1   Short title: plant reproductive tissues and prey consumption

2   Conspecifics, not plant reproductive tissues, reduce omnivore prey consumption

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Abstract

Plant reproductive tissues (PRTs) can decrease (via reduced consumption) or increase (via numerical response) an omnivores consumption of animal prey. Although PRTs can increase predation pressure through numerical responses of omnivores, PRTs may also suppress predation by increasing omnivore interactions with conspecifics. Despite this potential, studies of the impacts of PRTs on predation by omnivores often overlook the effect of these tissues on intraspecific interactions between omnivores. We designed three studies to examine how PRTs and conspecific density impact prey consumption by ladybeetle omnivores. First, we assessed how PRTs impact scale insect consumption by isolated ladybeetles. Second, we measured how PRTs influence ladybeetle prey suppression when numerical responses were possible. Third, because initial experiments suggested the consumption rates of individual ladybeetles depended upon conspecific density, we compared per capita consumption rates of ladybeetles across ladybeetle density. PRTs did not influence prey consumption by isolated ladybeetles. When numerical responses were possible, PRTs did not influence total predation on prey despite increasing ladybeetle density, suggesting that PRTs decreased per capita prey consumption by ladybeetles. The discrepancy between our lab and field studies is likely a consequence of differences in ladybeetle density - the presence of only two other conspecifics decreased per capita prey consumption by 76%. Our findings suggest that PRTs may not alter the population level effects of omnivores on prey when omnivore numerical responses are offset by reductions in per capita predation rate.

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Introduction

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43   Omnivory (i.e. consuming resources from multiple trophic levels) [1] is ubiquitous within

44   several taxa (e.g. birds, mammals, reptiles, insects, and fishes) and influences the structure and

45   function of communities [2-3]. Interactions between omnivores and their plant and animal prey

46   can account for up to 78% of species' links in food webs [4]. Despite their prevalence, we lack a

47   basic understanding about how plant reproductive tissues (hereafter, PRTs) affect interactions

48   between omnivores and their prey in natural systems. Some studies suggest that PRTs decrease

49   prey consumption by omnivores [5-6], whereas others suggest the opposite [7]. This discrepancy

50   may be exacerbated by methodological approaches and the spatial scale of the study [8-9]. For

51   instance, many omnivory studies focus on isolated omnivores feeding on a sub-set of possible

52   resources, which only allows omnivore consumption to depend on resource density and the

53   availability of PRTs [8,10]. Such approaches fail to allow important intraspecific interactions

54   (e.g., mating, cannibalism, and competition) and interspecific interactions (e.g., predation and

55   competition), whose occurrence may be altered by PRTs [9, 11-13]. Understanding how PRTs

56   and conspecific density affect prey consumption by omnivores may help predict when and where

57   omnivores exert top-down control on prey populations.

58   PRTs may suppress omnivore consumption of prey if these resources are equally (or

59   more) palatable than prey or provide critical habitat structure [14-16]. For example, when PRTs

60   (pollen) was available, omnivorous phytoseiid mites (*Iphiseius degenerans*) consume fewer prey

61   (larval *Euseius stipulatus*), leading to lower prey mortality [13]. Similarly, omnivorous big-eyed

62   bugs (*Geocoris punctipes*) consume fewer pea aphids (*Acyrthosiphon pisum*) and are less

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63   effective at regulating pea aphid populations when high quality plant tissue (lima bean pods) is

64   locally available [5].

65   In contrast, omnivore prey consumption may increase in the presence of PRTs if these

66   resources increase the local abundance of omnivores through a numerical response (i.e.

67   aggregation and enhanced fitness) [5, 15-18] or by lengthening omnivore persistence in habitats

68   with low prey densities [1, 17, 19-21]. For instance, habitat patches containing high densities of

69   PRTs (lima bean pods) had larger populations of omnivores and omnivores were less-likely to

70   emigrate from patches containing lima bean pods [17].

71   Elevated conspecific density, due to omnivore numerical responses to PRTs, may

72   increase the frequency of intraspecific interactions (i.e. interactions between conspecifics such as

73   mating, cannibalism, territoriality, competition) [22-23], thereby decreasing the per capita prey

74   consumption by omnivores [24-26]. For example, flatworm predators (*Stenostomum virginanum*)

75   reduce their per capita predation rates on protozoan prey in the presence of conspecifics [26].

76   Similarly, larval tiger salamanders lower their foraging rates when larger conspecifics are

77   present, likely to minimize their risk of being cannibalized [27]. While the effects of PRTs on

78   intraspecific (e.g., cannibalism) and intraguild interactions have been well-studied [see 9, 11-13],

79   few studies have aimed to understand how changing omnivore densities (associated with

80   numerical responses to PRTs) can indirectly affect prey population dynamics in the field.

81   Most empirical studies testing the impacts of PRTs on omnivore prey consumption have

82   used insect omnivores as model systems [see 5, 7, 17, 28-32]. Many insects, like omnivores

83   belonging to other taxa like foxes, sharks, and coyotes, are active predators [33-37], meaning that

84   they continuously search for prey [38]. This suggests that studies of omnivorous insects may

85   inform how non-insect omnivores impact prey populations.

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86   Here, we assessed how PRTs and conspecific density affect the foraging behavior of an

87 omnivorous salt marsh ladybeetle (*Naemia seriata*) feeding on scale insects (*Haliaspis*

88 *spartinae*). We used laboratory mesocosms to assess the impacts of PRTs [i.e. cordgrass

89 (*Spartina foliosa*) flowers] on ladybeetle per capita consumption of scale insects. We paired

90 laboratory mesocosms with a field study to assess the impact of cordgrass flowers on ladybeetle

91 and scale insect density under natural conditions, where numerical responses were possible.

92 Finally, to reconcile our laboratory and field studies, we conducted a laboratory no-choice

93 feeding assay to assess how conspecific density impacts ladybeetle per capita scale insect

94 consumption.

Methods

Study system

97   We assessed how PRTs and conspecific density influence the ability of the omnivorous

98 ladybeetle, *Naemia seriata* (hereafter ladybeetle), to suppress populations of its insect prey, the

99 armored scale insect *Haliaspis spartinae* (hereafter, scale insects). Scale insects are specialist

100 phloem-feeders on the foundational salt marsh plant, *Spartina foliosa* (hereafter, cordgrass). We

101 used this ladybeetle-scale insect model system for three reasons. First, ladybeetles in this system

102 are facultative omnivores, as access to cordgrass pollen facilitates ladybeetle survival in the

103 absence of other dietary resources [18]. Specifically, adult ladybeetles provided only access to

104 cordgrass pollen survived 1.97-times longer than ladybeetles provided access to no food

105 resources. This suggests that in the absence of other prey resources, adult ladybeetles likely

106 consume cordgrass pollen to promote their longevity. Second, adult ladybeetles show resource-

107 dependent aggregation in the field, with ladybeetles tending to preferentially aggregate to

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108   habitats containing both scale insects and cordgrass flowers over habitats lacking these resources

109   [18]. Third, adult ladybeetles often aggregate with conspecifics on cordgrass flowers (S. Rinehart

110   and J.D. Long *unpublished data*), suggesting that cordgrass flowers may be a hub of ladybeetle

111   intraspecific interactions (e.g. mating and territoriality).

Effect of cordgrass flowers on scale insect consumption by isolated ladybeetles

114   To test how Flower Access [2 Levels: Flower Access Present (FA+), Flower Access

115   Absent (FA-)] affects consumption of scale insects by individual adult ladybeetles, we conducted

116   a mesocosm experiment at the San Diego State University Coastal and Marine Institute

117   Laboratory (CMIL). On 20-July-2015, we collected 20 sediment plugs (15 x 15 cm; diameter x

118   deep) each containing a single flowering cordgrass stem infested with scale insects from

119   Sweetwater Marsh (South San Diego Bay; 32° 38' 15.8''N, 117° 06' 37.5''W). We observed

120   pollen on all cordgrass stems collected at this time. We planted cordgrass stems and field-

121   collected sediment in 2.6 L plant pots with holes for drainage (Elite Nursery Containers; 300

122   Series). We used toothbrushes to remove all non-scale insect resources (e.g., leafhoppers of

123   pollen) from cordgrass leaves and to standardized initial mean total scale insect density to $559 \pm$

124   73 insects stem^{-1} (mean $\pm$ SE). We collected ladybeetles from two sites, Sweetwater Marsh and

125   San Dieguito Lagoon (32° 58' 40.4''N, 117° 14' 32.8''W).

126   We placed all potted plants in an outdoor, flow-through seawater table. Plants were

127   rearranged randomly each week. We connected our seawater table to a tidal control system that

128   automatically changed tank tidal conditions [between high (plant pots submerged) and low (plant

129   pots not submerged)] at preset intervals creating tidal conditions like those experienced by

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130 cordgrass at Sweetwater Marsh at a tidal height of 1.5 m above sea-level. We let potted plants

131 acclimate to tank conditions for two weeks prior to the experiment.

132   On 03-Aug-2015, we randomly assigned potted cordgrass plants to a Ladybeetle (Present,

133 Absent) and a Flower Access treatment [Flower Access Present (FA+), Flower Access Absent

134 (FA-)]. All treatments had scale insects present (n=5). In the Ladybeetle Present treatment, we

135 introduced a single adult ladybeetle into each replicate. We replaced ladybeetles every other

136 week, as we experienced a 10% mortality rate each week. In FA- treatments, we placed

137 cordgrass flowers in 16 x 14 cm Glad Fold-Top plastic bags (The Glad Company; Oakland,

138 California). We secured bags to plants with a cable tie. These bags prevented ladybeetle access

139 to the flowers and thus indirectly manipulated their ability to access cordgrass pollen. In FA+

140 treatments, we did not restrict ladybeetle access to cordgrass flowers and pollen. However, we

141 controlled for the cable tie by attaching a cable tie to all cordgrass stems in FA+ treatments. We

142 prevented insect dispersal among replicates by covering each entire replicate with nylon insect

143 mesh (54 x 50 cm, height x width, mesh size = 1 mm). We maintained this experiment for 6

144 weeks until 14-Sept-2015.

145   To assess the effect of Flower Access and Ladybeetles on scale insect density, we

146 monitored adult and juvenile (hereafter "crawler") scale insect density every two weeks. Adult

147 and crawler scale insects can be distinguished by their mobility and morphology (e.g. Unlike

148 crawlers, adults are immobile and produce a white waxy test). We corrected for natural

149 fluctuations in scale insect density by pairing replicates from the Ladybeetle Present and

150 Ladybeetle Absent treatments and using the formula: $P_i (A_f/ A_i) - P_f$[39]. Here, P_i and P_f

151 represent the initial and final scale insect density of Ladybeetle Present treatments and A_i and A_f

152 represent the initial and final scale insect density of Ladybeetle Absent treatments. This

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153   correction allowed us to detangle natural variation in scale insect population dynamics from

154   effects of Flower Access. We then compared our corrected adult, crawler, and total scale insect

155   per capita consumption by ladybeetles between Flower Access (FA+, FA-) treatments using a

156   series of two-sample t-tests. All corrected scale insect consumption data were square-root

157   transformed. We conducted all statistical analyses in JMP v. 13 (www. jmp.com).

Effect of cordgrass flowers on ladybeetle aggregation and scale insect consumption

160   To assess how Flower Access [(Flower Access Present (FA+), Flower Access Absent

161   (FA-)] influences ladybeetle aggregation and consumption of scale insects, we conducted a fully-

162   factorial study at San Dieguito Lagoon. On 18-Aug-2016, we established 20 - 0.25m^2 circular

163   plots (separated by at least 1m) in a monospecific cordgrass stand infested with scale insects.

164   Although ladybeetles may feed on other prey resources (e.g., leafhoppers), they likely constitute

165   only a small portion of ladybeetle diets, as alternative prey resources are rare compared to scale

166   insects. For example, at the experimental site, scale insect density was $16,177 \pm 2,174$ per

167   0.25m^2 (mean $\pm$ SE), while leafhopper density was only 25 ± 2.8 per 0.25m^2 (mean $\pm$ SE; S.A.

168   Rinehart *unpublished data*). All plots started with at least four flowering cordgrass stems, a

169   cordgrass stem density of 22 ± 1.1 (mean $\pm$ SE), and zero ladybeetle egg clutches. We randomly

170   allocated plots to each treatment (n=10). In the FA- treatment, we covered all cordgrass flowers

171   with 16 x 14 cm Glad Fold-Top plastic bags (The Glad Company; Oakland, California) and

172   secured bags in place with a cable tie. In the FA+ treatment, we did not inhibit ladybeetle access

173   to cordgrass flowers. However, we controlled for the presence of cable ties in the FA+ treatment

174   by applying cable ties to all stems included in the study. We used plastic bags to inhibit

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175   ladybeetle access to cordgrass flowers rather than mesh bags, as plastic also inhibits the

176   transmission of plant volatile cues [40].

177   To assess how Flower Access influences ladybeetle aggregation, we monitored the

178   density of all ladybeetle life stages (adults, larvae, and egg clutches) in each plot weekly between

179   08-Aug-2016 and 22-Sept-2016. We determined the density of ladybeetle life stages using two-

180   minute timed searches. During timed searches, we examined all stems in each plot, starting at the

181   soil-air interface and working toward the apical meristem. All ladybeetle life stage densities were

182   log transformed. We tested for effects of Flower Access on the density of each ladybeetle life

183   stage using separate RM-ANOVAs with Flower Access as a fixed factor and week as the

184   repeated measure.

185   To understand how Flower Access influences ladybeetle suppression of scale insect

186   populations under field conditions, we recorded scale insect density on two focal cordgrass stems

187   (all focal stems had flowers present) in each replicate on two dates (18-Aug-2016 and 22-Sept-

188   2016). We summed the total scale insect density on focal stems in each plot for both timepoints

189   and used this value to calculate the change in scale insect density per plot over the five-week

190   study. The change in scale insect density was square-root transformed. We then compared the

191   change in scale insect density (per two focal stems) between Flower Access (FA+ vs. FA-)

192   treatments using a two-sample t-test.

193 **Effect of conspecific density on ladybeetle per capita scale insect**

194 **consumption**

195   Because 1) the impact of flower access on per capita consumption of scale insects

196   differed between our laboratory and field studies (no effect in the laboratory, decreased

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197   consumption in the field) and 2) intraspecific interactions between ladybeetles also varied

198   between these studies (absent in the laboratory, present in the field), we conducted a no-choice

199   feeding assay to examine the influence of ladybeetle density on per capita consumption of scale

200   insects. On 10-Nov-2017, we collected ladybeetles and flowering, scale-infested cordgrass stems

201   (clipped at the air-soil interface) from San Dieguito Lagoon two hours prior to the study.

202   Collected stems and ladybeetles were transported to the CMIL, where we counted the initial total

203   scale insect density per cordgrass stem. Cordgrass stems were then randomly allocated to each

204   Ladybeetle Density treatment: 0, 1, 2, or 3 per stem. We based the upper Ladybeetle Density

205   treatment on survey data showing that adult ladybeetles tend to aggregate in groups of 3 ± 0.6

206   individuals per cordgrass stem. Sample size was five for all Ladybeetle Density treatments

207   except the 0 treatment, which had three replicates. We then placed the clipped end of each

208   cordgrass stem into its own 13 x 13 cm (height x diameter) cylindrical plastic container filled

209   with 700 ml of tap water (to act as a vase) and enclosed the whole cordgrass stem and plastic

210   container in a 54 x 13 cm (length x width) bag made with white nylon insect mesh (6 mm mesh

211   opening). Finally, we introduced zero, one, two, or three adult ladybeetles to each replicate. We

212   accidentally added four ladybeetles to one of the three ladybeetle treatments. All replicates were

213   maintained at a mean temperature of 21.1°C with a 12:12 hour light-dark cycle (85.6 ± 5 μmol

214   photons • m-2 • s -1 (PAR); Philips Natural Light 40W). After three days, we removed

215   ladybeetles (no ladybeetles were lost or cannibalized during the study) and counted the final total

216   scale insect density on all stems. We then calculated the total scale insects consumed (between

217   all ladybeetles) and the per capita scale insect consumption of ladybeetles in all replicates.

218   Because there was no change in scale insect density in zero ladybeetle replicates during the study

219   (one-sample t-test: $t_{2.00} = 0.256$, $p = 0.589$), we removed this treatment from further analysis and

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220   attributed all reductions in scale insect density to ladybeetle feeding. Using our 1,2, and 3

221   ladybeetle treatments, we tested for the effects of ladybeetle density (consistent through the

222   study) on total scale insect consumption and the per capita consumption of ladybeetles using

223   linear regressions with ladybeetle density as the independent factor. Total scale insects consumed

224   (between all ladybeetles) and the per capita scale insect consumption were square-root

225   transformed prior to analyses.

226   On the 2nd and 3rd days of the assay (11-Nov-2017 and 12-Nov-2017), we conducted

227   behavioral observations of ladybeetles in all replicates. On each day, we recorded the location

228   (i.e., plant leaf, plant stem, plant flower, or mesh bag) of each ladybeetle in each replicate

229   between the hours of 08:00 and 10:00 am. We then calculated the number of ladybeetles in each

230   replicate that were on any part of the plant (e.g., leaves, stem, or flower) at the time of

231   observation. We tested for effects of ladybeetle density on the number of ladybeetles on any part

232   of the plant using a RM-ANOVA with Ladybeetle Density as a fixed factor and Observation Day

233   as the repeated measure.

Results

Effect of cordgrass flowers on scale insect consumption by isolated ladybeetles

237   Although ladybeetles have been observed consuming pollen (S.A. Rinehart *personal*

238   *observation*), consumption of adult, crawler, and total scale insects by isolated ladybeetles was

239   not affected by access to cordgrass flowers (Adults: $t_{6.59} = 0.052$, p = 0.96; Crawlers: $t_{5.32} =$

240   0.596, p = 0.576; Total: $t_{7.89} = 0.216$, p = 0.834; Fig 1).

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241 **Fig 1. Effect of PRTs on isolated ladybeetle foraging.** Control corrected mean (± SE)

242 consumption by isolated adult ladybeetles of a) adult, b) crawler, and c) total scale insects (n =

243 5).

Effect of cordgrass flowers on ladybeetle aggregation and scale insect consumption

246 In our field experiment, adult ladybeetle density depended on Flower Access ($F_{1,107}$ =

247 43.69, p <0.001; S1 Table) and week ($F_{5,107}$ = 6.73, p < 0.001). Ladybeetles increased with both

248 factors. Flower Access and week also had an interactive effect on local adult ladybeetle density

249 ($F_{5,107}$ = 6.65, p < 0.001, Fig 2a). This interaction resulted from the differential effects of Flower

250 Access on adult ladybeetle density through time. Specifically, adult ladybeetle density in plots

251 with flower access increased by 412%, while adult ladybeetle density in plots without flower

252 access actually decreased by 8% over the five-week study. Additionally, this effect was

253 strengthened by differences in the initial adult ladybeetle density between treatments, as plots

254 without flower access tended to have more adult ladybeetles than plots with flower access at the

255 start of the study [Initial Adult Ladybeetle Density: BF: 3.7 ± 0.56 (mean ± SE); UBF: 2.5 ± 0.34

256 (mean ± SE); Two-Sample T-Test (Factor = Flower Access): $t_{14.9}$ = 1.83, p = 0.087].

257 **Fig 2. Effect of PRTs on ladybeetle population dynamics in the field.** Mean (± SE) density of

258 ladybeetle a) adults, b) larvae, and c) egg clutches in 0.25m^2 manipulated field plots. Flower

259 Access treatments (n= 10) are as follows: Flower Access Present (FA+) and Flower Access

260 Absent (FA-).

261 Similar to effects on adult ladybeetles, larval ladybeetle density was impacted by Flower

262 Access ($F_{1,107}$ = 5.67, p = 0.019; S2 Table) and week ($F_{5,107}$ = 5.08, p <0.001). Regardless of

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263   flower access, larval ladybeetle density peaked in all plots at week two (Fig 2b). However, the

264   presence of cordgrass flowers increased larval ladybeetle density by 36% over the five-week

265   study, while removing access to cordgrass flowers decreased larval ladybeetle density by 40%

266   after five weeks.

267   The density of ladybeetle egg clutches depended upon time ($F_{5,107} = 22.3$, p <0.001; S3

268   Table), with clutch density peaking at week three in both treatments. Flower Access had no

269   effect on egg clutch density ($F_{1,107} = 0.38$, p = 0.539; Fig 2c), despite adult ladybeetles being 4x

270   more abundant in Flower Access Present plots.

271   Total scale insect density declined in both treatments over the five-week study (Fig 3).

272   However, there was no difference between Flower Access treatments in the change in scale

273   insect density during the study, despite the higher density of adult ladybeetles in plots with

274   flower access ($t_{13.07} = 0.347$, p = 0.734).

275   **Fig 3. Effect of PRTs on ladybeetle foraging in the field.** Mean (± SE) change in scale insect

276   density on two focal cordgrass stems in our $0.25m^2$ manipulated field plots (n = 10).

Effect of conspecific density on ladybeetle per capita scale insect consumption

279   In the presence of 1-3 conspecifics, adult ladybeetle density had no effect on the total

280   number of scale insects consumed (linear regression: $R^2 = 0.07$, p = 0.341; Fig 4a) and no

281   cannibalistic activities between ladybeetles occurred. This result suggests that as conspecific

282   density increased, per capita consumption of scale insects declined (linear regression: $R^2 = 0.489$,

283   p = 0.002 Fig. 4b). For example, adult ladybeetle per capita scale insect consumption (over three

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284 days) was 201 ± 58 (mean ± SE) for individual ladybeetles, but only 48 ± 20 (mean ± SE) for

285 ladybeetles with two conspecifics (i.e. three adult ladybeetle treatment).

286 **Fig 4. Effect of conspecific density on ladybeetle foraging rates.** Mean (± SE) per capita

287 consumption by adult ladybeetles of a) adult scale insects and **b)** total scale insects. Sample size

288 five for all ladybeetle density treatments except the 3-ladybeetle treatment (n = 4) and 4-

289 ladybeetle treatment (n= 1).

290   The number of ladybeetles observed on cordgrass plants (i.e., either leaves, stem, or

291 flower) was not affected by Ladybeetle Density ($F_{2,12} = 0.68$, p = 0.523) or Observation Day

292 ($F_{1,12} = 4.00$, p = 0.069; S4 Table, S1 Fig). For example, during the first observation day,

293 replicates with 1 ladybeetle had 0.6 ± 0.24 (mean ± SE) ladybeetles present on the cordgrass

294 plant, while replicates with 3+ ladybeetles had 1.0 ± 0.32 (mean ± SE) ladybeetles on the

295 cordgrass plant. Similarly, on the second observation day replicates with 1 ladybeetle had 0.2 ±

296 0.2 (mean ± SE) ladybeetles present on the cordgrass plant, while replicates with 3+ ladybeetles

297 had 0.4 ± 0.4 (mean ± SE) ladybeetles on the cordgrass plant. Thus, regardless of ladybeetle

298 density within the replicate, ladybeetle density on the cordgrass plant appears to remain constant-

299 suggesting that adult ladybeetles may avoid habitats already occupied by conspecifics.

Discussion

301   Plant reproductive tissues (PRTs) can increase or decrease prey consumption by altering

302 omnivore foraging behavior. In laboratory mesocosms, isolated adult ladybeetle prey

303 consumption was unaffected by cordgrass flowers (Fig 1). In the field, habitat patches containing

304 access to cordgrass flowers attracted 4x as many adult ladybeetles compared to habitats lacking

305 flower access (Fig 2a). However, elevated ladybeetle densities in habitats with cordgrass flower

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306   access did not result in greater loss of scale insect prey (Fig 3), suggesting that PRTs resources

307   reduced ladybeetle per capita consumption of scale insects. This discrepancy (PRTs had no effect

308   in the lab but reduced per capita prey consumption in the field), may be related to intraspecific

309   interactions (e.g., interference competition) between ladybeetles which were absent in the lab

310   study with isolated ladybeetles. This hypothesis is supported by our finding that increasing

311   conspecific density reduced per capita consumption of scale insects by ladybeetles. Overall,

312   these observations suggest that PRTs may not impact the population level effects of omnivores

313   on prey when numerical responses of omnivores are offset by reductions in their per capita

314   predation rates.

315   PRTs decreased per capita consumption by omnivores on animal prey in our field study

316   that allowed for intraspecific interactions between omnivores. Although access to PRTs (i.e.

317   cordgrass flowers) increased adult and larval omnivore populations (412% and 36%,

318   respectively), this did not translate into a change in animal prey density. Thus, our laboratory

319   study of isolated adult omnivores and our field study contradict each other - access to PRTs

320   reduced per capita consumption of animal prey by omnivores in the field but not the lab.

321   Omnivore feeding rates in the presence of PRTs may have differed in our laboratory and

322   field experiments for two reasons. First, local environmental conditions may alter omnivore

323   consumption of prey. For example, temperature can directly impact the metabolic rate of

324   ectothermic omnivores, altering their energetic needs and, in turn, their foraging rates. However,

325   we tried to minimize differences in environmental conditions between the laboratory and the

326   field by 1) standardizing the month (August) of both experiments and 2) running our laboratory

327   mesocosm study in outdoor seawater tables with natural tidal cycles (exposing experimental

328   units to the ambient environmental conditions in southern California).

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329   Second, the density of omnivores differed between our first laboratory (single omnivore)

330   and field (multiple omnivores) studies. Differences in omnivore density may explain our

331   conflicting findings if intraspecific interactions (e.g. mating, territoriality, or cannibalism) reduce

332   omnivore consumption of focal prey resources. This seems likely, since our laboratory no-choice

333   feeding assay found that conspecifics reduce ladybeetle per capita scale insect consumption (Fig

334   4). These findings parallel those of our field study, as ladybeetle populations in cordgrass flower

335   habitats, despite being nearly 4x larger, removed the same number of scale insects as ladybeetles

336   in plots lacking flower access (Figs 2 and 3). A recent meta-analysis suggests that the effects of

337   PRTs on omnivore prey consumption depends on the ability of omnivores to elicit numerical

338   responses. Specifically, in the presence of PRT, allowing omnivore numerical responses

339   increased omnivore prey rate on animal prey, while not allowing numerical responses decreased

340   omnivore predation rate on animal prey (Rinehart and Long *in prep.*).

341   While several studies have aimed to assess the impacts of PRTs on intraguild predation

342   and cannibalism [see 9, 11-13], few have tested how elevated omnivore conspecific density (due

343   to numerical responses to PRTs) may affect omnivore foraging behavior and local prey

344   mortality. Here, we found that the presence of only two other conspecifics (i.e. 3+ ladybeetle

345   treatment) decreased per capita prey consumption by 76% in just three days. Omnivores may

346   consume fewer animal prey in the presence of conspecifics if they trade-off between foraging on

347   prey and engaging in intraspecific interactions (e.g. mating or interference competition). For

348   example, in our laboratory feeding assay, we frequently observed a single ladybeetle occupying a

349   cordgrass plant at a time- regardless of ladybeetle density (i.e., 1,2, or 3+ ladybeetles). This

350   observation suggests that adult ladybeetles may reduce their foraging efforts to avoid interacting

351   with other ladybeetles at small spatial scales.

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352   Changes in omnivore conspecific density and the availability of PRTs may also influence

353   the rate of cannibalism between ladybeetles in our study system. For instance, post-aggregation

354   cannibalism may explain why adult ladybeetle densities were 4x lower in field plots that denied

355   ladybeetles access to flowers than those allowing ladybeetles access to flowers. However,

356   cannibalism is unlikely in this system for two reasons. First, we never observed cannibalism

357   between individual ladybeetles in the laboratory (including during our three-day no-choice

358   assay) or the field (S.A. Rinehart *personal observation*). Second, cannibalistic events are most

359   likely to occur when food resources, especially prey, are limited [12]. In all our studies,

360   ladybeetles never consumed all scale insects in their environment, suggesting that the availability

361   of prey was never limiting.

362   The effect of PRTs on prey consumption by omnivores is commonly attributed to

363   nutritional benefits- as plants and animals vary in their nutrient, vitamin, mineral, and water

364   content [41]. However, PRTs may also affect omnivore behavior by increasing habitat

365   complexity. For example, habitat complexity can alter omnivore predation rates and antagonistic

366   intraspecific interactions [42-43]. In our system, ladybeetles preferentially use cordgrass flowers

367   as habitat - field surveys of randomly-selected cordgrass stems (n=95 individual flowering

368   cordgrass stems) found that 88% of adult ladybeetles were found on cordgrass flowers versus

369   other tissues (S5 Table).

370   The rate of omnivore prey consumption can be influenced by several factors. Historically,

371   omnivory studies have focused on the impacts of PRTs on prey consumption and have found

372   evidence that PRTs can both increase and decrease the rate of prey consumption by omnivores

373   [5-7]. PRTs can increase local omnivore predation rates by attracting omnivores- as PRTs

374   provide omnivores additional food resources and habitat structure [14-16]. However, few studies

17

375 have tried to understand how local increases in omnivore conspecific density (due to aggregation

376 to PRTs) ultimately affect omnivore-prey interactions. Here, we show that omnivore numerical

377 responses to PRTs alter the foraging behaviors of omnivores, due to shifts in local conspecific

378 density. Overall, our findings suggest a need to assess the indirect effects of PRTs on omnivore

379 foraging behaviors to better understand how omnivory influences food web structure and

380 function.

Acknowledgements

Literature Cited

391 1. Pimm SL, Lawton JH (1978) On feeding on more than one trophic level. Nature 275: 542-

392   544.

393 2. Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation:

394   Potential competitors that eat each other. Annual Review of Ecology and Systematics 20:

395   297-330.

396 3. Polis GA, Strong DR (1996) Food web complexity and community dynamics. The American

397   Naturalist 147: 813-846.

398 4. Polis, GA (1991) Complex trophic interactions in deserts: An empirical critique of food-web

399   theory. The American Naturalist 138: 123-155.

400 5. Eubanks MD, Denno RF (2000) Host plants mediate omnivore-herbivore interactions and

401   influence prey suppression. Ecology 81: 936-947.

402 6. Badii MH, Hernandez-Ortiz E, Flores AE, Landeros J (2004) Prey stage preference and

403   functional response of *Euseius hibisci* to *Teranychus urticae* (Avari: Phytoseiidae,

404   Tetranychidae). Experimental and Applied Acarology 34: 263-273.

405 7. Maselou DA, Perdikis DCh, Sabelis MW, Fantinou AA (2014) Use of plant resources by an

406   omnivorous predator and the consequences for effective predation. Biological Control 79:

407   92-100.

408 8. Abrams PA, Ginzburg LR (2000) The nature of predation: Prey dependent, ratio dependent,

409   or neither? Trends in Ecology and Evolution 15: 337-341.

410 9. Shakya S, Weintraub PG, Coll M (2009) Effect of pollen supplement on intraguild predatory

411   interactions between two omnivores: The importance of spatial dynamics. Biological Control

412   50: 281-287.

413 10. Hassell MP (1978) The dynamics of arthropod predator-prey systems, Princeton University

414   Press, Princeton, New Jersey, U.S.A.

415 11. Groenteman R, Guershon M, Coll M (2006) Effects of leaf nitrogen content on oviposition

416   site selection, offspring performance, and intraspecific interactions in an omnivorous bug.

417   Ecological Entomology 31: 155-161.

19

418   12. Leon-Beck M, Coll M (2007) Plant and prey consumption cause a similar reduction in

419   cannibalism by an omnivorous bug. Journal of Insect Behavior 20: 67-76.

420   13. Calabuig A, Pekas A, Wäckers FL (2018) The quality of nonprey food affects cannibalism,

421   intraguild predation, and hyperpredation in two species of phytoseiid mites. Journal of

422   Economic Entomology 111: 72-77.

423   14. Abrams PA (1987) On classifying interactions between populations. Oecologia 73: 272-281.

424   15. Cottrell TE, Yeargan KV (1998) Influence of a native weed, *Acalypha ostryaefolia*

425   (Euphorbiacease), on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density,

426   predation, and cannibalism in sweet corn. Environmental Entomology 27: 1375-1385.

427   16. Musser FR, Shelton AM (2003) Predation of *Ostrinia nubilalis* (Lipidoptera: Crambidae)

428   eggs in sweet corn by generalist predators and the impact of alternative foods. Biological

429   Control 32: 1131-1138.

430   17. Eubanks MD, Denno RF (1999) The ecological consequences of variation in plants and prey

431   for an omnivorous insect. Ecology 80: 1253-1266.

432   18. Rinehart SA, Long JD (2018) Habitat use is linked to resource-specific performance of an

433   ecologically important marsh predator. Ecosphere 9: doi: e02273.10.1002/ecs2.2273.

434   19. Crawley MJ (1975) Numerical responses of insect predators to changes in prey density.

435   Journal of Animal Ecology 44: 877-892.

436   20. Pimm SL, Lawton JH (1977) Number of trophic levels in ecological communities. Nature

437   268: 329-331.

438   21. Walde SJ (1994) Immigration and the dynamics of a predator-prey interaction in biological

439   control. Journal of Animal Ecology 63: 337-346.

440   22. Wildy EL, Chivers DP, Kiesecker JM, Blaustein AR (2001) The effects of food level and

441   conspecific density on biting and cannibalism in larval long-toed salamanders, *Ambystoma*

442   *macrodactylum*. Oecologia 128: 202-209.

443   23. Gage MJ (1995) Continuous variation in reproductive strategy as an adaptive response to

444   population density in the moth *Plodia interpunctella*. Proceedings of the Royal Society of

445   London Biological Sciences 261: 25-30.

446   24. Mansour R, Lipcius R (1991) Density-dependent foraging and mutual interference in blue

447   crabs preying on infaunal clams. Marine Ecology Progress Series 72: 239-246.

448   25. Skalski GT, Gilliam JF (2001) Functional responses with predator interference: Viable

449   alternatives to the Holling Type II model. Ecology 82: 3083-3092.

450   26. Kratina P, Vos M, Bateman A, Anholt BR (2009) Functional responses modified by predator

451   density. Oecologia 159: 425-433.

452   27. Ziemba RE, Collins JP (1999) Development of size structure in tiger salamanders: The role

453   of intraspecific interference. Oecologia 120: 524-529.

454   28. Janssen A, Willemse E, Van Der Hammen T (2003) Poor host plant quality causes omnivore

455   to consume predator eggs. Journal of Animal Ecology 72: 478-483.

456   29. Robinson KA, Jonsson M, Wratten SD, Wade MR, Buckley HL (2008) Implications of floral

457   resources for predation by an omnivorous lacewing. Basic and Applied Ecology 9: 172-181.

458   30. Frank SD, Shrewsbury PM, Denno RF (2010) Effects of alternative food on cannibalism and

459   herbivore suppression by carabid larvae. Ecological Entomology 35: 61-68.

460   31. Frank SD, Shrewsbury PM, Denno RF (2011) Plant versus prey resources: Influence on

461   omnivore behavior and herbivore suppression. Biological Control 57: 229-235.

462   32. Maselou DA, Perdikis DCh, Sabelis MW, Fantinou AA (2015) Plant resources as a factor

463   altering emergent multi-predator effects. PLoS ONE 10: 1-16.

464   33. Schmitz OJ (2005) Behavior of predators and prey and links with population-level processes.

465   In: Barbosa P, Castellanos I, ed. Ecology of predator-prey interactions. New York, NY:

466   Oxford University Press. pp 256-278.

467   34. Preisser EL, Orrock JL, Schmitz OJ (2007) Predator hunting mode and habitat domain alter

468   nonconsumptive effects in predator-prey interactions. Ecology 88: 27744-2751.

469   35. Romero GQ, Antiqueria PAP, Koricheva J (2011) A meta-analysis of predation risk effects

470   on pollinator behavior. PLoS ONE 6: e20689. doi:10.1371/journal.pone.0020689.

471   36. Towner AV, Leos-Barajas V, Langrock R, Schick RS, Smale MJ, et al. (2016) Sex-specific

472   and individual preferences for hunting strategies in white sharks. Functional Ecology 30:

473   1397-1407.

474   37. Rinehart SA, Schroeter SC, Long JD (2017) Density-mediated indirect effects from active

475   predators and narrow habitat domain prey. Ecology 98: 2653-2661.

476   38. Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: The primacy of trait-mediated

477   indirect interactions. Ecology Letters 7: 153-163.

478   39. Peterson CH, Renaud PE (1989) Analysis of feeding preference experiments. Oecologia 80:

479   82-86.

480   40. Karban R, Shiojiri K, Huntzinger M, McCall AC (2006) Damage-induced resistance in

481   sagebrush: Volatiles are key to intra- and interplant communication. Ecology 87: 922-930.

482   41. Coll M, Guershon M (2002) Omnivory in terrestrial arthropods: Mixing plant and prey diets.

483   Annual Review of Entomology 47: 267-297.

22

484   42. Buck TL, Breed GA, Pennings SC, Chase ME, Zimmer M, et al. (2003) Diet choice in an

485   omnivorous salt-marsh crab: Different food types, body size, and habitat complexity. Journal

486   of Experimental and Marine Biology and Ecology 292: 103-116.

487   43. Corkum LD, Cronin DJ (2004) Habitat complexity reduces aggregation and enhances

488   consumption in crayfish. Journal of Ethology 22: 23-27.

Supporting information

S1 Table. Repeated measures ANOVA for mean adult ladybeetle density between Flower Access treatments across the field six-week study.

S2 Table. Repeated Measures ANOVA for mean larval ladybeetle density between Flower Access treatments across the six-week field study.

S3 Table. Repeated Measures ANOVA for mean egg clutch density between Flower Access treatments across the six-week field study.

S4 Table. Repeated Measures ANOVA for number of ladybeetles on cordgrass plants between Ladybeetle Density treatments at two timepoints.

S1 Fig. Effect of conspecific density on adult ladybeetle behavior in laboratory no-choice feeding assays. Mean (± SE) number of adult ladybeetles observed on cordgrass plant tissues in the laboratory no-choice feeding assay on the 2nd and 3rd days of the assay (n=5 per beetle density treatment).
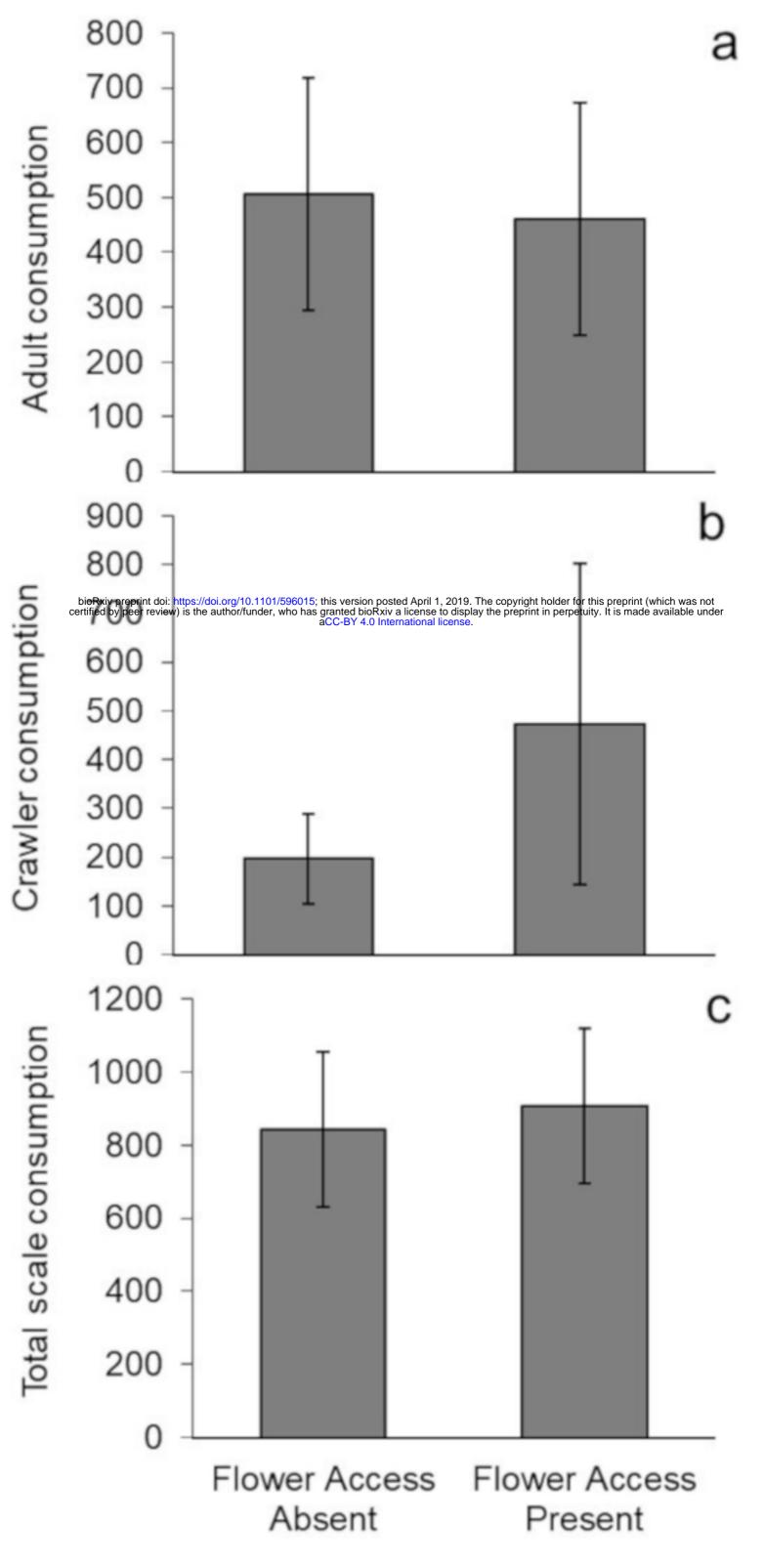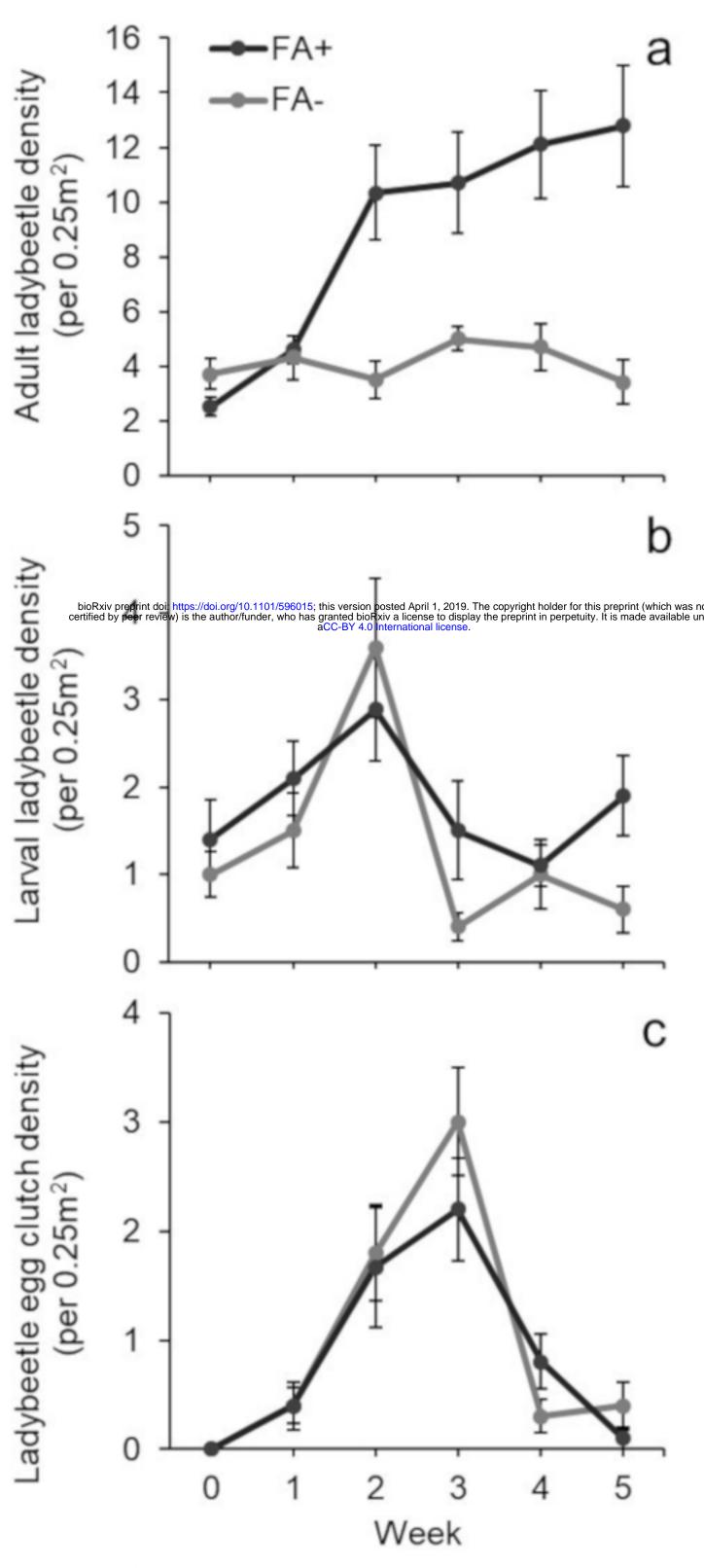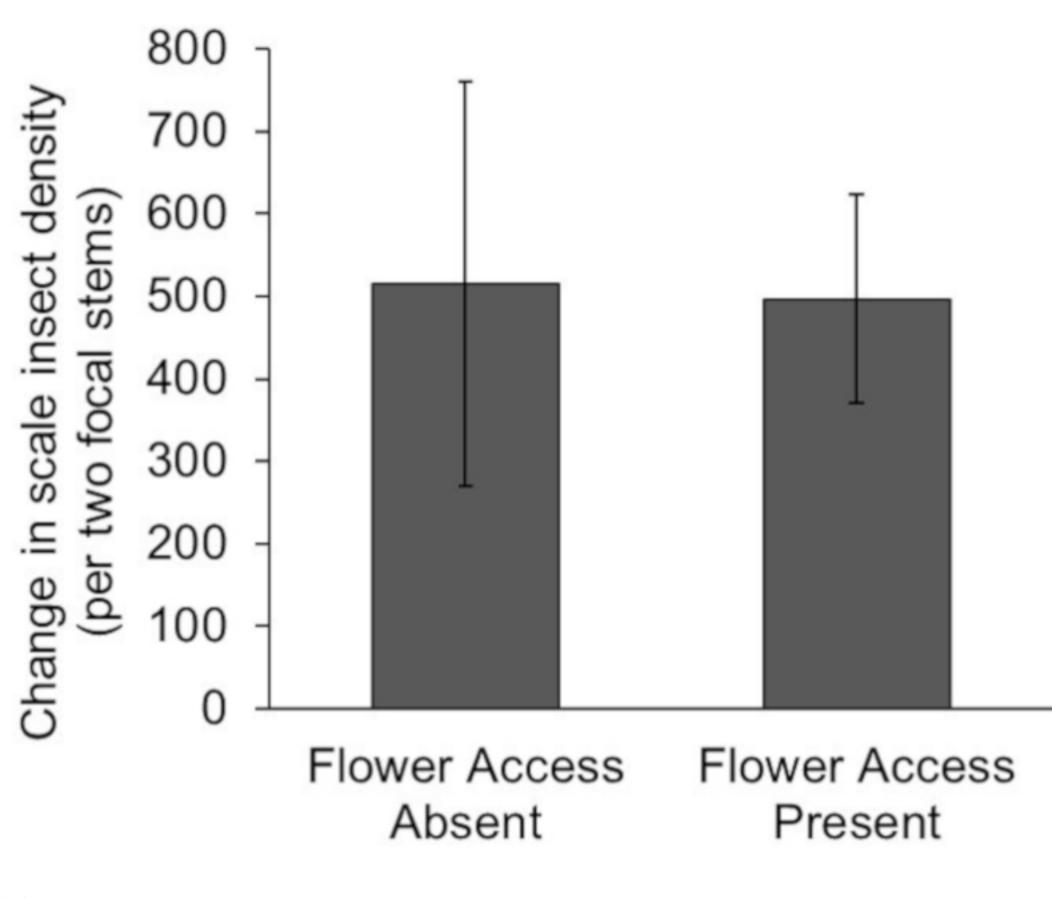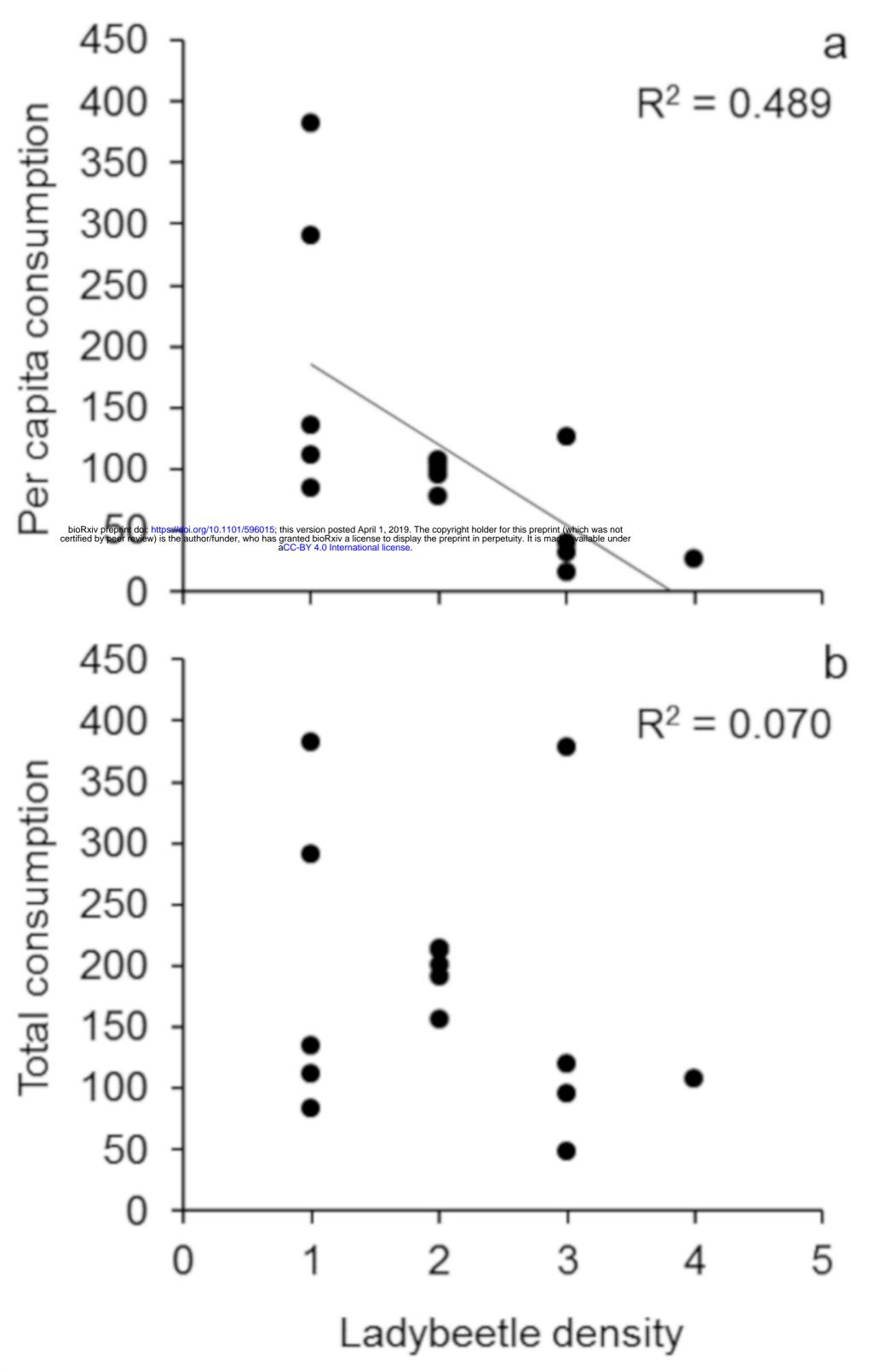
Figure 1

Figure 2

Figure 3

Figure 4