1   Selection of aphid prey by a generalist predator: Do prey chemical defences matter?

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19   Running Title: Do chemical defences affect prey selection?

20   <u>Abstract</u>

21   For predators, prey selection should maximize nutrition and minimize fitness costs. Here, we

22   investigate whether a generalist predator (*Chrysoperla carnea* lacewing larvae) rejected

23   harmful, chemically-defended prey (*Brevicoryne brassicae* aphids) when non-defended prey

24   (*Myzus persicae* aphids) were available. We tested: (1) the effect of consuming different prey

25   species on predator mortality; (2) whether naïve predators reject chemically-defended prey

26   during foraging when non-defended prey are available; (3) whether the relative abundance of

27   each prey affects the predator's prey choice; and (4) whether predators learn to avoid

28   consuming chemically-defended prey following exposure to both prey species. Consumption

29   of *B. brassicae* yielded greater *C. carnea* mortality than *M. persicae* consumption, but naïve

30   *C. carnea* did not reject *B. brassicae* in favour of *M. persicae* during foraging. When

31   presented at unequal abundances, naïve predators generally consumed each aphid species

32   according to their initial relative abundance, although, predation of non-defended prey was

33   less than expected where defended prey were initially more abundant, indicating high

34   consumption of *B. brassicae* impeded *M. persicae* consumption. With experience, *C. carnea*

35   maintained predation of both aphid species but consumed more *M. persicae* than *B.*

36   *brassicae*, indicating a change in behaviour. Although prey choice by *C. carnea* may change

37   with experience of available prey, prey chemical defences do not appear to influence prey

38   choice by naïve predators. This inability to avoid harmful prey could facilitate wider, indirect

39   interactions. *M. persicae* may benefit where high consumption of *B. brassicae* hinders

40   predators in the short term, and in the long term, increases predator mortality.

41   Keywords: Apparent commensalism, associational resistance, *Brassicacae*, predator

42   behaviour, trait-mediated indirect interaction

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INTRODUCTION

Predators can strongly affect the composition and persistence of their prey communities, and where prey are herbivorous, predators may indirectly affect plant diversity and biomass (Schmitz et al. 2000, Schmitz 2003, 2006). Through this mechanism (a 'trophic cascade'), predatory invertebrates deliver biological pest control, where predation of herbivorous crop pests improves or maintains crop plant production (Symondson et al. 2002, Snyder and Wise 2001). In many agricultural and natural communities, prey species co-occur in diverse assemblages, thus, to develop successful biological control schemes, it is necessary to predict how predatory invertebrates respond to the availability of multiple prey species. i.e., are predators selective in their prey choice? For predators, selecting the 'best quality available prey' means consuming prey that offer maximum nutrition and/or minimal costs - such as greater risk of wounding if prey are structurally-defended, or poisoning if prey possess chemical-defences, acquired from their food plants (Forbes 1989, Nishida 2002, Hayward and Kerley 2005, Magalhães et al. 2005, Opitz and Muller 2009).

Predators may choose between available prey species when locating prey habitats, locating prey within a habitat and when accepting located prey (Hoy and Smilanick 1981, Vinson 1976), using a variety of different cues. When plants are attacked by herbivores, they release volatile olfactory cues as a signal to attract the herbivore's natural enemies (Zhu et al. 1999, Dicke and van Loon 2000, Glinwood et al. 2011). The blend of volatiles varies depending on the identity of the herbivore attacking the plant, thus, predators may use plant volatiles to locate prey habitats and potentially, to differentiate between plants hosting different prey species (although this is more common for parasitoids than predators, Hatano *et al.* 2008). Generalist predators more commonly locate and select their prey using cues associated with prey themselves. For example, the scent of aphid honeydew or aphid alarm pheromone ((E)-β-farnesene) can be attractive to predators such as *Episyrphus balteatus*

69 (DeGeer) (Diptera: Syrphidae) hoverfly larvae and *Adalia bipunctata* (Linnaeus) (Coleoptera:

70 Coccinellidae) ladybird larvae (Francis et al 2004, 2005), yet isothiocyanates released by

71 *Brevicoryne brassicae* (Linnaeus) (Hempitera: Aphididae) aphids, as an indicator of chemical

72 defences, can be repellent to *A. bipunctata* (Francis et al. 2005). Should predators

73 successfully locate prey within a habitat, predators may register olfactory, or other cues (such

74 as aposematic coloration) associated with chemically-defended prey as a warning signal

75 against attack (Francis et al. 2004, Mappes et al. 2005). If cues are absent or not innately

76 recognized and harmful prey is accepted, then assuming harmful effects are sub-lethal,

77 predators may learn from experience to avoid the harmful prey when next foraging.

78   It is widely assumed that selectivity exhibited by generalist predators is a learned

79 behaviour (Dukas 2008). Coccinelid beetles for example can learn to recognise suitable prey

80 habitats and to select the most nutritious available prey. *Coccinella septempunctata*

81 (Linnaeus) (Coleoptera: Coccinellidae) larvae were shown to associatively learn the odours

82 of barley cultivars upon which it had previously located and fed on aphids (Glinwood et al.

83 2011), while *Coleomagilla maculata lengi* (Timberlake) (Coleoptera; Coccinellidae) have

84 been shown to reject poorer-quality, parasitized *Pieris rapae* (Linnaeus) (Lepidoptera:

85 Pieridae) eggs in favour of consuming more nutritious, unparasitized eggs at greater

86 frequency with greater experience (Boivin et al. 2008). In both studies however, the

87 behaviours were shown to be at least partially forgotten after forty-eight hours (Boivin et al.

88 2008; Glinwood et al. 2011). As prey that vary in levels of chemical defences can occur in

89 the same communities as non-defended prey (Kalule and Wright 2002b, Staley et al. 2010,

90 van Veen et al. 2009), we assess here whether a widespread predatory invertebrate rejects, or

91 learns to reject a harmful, chemically-defended aphid species if a better quality, non-defended

92 aphid species is available.

93   Among *Brassica* crops, predatory insects, such as ladybird, lacewing and hoverfly

94   larvae can feed on two widespread pest aphid species that can occur together on the same

95   plants, or in the same communities (Kalule and Wright 2002b, Snyder et al. 2006, 2008,

96   Staley et al. 2010). *Myzus persicae* (Sulzer) (Hempitera: Aphididae) is a non-defended

97   generalist aphid (Bridges et al. 2002), while *B. brassicae* is a specialist aphid that co-opts the

98   glucosinolate defence chemicals of its host plant as a defence against predators (Bridges et al.

99   2002, Kazana et al. 2007). Continued consumption of *B. brassicae* can be lethal to, or inhibit

100   the growth rates of generalist predators (Francis et al. 2001, Kos et al. 2011, 2012, Pratt et al.

101   2008); effects that can be stronger when *B. brassicae* feed on more chemically-defended crop

102   plant varieties (Chaplin-Kramer et al. 2011, Kos et al. 2011).

103   The aim of this study was to assess whether the generalist predator *Chrysoperla*

104   *carnea* (Stephens) (Neuroptera: Chrysopidae) lacewing larvae innately avoids, or learns to

105   avoid consuming chemically-defended *B. brassicae* where *M. persicae* are available, and

106   whether any selectivity behaviour varies depending on the variety of plant hosting the prey

107   species. We predict that *C. carnea* will learn to reject *B. brassicae* in favour of *M. persicae*

108   and for the strength of selectivity to vary depending on the aphid's host plant. First, we tested

109   the assumption that *B. brassicae* are more harmful for *C. carnea* to consume than *M.*

110   *persicae*. Second, we assessed the ability of naïve *C. carnea* to select between plants hosting

111   different prey species (*B. brassicae* or *M. persicae*). Thirdly, we assessed whether innate prey

112   choice of *C. carnea* was determined by the relative abundance of the two prey species, and

113   finally, we tested whether *C. carnea* learn to avoid consuming *B. brassicae* through

114   experience.

115

METHODS

The study system included two aphid species, chemically-defended *Brevicoryne brassicae* and non-defended *Myzus persicae*; and the shared predator *Chrysoperla carnea* larvae. Two widely studied *Brassica oleracea* (Linnaeus) (Brassicales: Brassicaceae) cabbage cultivars, Derby Day and f_1 Minicole, were used as aphid host plants. Derby Day is considered an herbivory-susceptible cabbage cultivar (Ellis et al. 1996, Verkirk et al. 1998, Staley et al. 2009) and Minicole to possess some herbivory-resistance (Verkirk et al. 1998, Schuler and van Emden 2000, Hariprasad and van Emden 2010). Populations of both aphid species have been reported to be lower on Minicole compared to Derby Day plants in lab and field experiments (Kalule and Wright 2002a, 2002b; Nesbit 2013), suggesting a difference in antibiosis between cultivars.

Derby Day (Nicky's Nursery Ltd., UK) and Minicole (E.W. King & Co. Ltd., UK) seeds were sown individually in John Innes N°.2 compost in 15 cell seed trays (each cell 65 x 65 mm and 60 mm deep) and grown in a glasshouse with daily watering. *M. persicae* and *B. brassicae* were maintained in monocultures in a controlled environment room (hereafter, CE room) at Lancaster University (day/night temp (^{o}C): 22/17, 15L:9D photoperiod) on plants of both cultivars. *C. carnea* larvae (2nd instar, supplied by Fargro Ltd., UK) were stored on arrival in buckwheat seed husks in a refrigerator at 4^oC, for 3 days before each experiment began. Twenty-four hours prior to testing, *C. carnea* larvae were weighed (mg), transferred to numbered Petri dishes (5 cm diameter, containing a small filter paper saturated with water and one *Rhopalosiphim padi* aphid (from a culture maintained on wheat) to prevent death from starvation) and assigned to treatments.

139   Predator survival on diets of different prey

140   To test the assumption that *B. brassicae* are more harmful for *C. carnea* to consume

141   than *M. persicae*, diet assays were employed. Survival was measured for *C. carnea* larvae

142   that were fed diets of *M. persicae* reared on Derby Day (MpDD), *B. brassicae* reared on

143   Derby Day (BbDD, to test against MpDD for species effects), or *B. brassicae* reared on

144   Minicole plants (BbM, to test against BbDD for *B. brassicae*-mediated host plant effects).

145   Regrettably, our stock of *M. persicae* on Minicole was contaminated with *Aphidius ervi*

146   (Haliday) (Hymenoptera: Braconidae) parasitoids at the time of this experiment, precluding

147   the possibility of a fully factorial experiment (although this treatment was not strictly

148   necessary to test our prediction). Ninety *C. carnea* were transferred individually to numbered

149   plastic pots (4.5 cm diameter, 4 cm depth, with perforated lids) containing a filter paper

150   saturated with water. Each *C. carnea* larva was fed in excess, with 20 mixed-age wingless

151   aphids according to their diet treatment (30 replicates per treatment). Aphids were replaced

152   every day, at which point the remains of dead aphids and all surviving aphids were removed.

153   Survival of *C. carnea* was recorded at the end of the experimental period of 7 days. The

154   experiment was repeated, giving 60 replicates per treatment in total. Predators were not used

155   more than once.

156

157   Innate predator selectivity between different aphid host plants

158   To test whether naïve *C. carnea* select between aphid species while locating aphid

159   host plants, predators were given free choice to visit a plant hosting *B. brassicae* and/or a

160   plant hosting *M. persicae*. Each assay exposed one *C. carnea* larva to two plants, one host to

161   *B. brassicae,* the other to *M. persicae*. Assays alternated in using Derby Day or Minicole as

162   host plants. Six assays were conducted per day over three days for two weeks, giving a total

163   of 36 assays, 18 per plant cultivar. A new predator and new aphid host plants were used in

164   each assay.

165   Twenty-four hours before each day of assays, plants and insects were pre-treated as

166   follows: Six plants (6 week old) per cultivar were re-potted (10 cm diameter, 9 cm depth

167   pots) and transferred to the CE room. Measurements of leaf number and height (mm, from

168   base of the stem to the tip of the budding leaf) were used to assign plants to assays, so the two

169   aphid host plants were of approximately equal size. Each plant was transferred to an

170   individual insect rearing cage (30 cm diameter, approx. 60 cm high). A Petri dish (5 cm

171   diameter) containing 20 mixed-age wingless aphids of the assigned aphid species was left at

172   the base of the stem overnight for aphids to colonize.

173   The assay arena was a Perspex observation box (30 x 30 x 30 cm Bugdorm1,

174   MegaView Science Co. Ltd, Taiwan, modified to have one transparent side to facilitate

175   observation) adapted from Wilby et al. (2013). Inside were two plants of the same cultivar,

176   one hosting *B. brassicae*, the other *M. persicae*, connected by a 15 cm Perspex bridge in

177   contact with the base of their stems. A single *C. carnea* larva was placed in the centre of the

178   bridge, which could visit one, both or neither of the plants. *C. carnea* were then observed for

179   45 minutes. Time and location were recorded when *C. carnea* visited a plant (defined as

180   having made physical contact with the plant), left a plant, foraged (defined as actively

181   seeking prey as opposed to resting immobile on the plant), captured an aphid or discarded a

182   consumed aphid. The bridge was rinsed with tap water between assays and plant

183   configuration (whether the plant with *B. brassicae* was on the left or right) alternated between

184   assays to control for any directional effects.

185

186   Innate prey selection in response to different prey abundances

187   To test whether innate prey choice of *C. carnea* was determined by the relative

188   abundance of the two prey species, predators were exposed to mixed populations of *B.*

189   *brassicae* and *M. persicae* at different relative abundances. *C. carnea* were randomly

190   assigned to ten treatment combinations of plant cultivar (Derby Day or Minicole) crossed

191   against aphid abundance ratio (number of *B. brassicae:* number of *M. persicae*: 0:20; 5:15;

192   10:10; 15:5; 20:0). Each treatment was replicated 3 times per day and the experiment was

193   repeated over six days, giving 18 replicates per treatment in total.

194   On the day of testing, aphids were transferred to Petri dishes (5 cm diameter)

195   according to the appropriate abundance ratio. Each Petri dish also contained a small water-

196   saturated filter paper, and approximately 2 cm^2 of fresh, randomly excised leaf material from

197   8 week old plants of the treatment cultivar. *C. carnea* were transferred to the aphid Petri

198   dishes, one per dish, and left for 5 hours, after which time the number of surviving aphids

199   was counted.

200

201   Predator associative learning

202   To test whether *C. carnea* learn to avoid consuming *B. brassicae* through experience,

203   predators were repeatedly exposed to mixed populations of *B. brassicae* and *M. persicae* (at

204   equal proportion). Thirty *C. carnea* larvae were exposed individually to mixed groups of 10

205   *B. brassicae* and 10 *M. persicae* in a Petri dish (5 cm diameter) for five hours, after which

206   time the number of surviving aphids was counted. The same *C. carnea* larvae were then

207   exposed to new, mixed-aphid groups, for the same five hour period, over four further

208   consecutive days, thus, predators were re-used in this experiment. The experimental protocol

209   was the same as described in previous section (involving a Petri dish, plant material and filter

210 paper), however, there were only two treatments of ten of each Derby Day-reared aphid

211 species, or ten of each Minicole-reared aphid species (15 replicates per treatment).

212

213 Statistical Analysis

214   Unless stated, data from the first and second experiments were analysed using

215 generalised linear mixed effects models (GLMMs) fit to a binomial distribution with a logit

216 link function. The significance of fixed effects was assessed by contrasting the deviance

217 between models with and without the fixed effect using chi-squared test statistics (hereafter:

218 analysis of deviance) (Crawley 2007, Zuur et al. 2009).

219   For the first experiment, survival of *C. carnea* (yes or no) fed MpDD and BbDD was

220 contrasted, with aphid species as the fixed effect. Survival of *C. carnea* fed BbDD and BbM

221 was contrasted with plant cultivar as the fixed effect (Crawley 2007; Zuur et al. 2009).

222 Temporal block was included as a random effect (factor: 1 or 2).

223   For the second experiment, to test whether *C. carnea* discriminated between plants

224 hosting different aphid species, we analysed whether a plant hosting one aphid species was

225 consistently visited first in an assay over the other (yes or no). To test whether *C. carnea*

226 registered any subsequent cues while foraging on plants, three further responses were

227 analysed: (a) plant fidelity - whether the first visit was exclusive (yes or no) or if *C. carnea*

228 also visited the other plant during the assay; (b) the time *C. carnea* spent foraging on a plant

229 (minutes spent on the plant minus time spent feeding minus time spent immobile), and (c)

230 whether predation occurred (yes or no). The fixed effects of all maximal models were aphid

231 species, plant cultivar and the interaction term. The random effects of all models were the

232 time of day (factor: 1:6), nested within the day (factor: Wednesday/Thursday/Friday), nested

233 within the week the assay was conducted (factor: week 1 or 2). Foraging time (mins) was

234   analysed using linear mixed effects (LME) models and analysis of deviance under maximum

235   likelihood (ML) parameter estimation.

236   For the third experiment, we assumed that if *C. carnea* were unselective they would

237   be expected to encounter and consume aphids of each species in proportion to their initial

238   abundance in mixed-prey populations, weighted by their respective feeding rates on the two

239   aphid species when presented alone to account for differences between prey species in

240   handling time or satiation. Differences in handling time or satiation between aphid species

241   were analysed using single-species treatment data. Aphid count was analysed using GLMMs

242   with Poisson errors and log-link function. Fixed effects in the maximal model included aphid

243   species, plant cultivar and the interaction term. The random effect was predator weight (mg).

244   The significance of fixed effects was assessed through analysis of deviance (Zuur et al.

245   2009). The mean final count of each aphid species per single-species treatment was obtained

246   using the parameter estimates from the minimum adequate model, and was used to obtain an

247   expected final count in the mixed-aphid treatments for each aphid species:

248   Expected final aphid count (mixed-species treatment) = [final count (single-species

249   treatment)/initial count (single-species treatment)] * initial count (mixed-species treatment)

250   Data from mixed-aphid treatments were used to test whether counts of each aphid species

251   when presented together deviated from expected counts. The response was:

252   Deviation from expected count = ln(observed final aphid count/expected final aphid count)

253   Fixed effects in the maximal LME model included aphid species, plant cultivar, aphid

254   abundance ratio (initial *B. brassicae*: *M. persicae*: 5:15; 10:10; 15:5) and all interaction

255   terms. Random effects included predator identification number, to account for aphid counts

256   from the same test, and predator weight. The significance of fixed effects was assessed by

257   analysis of deviance under ML parameter estimation (Zuur et al. 2009).

258   For the fourth experiment, data were split to test for (a) innate prey selection, using

259   only data from the first day when predators were naïve, and (b) selection resulting from

260   experience, using data from predators having been previously exposed to the aphids (1 to 4

261   exposures). All final count response data were analysed using GLMMs fit to a Poisson

262   distribution with a log-link function. Fixed effects for the innate prey selection analysis

263   included aphid species, plant cultivar and the interaction term, with random effects of

264   predator identification number (factor 1:30) to account for aphid counts from the same test,

265   and the starting predator weight. For the analysis of prey selection of experienced predators,

266   fixed effects included aphid species, plant cultivar, previous exposures (1 to 4) and all

267   interaction terms. The random effects included initial predator weight and a grouping term to

268   account for repeated measurements from the same predator (predator identification number)

269   across successive exposures.

270   All analyses used the 'lme4' package (Bates et al. 2012) for 'R.v.2.15.2' (R Core

271   Development Team 2012). Adequacy of best-fitting LME models and GLMMs fit to a

272   poisson distribution was assessed by inspecting the residuals against the fitted values, fixed

273   effects and random effects (Zuur et al. 2009).

274

275   **RESULTS**

276   Predator survival on diets of different prey

277   Diet assays were used to test whether *B. brassicae* are more harmful for *C. carnea* to

278   consume than *M. persicae*. Survival of *C. carnea* larvae was significantly greater for those

279   fed *M. persicae* (mean survival: 95%, ± SEM: 90-97%) compared to those fed chemically-

280   defended *B. brassicae* (mean survival: 83%, ± SEM: 77-88%) from Derby Day plants ($\chi^2_1 =$

281   4.435, *p* = 0.035). No significant difference was observed in survival of *C. carnea* given diets

282   of *B. brassicae* reared on Minicole (mean survival: 80%, ± SEM: 71-87%) or Derby Day

283   (mean survival: 83%, ± SEM: 77-88%) cabbage cultivars ($\chi^2_1 = 0.226$, *p* = 0.635).

284

285   Innate predator selectivity between different aphid host plants

286   To test whether naïve *C. carnea* select between aphid species while locating aphid

287   host plants, predators were given free choice to visit a plant host to *B. brassicae* and/or a

288   plant host to *M. persicae*. The first plant visited in an assay by *C. carnea* (Table 1a) was not

289   significantly affected by aphid species, by plant cultivar or by the interaction term between

290   the two factors. Additionally, there was no significant effect of aphid species or any other

291   fixed factor on: plant fidelity (Table 1b); the time *C. carnea* spent foraging on host plants

292   (Table 1c) or the occurrence of predation on plants (Table 1d). Of the 28 tests where

293   predators visited an aphid host plant, 10 tests yielded predation. The most number of attacks

294   observed in one test was six, with three kills and three aphids evading predation by dropping

295   from the plant; the least was one attack, with feeding lasting beyond the forty-five minute

296   experimental duration. Of the complete feeding times observed, the duration ranged from two

297   to thirty-one minutes.

298

299   Innate prey selection in response to different prey abundances

300   *C. carnea* were exposed to mixed populations of *B. brassicae* and *M. persicae* at

301   different relative abundances to test whether their innate prey choice of was determined by

302   prey relative abundance. After 5 hours exposure to *C. carnea,* the counts of *M. persicae* were

303 significantly lower than the counts of *B. brassicae* in the single species treatments ($\chi^2_1 =$

304 5.083, *p* = 0.024). The back-transformed parameter estimates for mean *B. brassicae* count

305 was 18.6 ± 0.7 aphids (a 7% reduction from the initial population size) and the mean *M.*

306 *persicae* count was 16.4 ± 0.9 aphids (a reduction of approximately 18% from the initial

307 population size). These parameter estimates were used to calculate the expected counts.

308 The interaction between aphid abundance ratio and aphid species was significant (χ^2_2

309 = 6.884, *p* = 0.032), as *M. persicae* counts were higher than expected when the aphid

310 abundance ratio was 15:5 in favour of *B. brassicae* (Fig. 1). However, aphid abundance ratio

311 did not significantly affect the degree of deviation from the expected counts of each aphid

312 species in mixed-species treatments (χ^2_2 = 1.019, *p* = 0.601) and the effect of aphid species

313 on degree of deviation was only marginally significant (χ^2_1 = 3.685, *p* = 0.055).

314

315 Predator associative learning

316 To test whether *C. carnea* learn to avoid consuming *B. brassicae* through experience,

317 predators were repeatedly exposed to mixed populations of *B. brassicae* and *M. persicae* (at

318 equal proportion). After the first 5 hour exposure of naive *C. carnea* to mixed-species aphid

319 populations, aphid counts were not significantly affected by aphid species, plant cultivar or

320 by the interaction term (Table 3a, Fig. 2a). In all subsequent exposures, when predators had

321 previous experience with the aphid species, *M. persicae* counts were lower than *B. brassicae*

322 counts and the counts of both species declined with progressive exposures (Table 3b, Fig.

323 2b).

324

325 **DISCUSSION**

326   The aim of this study was to assess whether a generalist predatory invertebrate

327   (*Chrysoperla carnea*, lacewing larvae) innately avoids, or learns to avoid consuming harmful,

328   chemically-defended prey (*Brevicoryne brassicae*) where non-defended prey (*Myzus*

329   *persicae*) are also available, and whether any selectivity that predators exhibit varies

330   depending on the variety of plant hosting the prey species. Our experiments found no

331   evidence that naïve *C. carnea* preferentially select *M. persicae* aphids when both prey species

332   are available, and even with experience of both prey species, *C. carnea* did not reject *B.*

333   *brassicae* entirely in favour of *M. persicae*. Continued consumption of *B. brassicae* by *C.*

334   *carnea* may influence how *C. carnea* affects the wider community, by increasing *C. carnea*

335   mortality rates (when consumed in isolation), and potentially, by reducing the strength of

336   predation experienced by other prey species.

337   Our results supported the assumption that *B. brassicae* are more harmful for *C.*

338   *carnea* to consume than *M. persicae*, as a diet of *B. brassicae* reduced survival of *C. carnea*

339   by approximately 12% compared to a diet of *M. persicae*. This is consistent with other

340   studies showing that *B. brassicae* chemical defences (Bridges et al. 2002, Kazana et al. 2007)

341   can increase mortality, or reduce the growth rates of generalist predatory invertebrates,

342   including *Adalia bipunctata* (Francis et al. 2001; Kazana et al. 2007; Pratt et al. 2008),

343   *Episyrphus balteatus* and *C. carnea* (Chaplin-Kramer et al. 2011, Kos et al. 2011, 2012).

344   Additionally, although the strength of *B. brassicae* chemical defences can vary depending on

345   the host plant's chemical defences (as Chaplin-Kramer et al. 2011, Kos et al. 2011), we found

346   no difference in survival of *C. carnea* fed *B. brassicae* from the two cabbage cultivars used in

347   this study. This lack of host plant effects may be due to host plants affecting biological

348   parameters of the predator we did not measure (such as predator growth rates or fecundity,

349   Chaplin-Kramer et al. 2011, Kos et al. 2011), or due to similar expression of chemical

350   defences by the two cultivars. However, as *C. carnea* survival was unaffected by the cultivar

351　hosting *B. brassicae*, this may help explain why *C. carnea* behaviour in the subsequent

352　experiments was unaffected by plant cultivar. If there was a difference in mortality between

353　*C. carnea* consuming *B. brassicae* from one cultivar compared to the other, then

354　theoretically, consuming the more harmful *B. brassicae* may provide a stronger stimulus for

355　deterrence or learning than consumption of the less harmful *B. brassicae*. As *C. carnea*

356　survival was only affected by differences in aphid species (chemically-defended or non-

357　defended), only a difference in species, not the additional difference in *B. brassicae* host

358　plant, is likely to provide a strong enough stimulus for discrimination or learning.

359　　　Given *B. brassicae* are more harmful to consume than *M. persicae*, it may be

360　expected that *C. carnea* would choose to feed on *M. persicae* over *B. brassicae* where

361　available. However, naïve *C. carnea* larvae did not display any innate preference for *M.*

362　*persicae* over *B. brassicae* during any stage of foraging: when locating occupied plants; when

363　locating prey within plants and when accepting prey (Table 1) (Hoy and Smilanick 1981,

364　Vinson 1976). Naïve *C. carnea* therefore were not innately deterred by any cues associated

365　with *B. brassicae* (Francis et al. 2005, Mappes et al. 2005). The results suggest that naïve *C.*

366　*carnea* consume the aphids they encounter first while foraging and support the widely held

367　assumption that any selectivity that generalist predatory invertebrates exhibit is a learned

368　behaviour (Boivin et al. 2010, Dukas 2008).

369　　　A lack of selectivity by naïve *C. carnea* was also shown in the third experiment, as *C.*

370　*carnea* generally predated according to the relative abundance of each aphid species (Fig. 1).

371　Interestingly however, when *B. brassicae* were more abundant than *M. persicae* (15:5 *B.*

372　*brassicae*: *M. persicae* treatment), there was some evidence that the high consumption of *B.*

373　*brassicae* negatively impacted on *M. persicae* consumption. The final count of *B. brassicae,*

374　although lower than expected*,* was not significantly different to the expected count, however,

375　counts of *M. persicae* were significantly higher than expected (Fig. 1). In a similar study,

376   Eisner et al. (2000) observed that larvae of the green lacewing *Ceraeochrysa cubana* (Hagen)

377   were deterred from feeding on moth eggs if only a few of those present in a cluster were

378   identified as being chemically-defended. Therefore, upon encountering and consuming *B.*

379   *brassicae* at a high frequency, *C. carnea* may have been deterred from feeding (especially as

380   other glucosinolate-sequestering herbivores can be unpalatable to their predators, Müller et

381   al. 2002, Vlieger et al. 2004), rejecting all available prey and releasing *M. persicae* from

382   predation.

383   Given repeated exposure to harmful and non-harmful prey, it may be expected that

384   predators would learn to select the non-harmful prey species (Boivin et al. 2010, Dukas

385   2008). After the first exposure, there was an initial change in response to the two aphid

386   species, where *M. persicae* counts were lower than *B. brassicae* by 0.91 ± 0.04 aphids in each

387   successive exposure. However, the difference did not become more marked over time. Thus,

388   although there was a change in behaviour, *C. carnea* did not learn from experience to avoid

389   *B. brassicae* consumption altogether. Welch & Lundgren (2014) recently assessed the ability

390   of three arthropod predators to learn to avoid chemically-defended western corn rootworm

391   *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae). Like *B. brassicae*, *D.*

392   *virgifera* does not display aposematic colouration to indicate chemical defences, and harms

393   predators upon attack. The rootworm's haemolymph can be unpalatable or can impede

394   feeding by coagulating around the predator's mouthparts. Interestingly, the predators did not

395   learn to avoid predating on the rootworm, rather *Gryllus pennsylvanicus* Burmeister

396   (Orthoptera: Gryllidae) crickets attacked rootworm as much as palatable maggots of the

397   house fly *Musca domestica* Linnaeus (Diptera: Muscidae), stone centipedes (Chilopoda:

398   Lithobiidae) showed little impediment resulting from the rootworms defences and *Lasius*

399   *neoniger* Emery (Hymenoptera: Formicidae) ants learned to attack successfully in groups,

400   rather than individually (Welch & Lundgren 2014). Here, the underlying cause of the

401   behavioural change requires further investigation, yet like the predators of the rootworm, it

402   may be possible that *C. carnea* bypassed or tolerated *B. brassicae* chemical defences. By

403   consuming more *M. persicae* than *B. brassicae*, *C. carnea* may have maintained an optimal,

404   mixed diet; by which the concentration of ingested defence chemicals from *B. brassicae* was

405   diluted by feeding on *M. persicae*, yielding a high nutritional payoff and facilitating the

406   increase in aphid consumption as the predator grows (as Fig. 1; Cruz-Rivera and Hay 2003;

407   Glendinning 2007).

408   The results suggest that prey chemical defences do not influence the prey choice of

409   naïve *C. carnea*. Rather, naïve *C. carnea* locate plants hosting prey at random and feed on

410   aphids they encounter first. If multiple species are encountered (for example, if they share a

411   host plant), then prey choice may be determined by the relative abundance of each prey

412   species (Fig. 2). However, prey choice may be affected *in situ* by how prey use a shared host

413   plant and by how the predator uses the plant to forage (Schmitz et al. 2004). For example, in

414   the plant selection assays, *C. carnea* used the stem to access the lower leaves and consumed

415   aphids they encountered first. If one aphid species colonises the stem or lower leaves more

416   than the other, then predators are likely to encounter and consume that species first at higher

417   frequency (*M. persicae* reportedly use the lower leaves of *Brassica* plants and *B. brassicae*

418   use leaves higher up the stem, Trumble 1980). Furthermore, if parts of the plant are

419   inaccessible and one prey species uses them as a refuge, this may affect prey encounter and

420   consumption rates as well (Eigenbrode et al. 1999, Fordyce and Agrawal 2001, Northfield et

421   al. 2012).

422   The lack of naïve preference between toxic and non-toxic prey, at least in the short

423   term, could lead to wider associational/apparent interactions. Associational interactions,

424   typically, involve chemically-defended species that reduce predation of non-defended species

425   (associational resistance) or are consumed incidentally due to the presence of palatable

426 species (associational susceptibility) (Wahl and Hay 1995; Barbosa et al. 2009). These

427 indirect interactions have mostly been observed between plant species (Barbosa et al. 2009,

428 Kostenko et al. 2012, Castagneyrol et al. 2013) and in aquatic systems (Hay 1986, Wahl and

429 Hay 1995), yet, although examples of 'associational' interactions in terrestrial systems are

430 sparse (Barbosa et al. 2009), indirect 'apparent' interactions have been widely reported in

431 terrestrial invertebrate communities (van Veen et al. 2006, Chailleux et al. 2014). In this body

432 of literature, apparent commensalism, where one species benefits from the presence of

433 another, through indirect interactions with a natural enemy, is analogous to associational

434 resistance (van Veen et al. 2005, 2009) and apparent amensalism, where one species suffers

435 from the presence of another, through indirect interactions with a natural enemy, is analogous

436 to associational susceptibility (Chaneton & Bonsall 2000). The mechanisms that determine

437 associational resistance or susceptibility and the effects of these apparent interactions in

438 applied agricultural systems however remain unclear (Barbosa et al. 2009, Chailleux et al.

439 2014). Here we report that continued consumption of *B. brassicae* may increase *C. carnea*

440 mortality and potentially reduce predator numbers – a density mediated indirect interaction

441 that could benefit *M. persicae*. In the short term, the effects of *B. brassicae* chemical

442 defences may potentially reduce predation of other herbivores (Fig. 1) – a trait-mediated

443 indirect interaction from which *M. persicae* benefit.

444   The occurrence of associational/apparent interactions may further change if *C. carnea*

445 can learn from cues not measured in this investigation. Our experiments did not account for

446 the ability of *C. carnea* to learn olfactory cues from plants host to different prey species

447 (Glinwood et al. 2011), or their ability to learn to select between prey that are at different

448 densities. Further studies could usefully explore these aspects of learning, along with the

449 duration over which any discriminatory behaviours can be retained (Boivin et al. 2008;

450 Glinwood et al. 2011). If predators fail to discriminate between toxic and non-toxic prey or if

451 selectivity is forgotten, associational/apparent interactions may be prevalent and furthermore,

452 may affect the predator's impacts on prey communities.

453

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683

684 **FIGURE LEGENDS**

685

686 Figure 1: The expected and observed counts of *Brevicoryne brassicae* and *Myzus persicae*

687 aphids alive after 5 hours exposure to predatory *Chrysoperla carnea* larvae, when presented

688 at different aphid abundance ratios (number of *B. brassicae*: number of *M. persicae*). Error

689 bars denote the standard errors of the means.

690

691 Figure 2: Counts of *Brevicoryne brassicae* and *Myzus persicae* aphids alive after 5 hours

692 exposure to *Chrysoperla carnea* larvae, that were naïve (left of the dashed line at 0 previous

693 exposures), or given previous exposure to their prey (right of the dashed line; 1-4 previous

694 exposures). The starting population was 10 aphids of each species. Error bars denote the

695 standard errors of the means.

696

TABLES AND TABLE LEGENDS

698   Table 1: Results of deletion tests for GLMMs without a fixed effect, for different response

699   variables associated with predator behaviour in aphid host plant choice tests: (a) of the plants

700   visited; the number of plants visited first by predators (n = 37 plants); (b) of the first visited

701   plants; the number of exclusive visits (as opposed to predators also visiting the other

702   respective aphid host plant) (n = 28 plants); (c) the time predators spent foraging on the host

703   plants (minutes) and (d) the number of plants where predation occurred (n = 37 plants). Fixed

704   effects included aphid species (*Brevicoryne brassicae* or *Myzus persicae*), plant cultivar

705   (Minicole or Derby Day). All fixed effects had one degree of freedom.

	Response variables							
	(a)		(b)		(c)		(d)	
	Plants visited first		Plant fidelity		Foraging Time (mins)		Plants yielding predation	
Fixed Effect	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Aphid Species	1.549	0.213	0.681	0.409	1.807	0.179	2.341	0.126
Plant Cultivar	0.003	0.954	0.096	0.757	0.874	0.350	0.055	0.814
Species: Cultivar	0.478	0.489	1.449	0.229	0.151	0.697	0.554	0.457

706

707   Table 2: The significance of fixed effects on the number of aphids alive after 5 hours

708   exposure to *Chrysoperla carnea* larvae, that were (a) naïve or (b) experienced of their prey.

709   Fixed effects included aphid species (*Brevicoryne brassicae* or *Myzus persicae*), plant

710   cultivar (Minicole or Derby Day) and the number of previous exposures predators had

711   received to the aphids (1-4 previous exposures). All factors had one degree of freedom.

712

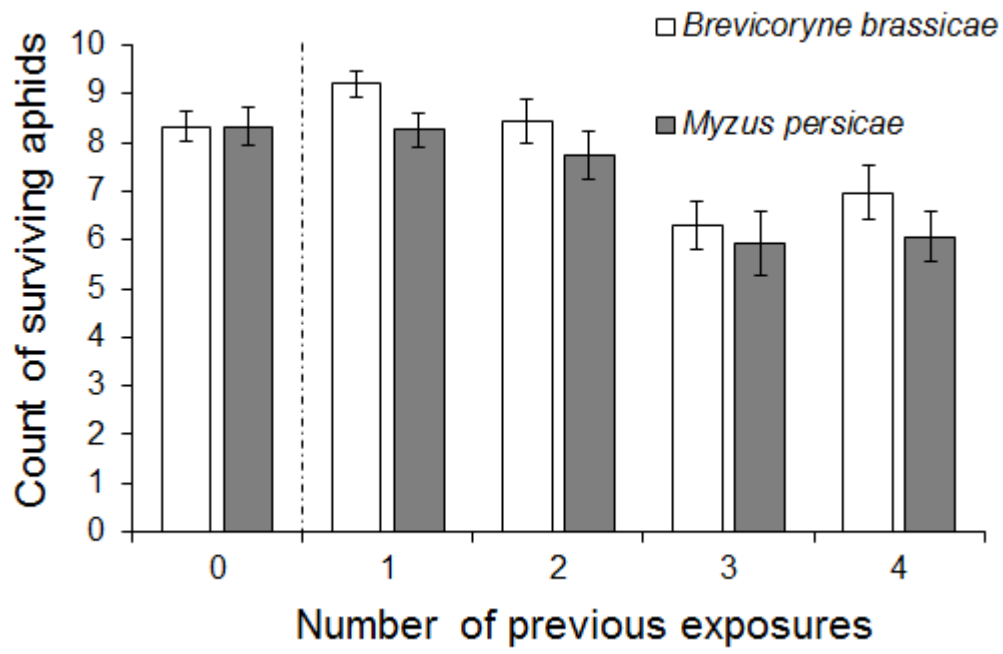| Predators:	(a) Naïve		(b) Experienced		
Fixed Effects	χ^2	p	Fixed Effects	χ^2	p
Aphid Species	0.288	0.592	Aphid Species	4.285	0.038
Plant Cultivar	0.000	1.000	Exposures	14.673	< 0.001
Aphid:Plant	0.000	1.000	Plant Cultivar	0.002	0.963
			Aphid:Exposures	0.016	0.897
			Aphid:Plant	0.121	0.728
			Exposures:Plant	0.071	0.790
			Aphid:Exposure:Plant	0.571	0.450

713

714   Figures
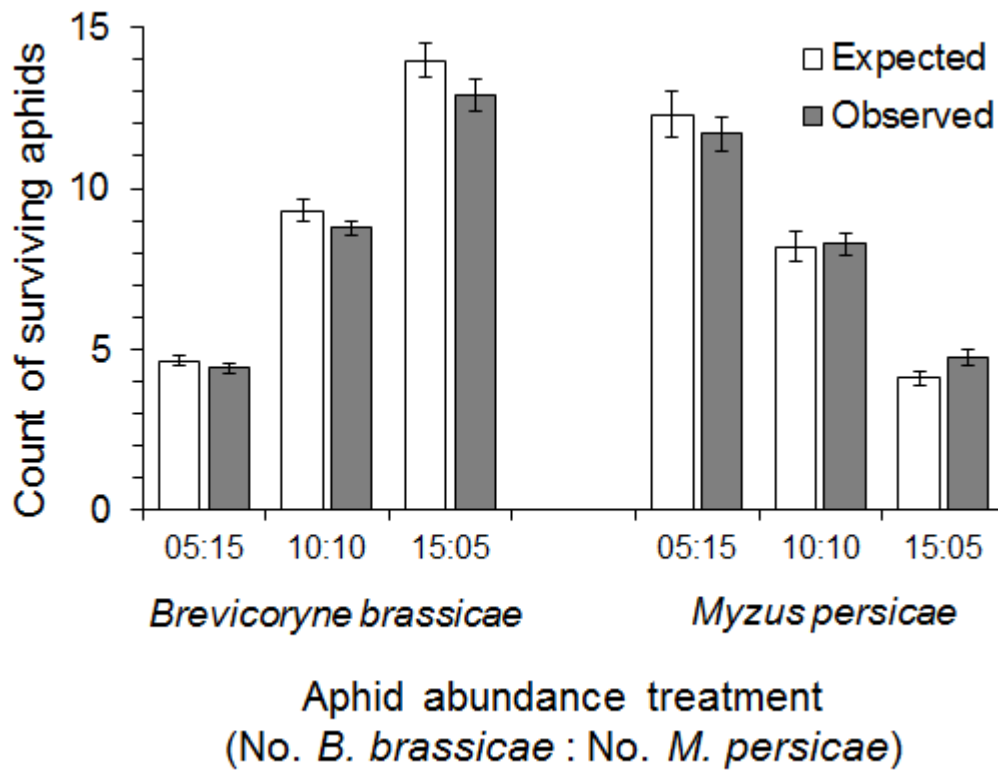
715

716   Figure 1.

717

718

719   Figure 2.

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