburg, MS (31°19'38" N, 89°17'25" W). Males and females were placed in large plastic
115 tubs (91.5 x 61 x 20.3 cm) containing aquatic plants, pond water, food, and substrate. Plants

116 (*Ludwigia palustris*) were collected from ponds locally and rinsed repeatedly to remove
117 invertebrates. Tubs were covered with no-see-um mesh and left for several weeks at the USM
118 Science Park, located approximately 8 km east of the Hattiesburg campus, during which time any
119 juveniles that were produced were removed for experiments (genus level identifications were
120 made using Larson et al. 2000). For experiments requiring adults, additional *L. f. rufus* were
121 collected from aquatic habitats and isolated in separate plastic cups containing 100 mL filtered
122 pond water and a wooden perch. Adults and juveniles were fed once daily using frozen
123 chironomid larvae or live mosquitoes until experimental trials began. All juveniles used in the
124 experiments were either 2nd or 3rd instars. Predation by either adults or juvenile predator stages
125 were easily distinguishable based on known behavior: mosquitoes killed by adults were wholly
126 consumed or dismembered, whereas juveniles pierce and suck prey leaving only an empty
127 exoskeleton. Prey (*Culex quinquefasciatus*) were obtained from laboratory colonies (F₄ or less)
128 that were originally collected as egg rafts from areas near campus.

129 **Experiment 1. Predator stage and consumption of different prey stages.** To quantify
130 predation rates on shared mosquito prey, both juvenile and adult beetles were used separately in
131 feeding trials. Feeding trials were conducted in small plastic aquaria (20.3 x 15.2 x 12.7 cm)
132 filled with 3.9 L filtered pond water collected from ponds in the study area. In each aquarium,
133 three different levels of plant stem density were used: 0, 3, and 6 stems (hereafter no, low, and
134 high plant densities). We used *Ludwigia palustris*, a plant that is commonly found in dytiscid
135 habitats in the study area at variable densities (Pitcher & Yee 2014). Testing predation on
136 mosquitoes under different plant densities has been shown to affect predator-prey interactions
137 (Savino & Stein 2011, Yee, 2010) and we predicted that increasing plant density would increase
138 refugia for prey and thus reduce predation rates. Prey density trials consisted of three levels: 5,

139 10, or 15 of either early (1st and 2nd) or late (3rd and 4th) instar *Culex quinquefasciatus*, hereafter
140 low, medium, and high prey. In some lentic systems different levels of mosquito prey can also
141 affect predation rates (Alto et al. 2012). *Culex quinquefasciatus* is often found in open water
142 (Vinogradova 2000) and often cohabitates with these predators (unpublished data). Inclusion of
143 different sized prey let us examine how predator life stages affect predation across prey life
144 history stages. Plant density (3), prey density (3), and prey stage (2) were crossed to yield 18
145 combinations that were replicated 5 times for each predator stage. Uneaten mosquitoes were
146 counted after 4 hrs in each aquarium. Aquariums were placed in an incubator at 27° C on a 14:10
147 (dark:light) photoperiod (approximate summer conditions for the study area).

148 To assess differences in prey consumption a four-way analysis of variance (ANOVA) was
149 used to determine if differences existed among the different plant densities (3), prey densities (3),
150 prey stages (2), and predator stage (2). A $\log_{(x+1)}$ transformation was applied to the raw data to
151 meet assumptions of normality. Tukey's test were then conducted to assess differences among
152 specific treatment levels while controlling for experimental-wise error rates. All statistical
153 analyses were conducted in SAS (SAS 2004).

154 **Experiment 2. Single and multiple predator stages and prey consumption.** We examined
155 how single and mixed predator life history stages affected consumption of early and late instar
156 prey. Specifically, we placed either two adult predators, two juveniles, or one of each into
157 aquaria established in the same manner as described above, with 10 prey of each stage offered in
158 the single prey treatment levels and 10 of each in the combined level. For these trials, beetles
159 were starved 24 hrs prior to introducing them into aquaria to standardize hunger levels; trials ran
160 for four hours. We discarded one replicate of the mixed predator treatment level from analysis as
161 the adult beetle killed the juvenile. We also prepared 6 replicates of two juveniles and a juvenile

162 and adult predator without prey to evaluate potential predation among predators (we assumed
163 that adults were unlikely to kill one another) and three replicates with no predators (control) and
164 collected data as above.

165 A two-way ANOVA was used to assess differences in consumption of different prey stages
166 (early, late) across predator combinations (juvenile alone, adult alone, juvenile and adult). Raw
167 data met assumptions and differences among levels of significant treatment effects were assessed
168 using a Tukey adjustment.

169 **Experiment 3. Adult predator selection of prey.** Experiment 1 did not produce differences in
170 predation rates among prey densities or plant densities (see Results). These treatments were
171 subsequently excluded from this study, and we used three sprigs of plant for all replicates.
172 Furthermore, only late instar prey were utilized as adult dytiscids were observed to consume
173 significantly more late compared to early instar mosquito larvae. Specifically, we used three
174 different prey treatment levels to examine prey preference for adult beetles only: 10 dead
175 mosquito larvae, 10 living larvae, and 5 dead and 5 living. Larvae were freshly killed by placing
176 them in water in a microwave for approximately 1 minute. Each treatment level was replicated
177 six times yielding 24 experimental units. All other aspects of this experiment (e.g., aquarium
178 size, time until data collected) were the same as the ones described above.

179 A one-way ANOVA was used to test for differences between different prey treatment levels
180 (percent of prey eaten by adult dytiscids in the living, dead, of the combination of living and
181 dead treatment levels). Raw data met assumptions of the analysis.

182 **Results**

183 **Experiment 1. Predator stage and consumption of different prey stages.** We detected
184 significant effects of predator stage and a prey stage by predator stage interaction; other effects

185 were not significant (Table 1). Specifically, adult beetles consumed more late instar mosquitoes
186 compared to juvenile beetles, whereas both predator stages consumed a similar but lower number
187 of early instar mosquitoes (Fig. 1).

188 **Experiment 2. Single and multiple predators stages and prey consumption.** No prey died in
189 the no predator controls, however in two replicates of the controls without prey juveniles were
190 killed by adults (33%). About 30% more prey were consumed when an adult and juvenile were
191 together than when either stage was alone (Fig. 2A) ($F_{2,46} = 6.01$, $P = 0.005$). The highest
192 consumption was on early instar prey offered alone, followed by either early instars in
193 combination with late instars or late instars by themselves (Fig. 2B) ($F_{3,46} = 31.51$, $P < 0.001$).
194 Late instar prey offered with the early stage were consumed least overall (Fig. 2B). The
195 interaction between predator combination and prey combination was not significant ($F_{6,46} = 1.99$,
196 $P = 0.087$).

197 **Experiment 3. Adult predator selection of prey.** Adults ate three times as many dead prey
198 compared to living prey when both types were offered simultaneously (Fig. 3) ($F_{3,16} = 5.944$, $P =$
199 0.007). In addition, the overall consumption of live or dead prey did not vary when these types
200 were offered alone or in combination, indicating that prey density did not affect prey selection.

201

202 **Discussion**

203 It has been assumed that predators species are interchangeable in their effects on prey
204 (Fretwell 1987), however such an assumption is likely wrong, given that different predators may
205 act in dissimilar ways to enhance or weaker overall predation pressure in food webs (Schmitz
206 2007). However, little attention has been paid to predators with complex life cycles, wherein
207 different life history stages may exert different forces on shared prey. Our goal was to test for

208 consumption differences for adults and juveniles of *L. f. rufus* on a shared prey, which would
209 allow us to examine the specific nature of predation effects of a predator with a complex life
210 cycle on a shared prey. Our hypothesis that adult and juvenile predators would display different
211 effects on prey populations was generally supported. We found that adult *L. f. rufus* consumed
212 more late instar mosquito larvae compared to juveniles; adults also consumed more dead than
213 living prey. The higher consumption of larger prey by adult predators may be due to energetic
214 differences, as larger prey are likely an easier target for adults compared to juvenile predators
215 and have a higher caloric value. Adult beetles are fast-moving adept swimmers, whereas larvae
216 generally walk along the bottom or on surfaces and often sit and wait for prey, and thus capture
217 of larger prey is likely easier for adults compared to juveniles. However, we found no differences
218 in predation on early instars, suggesting that both juveniles and adults can equally affect small
219 mosquitoes. Although we found no significant differences between prey sizes within each
220 predator stage consumption of early and late instars for adult predators did approach significance
221 ($P = 0.084$), whereas juveniles did not ($P = 0.180$). This would seem to bolster the possibility that
222 the larger, more active adult predators are more adept in consuming larger versus smaller prey.
223 At present, no other study has compared predator consumption for different dytiscid life history
224 stages across prey sizes within a prey species. Aditya and Saha (2006) did find that feeding rates
225 of adult *Rhantus sikkimensis* were higher on small chironomid prey versus larger ones, a finding
226 that is opposite of ours. Moreover, Lundkvist et al. (2003) found differences in mosquito size
227 preferences for three species of dytiscids, and concluded that there should exist an inverse
228 relationship between predator size and prey size, a prediction our data does not support.

229 The differences between consumption by beetles for a single prey type in our study are
230 broadly consistent with work by Klecka and Boukal (2012) who showed that adult and juvenile

231 dytiscids (*Acilius* sp.) exhibited preferences for different prey, with juveniles preferring *Culex* sp.
232 and adult beetles preferring chironomids. This could be explained by differences in prey
233 movement and location. Because of a lack of refugia, chironomids were an easy target for
234 predators, and likely required low effort by adults to obtain them (Klecka and Boukal 2012).
235 Regardless of the mechanism, such ontogenetic diet shifts (ODS) might be expected as a way to
236 reduce intraspecific competition, and would also be predicted when animals change in
237 morphology, size, and behavior over their life cycle (Ohba 2009, Klecka & Boukal 2012). Such
238 shifts may not always be perfect, allowing a degree of overlap that would bring adults and
239 juveniles into direct competition. Indeed, Klecka and Boukal (2012) did show that diet overlap
240 was pronounced for life history stages in two species of dytiscids, but did not offer any
241 mechanism for how species may limit intraspecific competition. Instead of dampening
242 competition, we suggest that with greater diet overlap there may be more opportunities for
243 predation among the predators (i.e., intraguild predation (IGP)). We found some evidence for
244 IGP, but not symmetrical, as juveniles succumbed to predation by adults one third of the time in
245 the absence of prey and in one of our replicates when prey were present. As IGP (e.g., Nilsson &
246 Söderström 1988) and instances of cannibalism (e.g., Dending 1988, Hicks 1994, Yee, 2010)
247 exist among dytiscids, these interactions could further complicate the way in which changes in
248 predator life history may interact with prey, to perhaps change overall predation rates among life
249 history stages.

250 We did determine that the combined feeding of an adult and juvenile predator increased prey
251 consumption 30% over single predator stage trials. One explanation for this increased feeding is
252 due to predator spatial niches and foraging behavior. Adult *L. f. rufus* are active predators
253 (Pitcher & Yee 2014) whereas *L. f. rufus* larvae are mostly sit-and-wait predators (personal

254 observation); adults also move actively through the water column, whereas juveniles of this
255 species remain relatively motionless at the bottom or on plants. This suggests inherent spatial
256 differences among life history stages, and coupled with differences in how these predator stages
257 feed, may help to explain the synergistic effects with mixed versus single predator stages for
258 dytiscids. Such behavioral differences among dytiscid larvae in feeding mode and hunting
259 domain have been documented for larval dytiscids (Yee 2010), however this is the first study to
260 look at the potential role of larvae and adults to affect shared prey. One consequence of this work
261 is to suggest that there may be compounding effects upon prey populations in nature by predators
262 with complex life cycles (Wilbur 1980). To determine if this is the case, additional experiments,
263 wherein adult and juvenile predators of various densities are used, will need to be conducted.

264 Unintentionally, we also tested the effect of multiple predators of each prey stage. In
265 Experiment 1, single adult beetles ate more large prey but there were no differences between
266 prey sizes within beetle stage (Fig. 1), whereas in Experiment 2 when two adult predators were
267 tested they generally ate more early instars (predator effect combines data from adults and
268 juveniles, Fig. 2B). The experimental design was not identical between trials, however
269 differences in plant density and prey density that were investigated in Experiment 1 were non-
270 significant, and thus were eliminated in Experiment 2. Given this, differences in consumption
271 would seem to point to potential interactions between predators, an effect found in some other
272 studies. Aditya and Saha (2006), who tested predation of adults of the dytiscid *Rhantus*
273 *sikkimensis* at two different predator densities on mosquito and chironomid prey, noted
274 significant differences in prey consumed with two predators consuming more prey than three.
275 However, Chandra et al. (2008) found higher predation rates of two juvenile *Acilius sulcatus*
276 feeding on *C. quinquefasciatus* compared to one juvenile, although variation in prey

277 consumption was also affected by prey density and volume. The interaction of multiple predators
278 on shared prey is understudied in aquatic insects in general, and dytiscids specifically, but as the
279 presence of multiple predators is the norm in natural temporary water bodies such data that
280 explores predator density are needed.

281 We also showed that adult *L. f. rufus* ate more dead mosquitoes compared to live ones. If
282 adult dytiscids are a good bio-control agent then we would expect living prey to be preferred
283 when given the choice between dead and living mosquitoes. Velasco and Millian (2008) found
284 that adult dytiscids chose to scavenge on dead animal material rather than to hunt living prey. A
285 similar result was observed by Kehl and Dettner (2003) who also tested prey preference by
286 giving the dytiscid *Scarodytes halensis* mixed treatments of dead and living plankton (Copepoda
287 and Cladocera). In our experiment, adult *L. f. rufus* had the ability to attack living prey when
288 given no choice, but attacked fewer living prey when dead prey were available. Scavenging on
289 dead animal material is common in dytiscids (Hicks 1994, Larson et al. 2000), and could be
290 favored if it requires lower energy expenditure. Scavengers (especially ones that are capable of
291 flight) can potentially transfer energy between adjacent ecosystems (Payne & Moore 2006).
292 Considering the prevalence of this species in local water bodies (Pitcher & Yee 2014), the rate at
293 which it scavenges, and potential mobility, this could possibly impact nutrient cycles in areas
294 that they inhabit, although such speculation requires more testing.

295 Our results showed that beetles of both stages caused a significant decrease in mosquito
296 densities, and support the results of others for dytiscids' ability to decrease mosquito larvae
297 populations (e.g., Formanowicz 1982, Culler & Lamp 2009, Chandra et al., 2008). For example,
298 Chandra et al. (2008) observed that in a 24 hr period, juvenile *Acilius sulcatus* (Coleoptera:
299 Dytiscidae) ate on average 34 out of 200 late instar *C. quinquefasciatus* (~17%). The juvenile

300 dytiscids used in our experiment consumed 28% of the late instar *C. quinquefasciatus* larvae
301 offered, even though the amount of time for this study's trials were shorter than those by
302 Chandra et al. (2008). It is still unclear the degree to which adult dytiscids or larvae are
303 important predators on mosquitoes in natural wetlands (Lundkvist et al. 2003, Shaalan and
304 Canyon 2009), however it is likely that they do represent an important predator under a variety
305 of circumstances, especially in fishless environments (Larson et al. 2000). Many different control
306 agents are utilized for population suppression of mosquito larvae including vertebrate predators
307 such as non-game fish (Kern 2004). In an experiment that tested prey preference of dytiscids and
308 mosquito fish it was observed that mosquito fish did not show a preference for mosquitoes,
309 however dytiscids did (Culler & Lamp 2009). Compilation of knowledge surrounding different
310 species of dytiscids may allow researchers to construct better bio-control strategies that are more
311 efficient than single species approaches.

312 Plant density had no significant effect on consumption of mosquito prey. Different plant
313 densities were utilized because we predicted that higher plant densities would provide refugia for
314 prey. Elsewhere (Yee 2010), the presence of plants altered the behavior of larval dytiscids when
315 attacking their prey. One possible explanation for the lack of an effect of plants could be that the
316 plant stem densities used may not have been appropriate to allow prey to use as shelter or as a
317 vantage point for predators. Another explanation could be that *Culex* sp., including *C.*
318 *quinquefasciatus*, are open water dwellers and would not utilize plant refugia (Clements 1999).
319 Thus, even when offered plants as shelter, they may aggregate in the open water areas of the
320 habitat, where they would be vulnerable to predators. However, mosquitoes staying at the surface
321 regardless of plant density may also be a form of anti-predator behavior (Ohba & Ushio 2015).
322 Such interactions between habitat factors, prey type, and predator life history and species in

323 dytiscids have not been explored in detail.

324 We detected no significant relationship of prey density on consumption rates. Formanowicz
325 (1982), also did not find prey density to affect consumption rates across five different prey
326 densities for three different species of juvenile dytiscids. He also noted no difference between
327 predator searching times, handling time, and prey densities. In this case, it did not seem to matter
328 what density of prey that was administered, suggesting that the dytiscids take the same amount of
329 time to recognize, handle, and consume each prey. Additionally, Formanowicz (1982) attributed
330 his results to the many different ways that juvenile dytiscids can hunt for prey. For instance, at
331 low densities of prey juveniles would actively search at all times, whereas in high densities of
332 prey they utilized a sit and ambush tactic (Formanowicz 1982). Others have found that prey
333 density affects consumption of prey (Aditya & Saha 2006), however explanations for why this
334 might occur are lacking.

335 It is clear that adult and juvenile *L. f. rufus* have different effects on a shared mosquito prey.
336 The compounding effect that both life stages of dytiscids may have on shared prey populations is
337 an underexplored area of research, but could be useful in understanding the degree to which
338 dytiscids serve, for instance, as biocontrols of mosquitoes in natural wetlands. Moreover,
339 research on intraguild predation would also be a necessary area of inquiry, where we hypothesize
340 that adult dytiscids would play the role top predator, the juvenile as the intermediate prey, and
341 the mosquito larvae as the basal resource. Our work points to an asymmetry in predation for
342 different life-history stages of *L. f. rufus*, an area that has not been identified previously.

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462 **Table 1.** Results of 4-way ANOVA showing effects of predator stage (juvenile, adult), prey
 463 stage (early or late instar mosquito larvae), plant density (low, medium, high), and prey density
 464 (5, 10, or 15 mosquito larvae) and all their interactions on consumption rates of mosquito prey.
 465 Significant effects are presented in bold.

Factor	df	F	p-value
Predator Stage (D)	1, 108	4.48	0.0367
Prey Stage (P)	1, 108	0.02	0.8835
Plant Density (L)	2, 108	0.13	0.8823
Prey Density (S)	2, 108	0.11	0.8919
D x P	1, 108	9.48	0.0026
D x L	2, 108	0.13	0.8782
D x S	2, 108	0.09	0.9163
P x L	2, 108	0.24	0.7892
P x S	2, 108	1.67	0.1926
L x S	4, 108	0.39	0.8122
D x P x L	2, 108	0.37	0.6898
D x P x S	2, 108	0.08	0.9222
D x L x S	4, 108	0.28	0.8895
P x L x S	4, 108	0.29	0.8839
D x P x L x S	6, 108	0.08	0.9901

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467 **Figure legends**

468 **Fig. 1** Results of the significant interaction between predator stages (juvenile and adult beetles)
469 and prey stages (early and late instar *Culex quinquefasciatus*) on mean (\pm SE) consumption rates.
470 Means that do not share a letter are significantly different based on mean separation with a
471 Tukey correction.

472 **Fig. 2** Effects of single and combined predator life history stages on different stages of shared
473 prey, *Culex quinquefasciatus*. A) Significant effect of predator stage (2 juvenile, 2 adult, or 1 of
474 each *Laccophilus fasciatus rufus*) on mean (\pm SE) percent consumption of larval *Culex*
475 *quinquefasciatus*. B) Significant prey stage effect for early (1st, 2nd) and late (3rd, 4th) instars of
476 prey offered either alone or in combination. In all panels means that do not share a letter are
477 significantly different based on mean separation with a Tukey correction.

478 **Fig. 3** Results of a one-way ANOVA on mean (\pm SE) consumption of mosquitoes by adult
479 dytiscids. Treatment levels included either 10 dead, 10 live, (noted as “10 prey” in the legend) or
480 a mixture of 5 living and 5 dead late instar mosquitoes (*Culex quinquefasciatus*). Means that do
481 not share a letter are significantly different based on mean separation with a Tukey correction.

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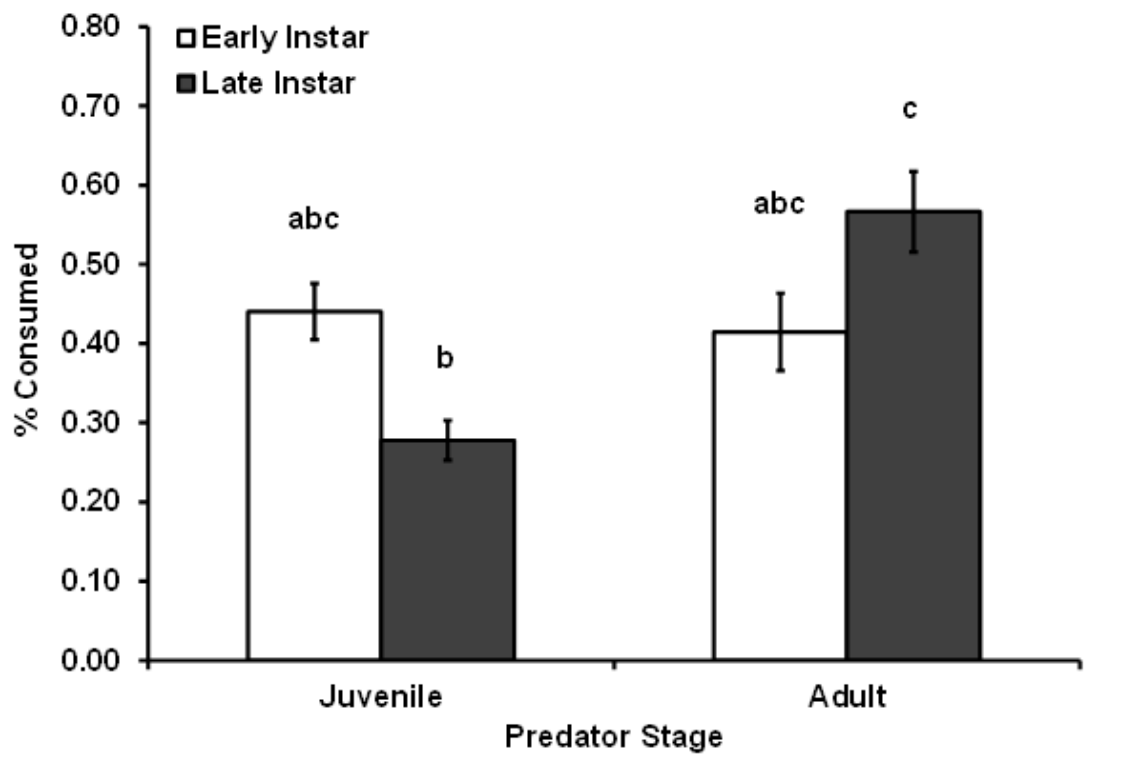
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508 Fig. 1

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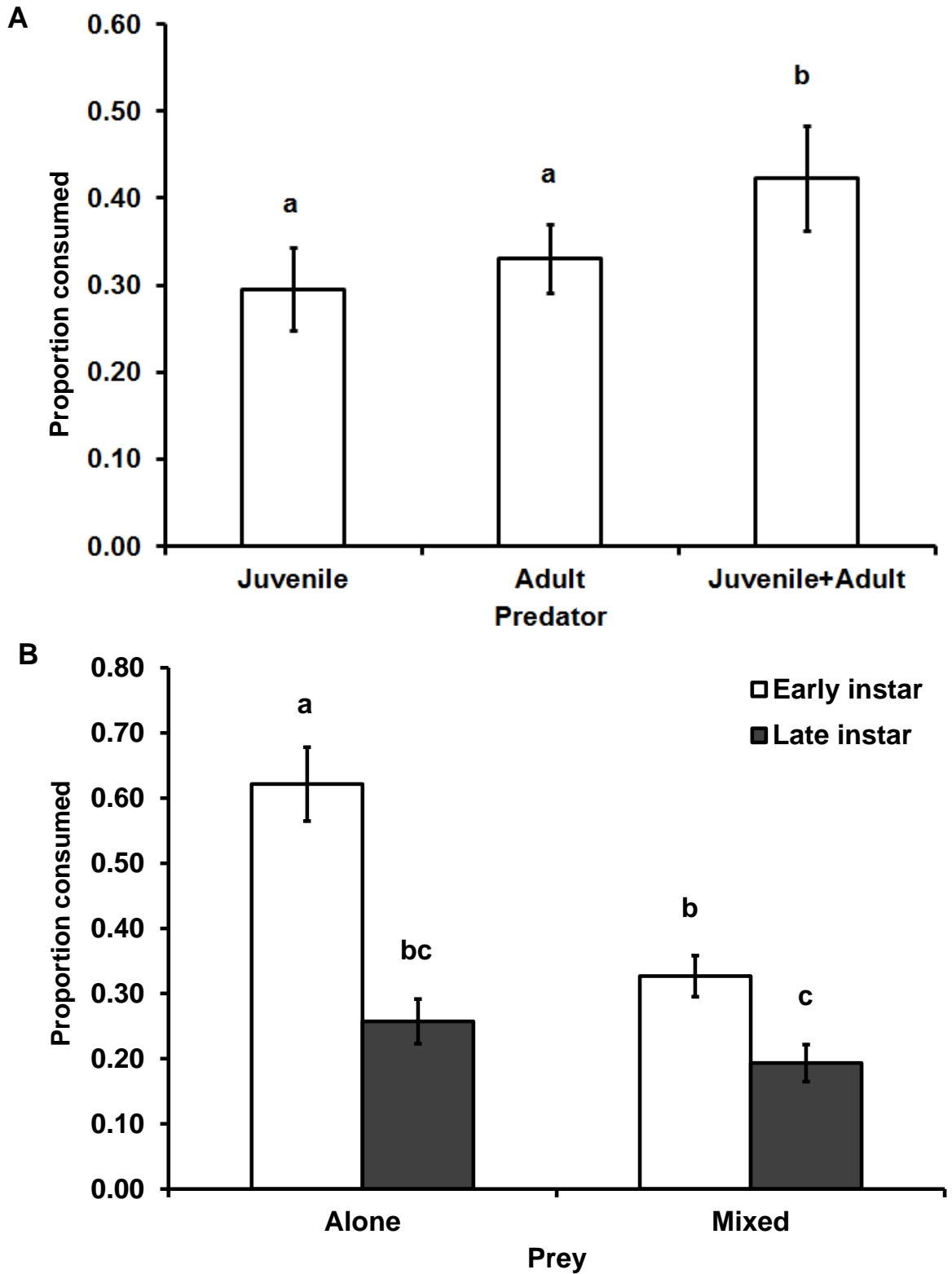


Fig. 2

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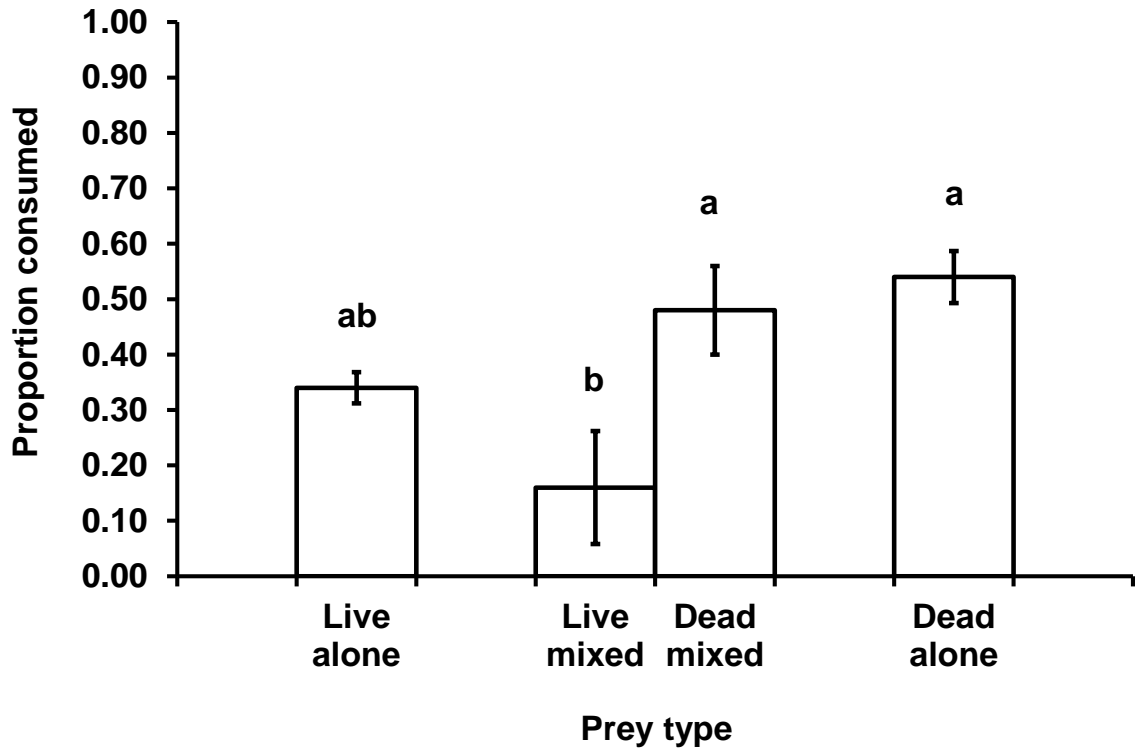


Fig. 3