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- 1 **Title:** Attractiveness of uninfested vegetables to the omnivorous predators
- 2 Dicyphus bolivari and D. errans (Hemiptera: Miridae) and their relative suitability
- 3 for oviposition
- 4
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- 10 11

12 **1. Introduction**

13 Augmentative biological control with parasitoids and predators has been 14 practiced for decades to control the main pests in greenhouse crops (Van 15 Lenteren and Woets, 1988). Biological control programmes initially applied in 16 the Mediterranean Basin in the 1980s and 1990s were based on the northern 17 European experience, and underwent a rapid expansion in the early 21st 18 century, especially the release of generalist predators (Albajes and Alomar, 19 1999). Several species of Miridae (Hemiptera: Heteroptera) have received 20 special attention for their capacity to control the key pests in various vegetable crops (Castañé et al., 2004; Perdikis et al., 2008; Ingegno et al., 2013). These 21 22 mirids are polyphagous and are also characterized by their facultative omnivory 23 (Alomar and Albajes, 1996; Ingegno et al., 2011), that is, their capacity to feed 24 on both prey and plant resources (Coll and Guershon, 2002; Albajes and 25 Alomar, 2008). The ability of mirids to feed facultatively on plants may allow 26 them to survive on the crop when prey is scarce or absent, establish 27 themselves early in the season, and prevent pests from reaching damaging 28 densities (Albajes and Alomar, 2008), although their use may also lead to some 29 crop plant damage, (Castañé et al., 2011; Calvo et al., 2012b). 30 31 In the Mediterranean region, predatory bugs such as *Dicyphus bolivari* Wagner, 32 (recently D. maroccanus has been synonymized with D. bolivari, Sánchez and

33 Cassis, 2018), *Dicyphus errans* (Wolff), *Dicyphus cerastii* Wagner, *Macrolophus*

costalis Fieber, Macrolophus pygmaeus (Rambur) and Nesidiocoris tenuis

35 (Reuter) can be found on vegetable and ornamental crops but also on many

36 non-crop plants (Carvalho and Mexia, 2000; Gabarra et al., 2004; Arnó et al.,

- 37 2010; Perdikis et al., 2011; Aviron et al., 2016; Leman et al., 2018). However, in
- 38 Europe, only two mirid bugs are currently commercialized, *M. pygmaeus* (sold
- 39 under its former name, *M. caliginosus*) and *N. tenuis*, which both have
- 40 characteristics that limit their usefulness as biological control agents: the
- 41 establishment of *M. pygmaeus* on crop plants after release in the greenhouse is
- 42 too slow, so that, it takes too long to reproduce, spread in the greenhouse, and
- 43 start pest suppression (Trottin-Caudal et al., 2012), whereas *N. tenuis* can
- 44 injure the crop plant under certain conditions (Castañé et al., 2011). In order to

45 overcome these disadvantages, there is interest in researching other native predators, including D. bolivari and D. errans (Ingegno et al., 2017, 2019). The 46 former species has been mainly studied in the northeastern Iberian Peninsula 47 48 under the name D. tamaninii. However, a recent revision of Mediterranean mirid 49 bugs (Sánchez and Cassis, 2018) identified the species collected in that part of 50 the Iberian Peninsula as D. bolivari, so results reported for D. tamaninii there 51 should be attributed to *D. bolivari*. *Dicyphus errans* has been mainly studied in 52 northern Italy, where it is common (Tavella et al., 1997; Ingegno et al., 2008, 53 2013).

54 Research has focused not only on assessing the potential for 55 augmentative releases, but also on identifying the factors that enhance natural crop colonization (Gabarra et al., 2004; Aviron et al., 2016) and on early 56 57 attraction of the predator into the greenhouse when crop plants have not yet 58 been infested by pests in order to keep pest numbers below economic 59 thresholds throughout the season (Perdikis and Lykouressis, 1996; Messelink et al., 2015). Early predator establishment on the crop plant for conservation 60 61 biological control relies on the crop plants attract naturally occurring predators 62 from a certain distance to lay eggs into them (Gabarra et al., 2004). If predators 63 are not attracted to crop plants from a distance, colonization may occur too late 64 to provide efficient biological control. In this case, early inoculation of crop seedlings in the nursery has been shown to be feasible and is routinely done for 65 66 commercial bugs such as *N. tenuis* and *M. pygmaeus* (Calvo et al., 2012a; Backer et al., 2014). This technique has been tested with D. bolivari and D. 67 68 errans on tomato and yielded good establishment and distribution of the 69 predators on the plants and no plant damage on seedlings was observed 70 (Madeira et al., 2018).

71 There is little information available about plant colonization processes or 72 the cues that mirid predators use to locate host plants from a distance (Ingegno 73 et al., 2016). Studies on olfactory orientation of omnivorous mirid bugs have 74 aimed to identify volatiles released by infested plants and their attractiveness to predators. Most of these have been done with a few commercial species (e.g. 75 76 Ingegno et al., 2011; Lins et al., 2014; Pérez-Hedo and Urbaneja, 2015; Naselli 77 et al., 2017; Rim et al., 2017), but few have examined the response of native 78 species such as *D. bolivari* or *D. errans* to crop plants (e.g. Ingegno et al., 2013, 79 2017). Previous studies have shown that *M. pygmaeus* and *N. tenuis* respond to volatiles from infested plants, but have not addressed whether mirids are also 80 81 attracted by host plants that are not yet infested, a feature that would enhance 82 crop colonization early in the season.

The first aim of this study was to determine whether *D. bolivari* or *D. errans* are attracted by uninfested crop plants (tomato, pepper, cucumber), a feature that would facilitate early greenhouse colonization before insect pest establishment. To this end, responses of adult predators to plants was studied in a Y-tube olfactometer. The second aim was to test whether the predators are willing to lay eggs on uninfested seedlings and if they expressed oviposition preferences among crop plants. To this end, predator adults were allowed tochoose between pairs of uninfested seedlings for oviposition.

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92 **2. Material and methods**

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94 2.1. Plants and insects

95 Experimental plants of tomato (Solanum lycopersicum L., cv. Roma VF), sweet 96 pepper (Capsicum annuum L., cv. Estrella), cucumber (Cucumis sativus L., cv. 97 Negrito) and marigold (Calendula officinalis L. cv. Fitó, Doble variada) were 98 grown in a climate-controlled room (25 ± 2 °C and 16:8 h L:D photoperiod). The 99 seeds were sown in peat substrate (Klasmann-Deilmann®, Geeste, Germany) 100 in pots (Ø 5.5 cm, height 10 cm) with no pesticide or fertilization application, and 101 they were watered as needed. Low nitrogen peat substrate was used to avoid 102 plant nitrogen contents to interfere with the selection of host plant species as 103 seen by Vankosky and VanLaerhove (2017).

104 The herbivore Bemisia tabaci Gennadius (Hemiptera: Aleyrodidae) and 105 the predators *D. bolivari* and *D. errans* were reared under controlled conditions 106 (25 ± 2 °C and 16:8 h L:D photoperiod) at the Universitat de Lleida (Catalonia, 107 NE Iberian Peninsula). Laboratory colonies of insects were started from 108 specimens collected on local plants (B. tabaci), from individuals provided by the 109 laboratory of Entomology of the Catalan Agricultural Research Institute IRTA-110 Cabrils (Catalonia) and initially collected in that area on various local plants (D. 111 bolivari), and from individuals reared at the Università di Torino (D. errans) on 112 several crop and non-crop plants.

113 The *B. tabaci* colony was reared on cabbage (*Brassica oleracea* L., cv. 114 acephale) plants in a climate-controlled room. Every two to three weeks, new 115 host plants were supplied as needed.

116 The mirid colonies were reared in our laboratory in 2-L glass jars for at 117 least 5 generations before trials, fed ad libitum with frozen eggs of Ephestia 118 kuehniella Zeller (Lepidoptera: Pyralidae) (BIOCARE GmbH, Germany) as prey, 119 and provided with water by means of a wet cotton and also French green bean 120 pods (*Phaseolus vulgaris* L.) and or tomato stems as egg-laying substrates. 121 Twice a week, the mirid colonies were provided with food, and the water and 122 egg-laying substrates were replaced. The substrates with mirid eggs were 123 placed in new rearing jars.

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125 2.2. Y-tube olfactometer bioassay

The Y-tube olfactometer consisted of a Y-shaped glass tube of 3.8 cm inner
diameter, 18 cm long for each arm tube and 20 cm long for the main tube. The
two arms were connected via a plastic tube to two identical glass bottles (2.8 L),
in which volatile sources had been placed. The glass bottles were kept behind a
panel to prevent the insects from visually detecting the plants.

131The bottles were connected to an air pump (Kn LAB Laboport, type132N86KN-18) that produced a unidirectional humidified airflow regulated at 250

mL/min from the bottles to the base of the main tube of the olfactometer. The airflow passed through a water filter (Analytical Research Systems, model VCS-HADS-2AFM2C) before it entered the bottles. The bioassays were conducted in a dark room ($25 \pm 2 \,^{\circ}$ C) with the Y-tube illuminated by a 28- to 35-W cool white fluorescent tube positioned 57 cm above the arms, providing a light intensity of 2643 lux. The Y-tube was positioned vertically, as in another study with *Dicyphus* species (Ingegno et al., 2013).

140 The olfactory bioassays were conducted between 12:00 and 16:00 h. 141 Males and females of *D. bolivari* and *D. errans* were used. Except for the 142 bioassay with mated females, newly moulted adults were separated by sex (<24 143 h) and used when they were between 6 and 14 days old. Before the bioassay, 144 each individual was transferred to a transparent vial (Ø 1 cm, height 10 cm) and 145 starved for 3 to 4 h. Insects were individually introduced at the downwind end of 146 the entry main arm and observed until they walked at least 5 cm up one of the 147 side arms or until five minutes had elapsed. Insects not choosing a side arm 148 within five minutes were considered as having made no choice and were not 149 counted in the data analysis. Each insect was tested only once and then 150 discarded. To minimize any spatial effect on choices, the volatile source bottles 151 were switched between the right and left side arms after five individuals had 152 been tested. After each use, the olfactometer setup was cleaned with neutral 153 soap, washed with acetone (99%) and placed in the oven at 60° C for at least 2 154 hours.

The plants used for this trial had the following characteristics: Tomato (5fully developed leaves, \pm 27 cm); sweet pepper (8 fully developed leaves, \pm cm); cucumber (4-5 fully developed leaves, \pm 23 cm); marigold (10-12 fully developed leaves, \pm 18 cm).

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160 The following bioassays were conducted for both *Dicyphus* species:

- 162 i. Response to volatiles emitted by uninfested plants vs. clean air.
 - a. Tomato vs. clean air; (species and sex, $n \ge 300$);
- b. Sweet pepper vs. clean air; (species and sex, $n \ge 200$);
- 165 c. Cucumber vs. clean air (species and sex, $n \ge 200$).
- 166ii. Response to volatiles emitted by uninfested tomato vs. clean air by mated167females and unmated females (species, $n \ge 200$). After the experiment, 20%168of females assumed to be mated were kept to confirm the status; more than
- 169 **60% were mated**.
- iii. Response to volatiles emitted by uninfested tomato *vs.* uninfested marigold plant (species and sex, $n \ge 200$).
- 172 iv. Response to volatiles emitted by uninfested tomato *vs.* tomato previously
- infested by *Dicyphus* species (species and sex, $n \ge 150$). Three six-day-old
- 174 couples of the respective *Dicyphus* species were released in a transparent
- insect-rearing tent (BugDorm®-2120, 60x60x60) with three tomato plants.

176 The plants were infested for five days, and after infestation the plants with 177 Dicyphus eggs were used in the bioassay.

- 178 v. Response to volatiles emitted by uninfested tomato vs. marigold plant 179 infested by *B. tabaci* (species and sex, $n \ge 150$). About fifty adults of *B. tabaci* 180 were released in a transparent methacrylate cylinder (\emptyset 20 cm, height 35 cm) 181 with one marigold plant. Plants were infested for ten days, and after 182 infestation the plants with *B. tabaci* eggs and nymphs were used in the bioassay.
- 183
- 184

185 2.3. Oviposition choice bioassay

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187 To test *D. bolivari* and *D. errans*, for oviposition preferences among host plants, 188 we provided bugs with free-flight, pairwise choices of the four plants tested in 189 olfactometer bioassays. We only used uninfested plants, and plant size was 190 similar to that of the plants used in the olfactometer experiments. For each 191 pairwise choice test, ten combinations of two plants, including pairs of the same 192 plant, were exposed for five days to three pairs of a *Dicyphus* species. The 193 insects were six- to nine-day-old adults when tested to ensure that they were 194 ready to oviposit (Madeira et al., 2018). Each of the ten combinations was 195 replicated six times. These bioassays were conducted inside transparent insect-196 rearing tents (60x60x60 cm, Insect Rearing BugDorm®-2120F, from BugDorm 197 Store) under controlled conditions ($25 \pm 2 \, {}^{\circ}C$ and 16:8 h L:D daylength).

198 After exposure to the predators for five days, all plants were isolated in a 199 laboratory chamber (25 ± 2 °C and 16:8 h L:D daylength). Oviposition 200 preference was assessed by counting the number of nymphs that emerged from each plant from 6 to 15 days after predator removal; it was assumed that 201 202 eclosion rates would be similar across host plants. Each replicate was 203 terminated after three consecutive days with no nymph emergence. 204

- 205 2.4. Data analysis
- 206

207 In the olfactometer bioassays, the dependent variable 'response' (proportion of 208 responses to one source) was analysed using generalized linear modelling 209 (GLM) based on a binomial distribution with a logit link function. The 210 explanatory variables used in the models were 'species' (D. bolivari vs. D. 211 errans) and 'sex' (female vs. male) as factors and their two-way interactions. 212 One of the models also included the explanatory variable 'mating status (Mated 213 vs. Unmated). After these analyses, at each olfactometer bioassay, responses 214 were analysed using a Chi-squared test 215 In the oviposition preference bioassays, the dependent variable

216 'offspring' (number of nymphs) was analysed using GLM based on a Poisson 217 distribution with a log link function, and the model included the explanatory 218 variables 'combination' (10 combinations of two plants) and 'species' (D. bolivari 219 vs. D. errans as factors and their two-way interactions). The total number of

offspring on each individual plant within each combination was analyzed using a
Chi-squared test. Statistical analyses were performed using R software version
3.5.3 (R Development Core Team 2019).

- 223
- 224

225 **3. Results**

226 3.1. Experiments in the olfactometer

227 In the olfactometer experiments, we tested a total of 1538 adults of *D. bolivari* or 228 D. errans, of which 1153 individuals selected an odour source in five minutes, 229 therefore representing a 75% success rate. GLM-binomial distribution analyses 230 were performed to determine whether the predator species, sex, and female 231 mating status significantly influenced insect choice; then, significant factors 232 were analysed by χ^2 tests. Only sex for uninfested tomato vs. uninfested 233 calendula resulted significant (χ^2 =5.35; df=1, P=0.02)(Fig. 1). Neither of the two 234 predators was attracted by uninfested host plants; that is, when tomato 235 $(\chi^2=1.15; df=1, P=0.28)$, pepper $(\chi^2=1.60; df=1, P=0.21)$, or cucumber $(\chi^2=0.10; \chi^2=0.10)$ 236 df=1, P=0.75), were each tested against clean air in the Y-form olfactometer, no 237 significant differences between the two choices were found (Fig. 1). Female 238 mating status did not alter this result (χ^2 =0.01; df=1, P=0.92); 48 vs. 49% of 239 (mated vs. unmated) females preferred the tomato plants to clean plants.

In contrast, tomato was preferred by females when it was tested against calendula (χ^2 =26.04; df=1, P<0.001). When the calendula was infested by whiteflies there was preference for uninfested tomato (χ^2 =2.10; df=1, P=0.15). Tomato plants bearing eggs of the predator became more attractive to the predator than tomato plants that had not been infested by the predator (χ^2 =6.53; df=1, P=0.01).

246

247 3.2. Dual-plant choice experiments for oviposition preference

248 Predator preference for host plants for oviposition was measured by the number 249 of nymphs eclosing from eggs laid during five days of predator-plant interaction. 250 There was a significant interaction between species and plant combination 251 factors (χ^2 = 43.64, df = 9, P < 0.001); for this reason, each predator species 252 was analysed separately. For both species, the number of nymphs per tent was 253 significantly different according to the plant combination contained in the tent 254 (Fig. 2), being lower in cages with only cucumber or pepper plants or their 255 combination than in cages with at least one tomato or calendula plant (Fig. 2). 256 When predator preference for host plants to lay eggs on was examined 257 according to the total number of nymphs produced on each individual plant, 258 tomato and calendula were preferred to pepper or cucumber by the two 259 predators (Fig. 3). Predator preference when tomato and calendula were 260 combined in the same cage varied with the predator species; D. bolivari 261 preferred calendula to tomato for ovipositing, whereas D. errans preferred 262 tomato (Fig. 3).

263

264

265 **4. Discussion**

266 None of the three crop plants tested in the Y-tube olfactometer (tomato, 267 sweet pepper and cucumber) were themselves more attractive to the bug 268 species than clean air. This would indicate that uninfested plants do not emit 269 volatiles that attract these predatory mirid bugs independent of other factors. 270 Similar results were recorded for *N. tenuis* on tomato (Lins et al., 2014). 271 However, a preference for uninfested crop plants over clean air has also been 272 found with Y-tube olfactometry for *M. pygmaeus* (Ingegno et al., 2011; Lins et 273 al., 2014) and N. tenuis (Naselli et al., 2017; Rim et al., 2015) on tomato and 274 eggplant (Solanum melongena L.). Similar results were found for three 275 neotropical predatory mirids on tomato (Silva et al., 2018), by Abbas et al. 276 (2014) on tomato and D. maroccanus (today synonymized to D. bolivari 277 according to Sánchez and Cassis, 2018), and by Pérez-Hedo and Urbaneja 278 (2015) on sweet pepper for N. tenuis, M. pygmaeus, and D. maroccanus. Other 279 authors have emphasized the importance of plant genotypes in explaining 280 variability of results regarding the attractiveness of uninfested plants to natural 281 enemies (Rapusas et al., 1996).

282 The lack of response of *D. bolivari* and *D. errans* to uninfested crop 283 plants could hamper the early colonization of greenhouse crops by these 284 naturally occurring predators. Only when the herbivores enter greenhouses and 285 start feeding on the plants will they become attractive to natural enemies, as many authors have also shown (e.g. Reddy, 2012). As shown in the present 286 287 work, if the predator is allowed to oviposit on the seedlings in the nursery, plants 288 become attractive to the predator and this may also cause the predator to 289 recognize volatiles emitted by the plant and move close to it. Moayeri et al. 290 (2007) also reported that plants previously exposed to omnivore predator 291 females for feeding became attractive to conspecific males, but the authors 292 inferred that this behavior improved mate finding by males, rather than plant 293 colonization for feeding and reproduction, an explanation also invoked by Ingegno et al. (2016) in their electroantennography (EAG) studies with two 294 295 Macrolophus species. Thus gender and sexual behaviour may have an effect 296 on the plant preferences of omnivorous predators, independent of the role of 297 plant volatiles in host plant discovery. Our results suggest that the gender of 298 predators did not influence plant selection except when uninfested tomato 299 plants were tested against uninfested calendula, in which case the females of 300 both species were more discriminating in the olfactometer.

301 Several studies have been devoted to determining which non-agricultural 302 plants present in habitats surrounding or close to greenhouses can serve as 303 refuges for predatory mirid bugs, from which they could disperse to colonize 304 greenhouse crops (Tavella and Goula, 2001; Gabarra et al., 2004; Alomar et al., 305 2006; Ingegno et al., 2016, Balzan, 2017). Among these, *Calendula* spp. have 306 received particular attention with regard to *M. pygmaeus* and *D. bolivari* (Alomar 307 et al., 2006; Lambion, 2011; Ardanuy et al., 2019). Surprisingly, *D. bolivari* and 308 D. errans preferred the odour of tomato to calendula, even when calendula 309 infested by whiteflies was tested against uninfested tomato, which was not 310 preferred over clean air. In contrast with that found for other omnivorous mirids, 311 it seems that *Dicyphus* species are not attracted by uninfested plants indicating 312 that no olfactory cues can be expected from greenhouse crops early in the 313 season to favour early entrance of predators into greenhouses. For this reason, 314 transplantation of young plants with predator eggs into the greenhouse can 315 enhance early crop colonisation (Madeira et al., 2018). This has been also 316 tested for other omnivorous predators like *M. pygmaeus* (Lenfant et al., 2000) or 317 N. tenuis (Calvo et al., 2012b; Perdikis et al., 2015).

318 Although none of the four plants alone were attractive in the olfactometer, 319 they still received oviposition in the enclosures, probably because other short-320 distance cues allowed them to recognize the plants as a suitable source of food 321 and potentially, prey. Plant selection by omnivorous predators for phytophagy, 322 oviposition, or sources of prey is probably a more complicated process than for 323 predators which are strictly carnivorous (Coll and Guershon, 2002). The 324 process can likely be influenced by both the plant and the presence/absence of 325 prey, as seen in another *Dicyphus* species (Sanchez et al., 2004). Plant guality 326 features like nitrogen content have been found to affect oviposition preference 327 (Groenteman et al., 2006; Vankosky and VanLaerhoven, 2017). Other authors 328 have implicated plant stickiness and hairiness as influencing D. hesperus 329 female oviposition decisions (Sanchez et al., 2004), and differences in these 330 plant traits could explain our results which showed tomato and marigold were 331 preferred over pepper for oviposition. Host plant selection by omnivore females 332 can be a combination of different cues that remain unidentified and more work 333 is warranted to better understand this important issue (Vankosky and 334 VanLaerhoven, 2017).

The two predators achieved very different fecundities on the four plants 335 336 tested. This means that pre-plant inoculation of the four plants tested is feasible, 337 but the numbers of adults to be released in the nursery, and their duration of 338 exposure to the seedlings, will vary among crops. Three pairs of predators 339 produced anywhere from three to 17 nymphs per plant in five days. This density 340 of predators per seedling would probably be too high in seasons with low pest pressure, but more suitable under high pest pressure. Initial release rates 341 342 recommended for *M. pygmaeus* and *N. tenuis* in greenhouse tomatoes range 343 from 0.5 to 1.6 adults per plant (Arnó et al., 2009), values not dissimilar from the 344 number of nymphs per plant achieved in this work.

Marigold plants did not seem to be a good companion plant for inoculation of *D. bolivari* in seedlings, whereas marigold might be inoculated with *D. errans* in the nursery and then moved to the greenhouse as a banker plant. Although predatory bugs have been tested for preferences among odor sources (e.g. Ingegno et al., 2011; Silva et al., 2018), it remains unknown how well these experiments reflect actual behavior in the field (Ballhorn and Kautz, 2013). In this study, we found that orientation to volatile cues does not always

- 352 reflect oviposition free choice under short-distance cues, as *D. bolivari* showed 353 contradictory results for tomato and calendula between the olfactometer and 354 oviposition assays.
- 355 In conclusion, some results indicate the need to inoculate D. bolivari or 356 D. errans in nursery plants, because uninfested plants do not have the capacity 357 to attract either of the predators from a distance. In addition to making the 358 plants more attractive to the predators when they have been transplanted in the 359 greenhouse, inoculation of young plants with predator eggs allows predator 360 populations to become established on the crop early in the season.
- 361 Diversification of the nursery by inoculating several crops with predators could 362 potentially increase oviposition on those crops less attractive to them, although 363 this effect merits further investigation.
- 364

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- 372 373

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- 547 Figure captions
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Fig. 1. Percentage of responses (mean \pm SE) of D. bolivari and D. errans adults in a Y-tube olfactometer to the odours of clean air vs. uninfested tomato, clean air vs. uninfested pepper, clean air vs. uninfested cucumber, females: uninfested tomato vs. uninfested calendula, males: uninfested tomato vs. uninfested calendula, uninfested tomato vs. infested calendula (with B. tabaci) and uninfested tomato vs. tomato previously visited (by the predator). * P < 0.05; **P ≤ 0.01.

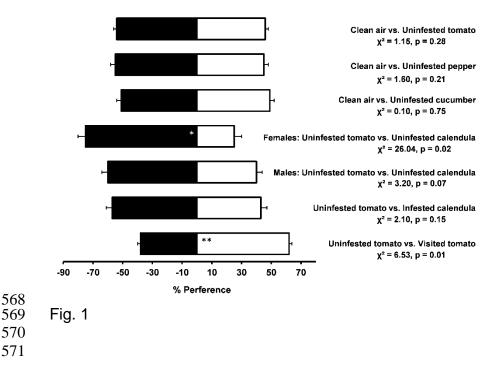
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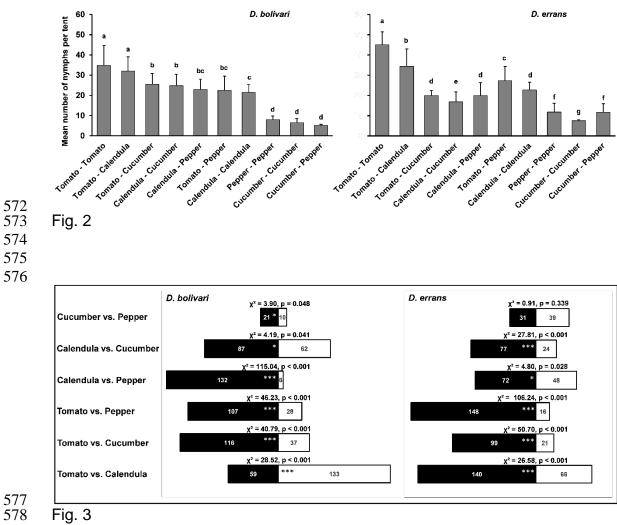
Fig. 2. Mean number + SE of nymphs per tent produced by three predator couples of two predatory species left for 5 days in a tent with a combination of two plants, as shown on the X axis. Means followed by different letters are significantly different (P < 0.05).

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Fig. 3. Total number of D. bolivari and D. errans nymphs that emerged per plant when different combinations of two plants were offered to predators within tents for oviposition for 5 days. In each plant comparison and predator species, chi

- 565 squared and significance are shown. * P < 0.05; ***P < 0.001.
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