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Abstract

Plants damaged by herbivores are known to release odors attracting parasitoids. However, there is currently no information how leguminous plants damaged by the pod borer *Maruca vitrata* attract the exotic larval parasitoid *Therophilus javanus*, which was imported into Benin from the putative area of origin of the pod borer in tropical Asia for assessing its potential as a biological control agent. In this study, we used Y-tube olfactometer bioassays to investigate *T. javanus* response towards odors emitted by four *M. vitrata*-damaged host plants: cowpea *Vigna unguiculata*, the most important cultivated host, and the naturally occurring legumes *Lonchocarpus sericeus*, *Sesbania rostrata* and *Tephrosia platycarpa*. Olfactory attraction of *T. javanus* was influenced by the species of plant damaged by the pod borer. Moreover, odors released from *M. vitrata*-infested host plant organs (flowers and pods) were discriminated over non-infested organs in cowpea and *T. platycarpa*, respectively. These results are discussed in the context of the possible impact of *M. vitrata* host plants on *T. javanus* foraging activity and subsequent establishment in natural environments following experimental releases.

Keywords Biological control; natural enemy; olfaction; attraction; cowpea; host plant volatiles

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Cotonou, August 13, 2018

Dear Editor of Biological Control

On behalf of the below listed co-authors, I am submitting an original manuscript titled:

Volatiles from *Maruca vitrata* (Lepidoptera, Crambidae) host plants influence olfactory responses of the parasitoid *Therophilus javanus* (Hymenoptera, Braconidae)

by Djibril Aboubakar Souna, Aimé Hippolyte Bokonon-Ganta, Elie Ayitondji Dannon, Nazyhatou Imorou, Benjamin Agui, Antonino Cusumano, Ramasamy Srinivasan, Barry Robert Pittendrigh, Anne-Nathalie Volkoff, and Manuele Tamò

This manuscript is intended to be published as an **original article** and is formatted accordingly. It reports, for the first time, observations on olfactory responses by foraging exotic parasitoids *Therophilus javanus*, introduced into West Africa for the prospective biological control of the legume pod borer *Maruca vitrata*. These observations are vital for further assessing the possible impact of *M. vitrata* host plants on *T. javanus* foraging activity and subsequent establishment in natural environments following experimental releases

We hope you will find this article of interest and suitable for publishing in your journal. The manuscript has not been published elsewhere and we are not considering submitting it anywhere else unless a decision has been made by your journal.

With kind regards



Manuele Tamò, PhD
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Highlights

The foraging behavior of *T. javanus* is influenced by pod borer *M. vitrata* host plants

Among wild host plant species, *T. javanus* is more attracted by odors of *T. platycarpa*

In cowpea, the cultivated host, infested pods are more attractive to *T. javanus* than infested flowers

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3

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21 **Abstract**

22 Plants damaged by herbivores are known to release odors attracting parasitoids. However, there is
23 currently no information how leguminous plants damaged by the pod borer *Maruca vitrata* attract
24 the exotic larval parasitoid *Therophilus javanus*, which was imported into Benin from the putative
25 area of origin of the pod borer in tropical Asia for assessing its potential as a biological control
26 agent. In this study, we used Y-tube olfactometer bioassays to investigate *T. javanus* response
27 towards odors emitted by four *M. vitrata*-damaged host plants: cowpea *Vigna unguiculata*, the
28 most important cultivated host, and the naturally occurring legumes *Lonchocarpus sericeus*,
29 *Sesbania rostrata* and *Tephrosia platycarpa*. Olfactory attraction of *T. javanus* was influenced by
30 the species of plant damaged by the pod borer. Moreover, odors released from *M. vitrata*-infested
31 host plant organs (flowers and pods) were discriminated over non-infested organs in cowpea and
32 *T. platycarpa*, respectively. These results are discussed in the context of the possible impact of *M.*
33 *vitrata* host plants on *T. javanus* foraging activity and subsequent establishment in natural
34 environments following experimental releases.

35 **Keywords:** Biological control, natural enemy, olfaction, attraction, cowpea, host plants

36

37 **1. Introduction**

38 *Maruca vitrata* Fabricius (Lepidoptera: Crambidae) is an insect pest of leguminous plants recorded
39 on thirty-nine host plants species in Africa (Sharma et al., 1999; Arodokoun et al., 2003). In West
40 Africa, cowpea *Vigna unguiculata* Walp (Leguminosae) is the main cultivated host plant attacked

41 by *M. vitrata* caterpillars and this pest can cause yield losses between 20-80% (Jackai and Daoust,
42 1986). Of the several host plants identified in Benin, the caterpillar primarily feeds on *Pterocarpus*
43 *santalinoides* L'her. Ex De, *Pueraria phaseoloides* (Roxb.) Benth. and *Centrosema pubescens*
44 Benth during the dry season, *Lonchocarpus sericeus* (Poir.) H.B. & K., *L. cyanescens* (Schum. &
45 Thonn.) Benth and *Sesbania rostrata* Bremek. & Oberm during the rainy season and *Tephrosia*
46 *platycarpa* Guill. & Perr (all Leguminosae) during the short intermediate season (Arodokoun et
47 al., 2003).

48 In view of the lack of host-specificity of local hymenopteran parasitoids attacking *M.*
49 *vitrata* in West Africa (Arodokoun et al., 2006), and the confirmation of tropical Asia as the
50 putative area of origin of the pod borer (Periasamy et al., 2015), Tamò et al. (2012) argued for the
51 introduction of parasitoids from Asia into West Africa as a classical biological control approach.
52 However, the first classical biological control candidate tested in West Africa, the larval parasitoid
53 *Apanteles taragamae* Viereck (Hymenoptera: Braconidae), failed to establish substantial
54 populations because of its inability to recognize major host plants of *M. vitrata* (Dannon, 2011).
55 In fact, the wasp was collected in Taiwan from *M. vitrata* caterpillars feeding on *Sesbania*
56 *cannabina* (Retz.) Pers., but, surprisingly, it was not attracted by local *Sesbania* species in Benin
57 (Dannon et al., 2012). Recent studies by Srinivasan et al. (2014) in tropical Asia have identified
58 parasitoids more closely associated with and specific to *M. vitrata* feeding on yard-long bean (*V.*
59 *unguiculata* subsp. *sesquipedalis*), including *Therophilus javanus* (Bhat & Gupta) (Hymenoptera:
60 Braconidae), which was introduced into Benin for preliminary assessment.

61 Parallel studies investigating the reproductive potential of *T. javanus* have evidenced its
62 considerable fecundity and suitability for mass rearing (Aboubakar Souna et al., 2017). However,
63 long-term reduction of *M. vitrata* populations depends mainly on how efficiently foraging *T.*

64 *javanus* females will be able to detect and parasitize *M. vitrata* caterpillars throughout the cropping
65 season and particularly during the offseason on alternative host plants.

66 It is well documented that odors emitted by plants can attract herbivorous insects and
67 foraging parasitoids (Bruce et al., 2005; Wäckers, 2005). However, the odors may differently affect
68 the behavior of the visiting insects (Pichersky and Gershenzon, 2002). For example, odors released
69 from non-damaged plants can attract herbivore insects for feeding and/or reproduction but, when
70 damaged, the plants will produce volatiles that can reduce herbivore oviposition and attract natural
71 enemies (Bruce et al., 2005; Bruce and Pickett, 2011; Allmann et al., 2013). Herbivore-damaged
72 plants are known to emit herbivore-induced plant volatiles (HIPVs), commonly used by parasitoids
73 as host-searching cues (Vet and Dicke, 1992; Hare, 2011; Aartsma et al., 2017).

74 There are few studies conducted on insect olfactory responses to the pod borer host plants
75 odors. Cowpea plants emitted volatiles attracting adult *M. vitrata* for feeding and oviposition
76 (Wang et al., 2014; Feng et al., 2017). The pod borer larval parasitoid *A. taragamae* was attracted
77 by odors released from caterpillar-infested cowpea flowers (Dannon et al., 2010). The objective of
78 our study was therefore to document the olfactory response by foraging females of the exotic larval
79 parasitoid *T. javanus* to odors of cowpea and three key alternative host plants *L. sericeus*, *S.*
80 *rostrata* and *T. platycarpa*.

81 **2. Materials and methods**

82 **2.1 Insects**

83 Insect colonies were reared at the laboratories of the International Institute of Tropical Agriculture
84 Benin (IITA-Benin) near Cotonou, Benin (12:12 L:D photoperiod; 26°C ± 1.1°C average

85 temperature; $76\% \pm 7\%$ relative humidity), with the methodology described in detail by Aboubakar
86 Souna et al. (2017), and briefly summarized below.

87 Five 4-day-old mated adult *M. vitrata* females were placed in transparent cylindrical plastic
88 cups (3 cm diameter x 3.5 cm height) and kept for 24 h to allow for oviposition. First instar
89 caterpillars were transferred to large cylindrical plastic containers (11 cm height x 16.5 cm
90 diameter) and reared until pupation using sprouting cowpea seeds as rearing substrate.

91 *T. javanus* parasitic wasps were reared on 3-day-old *M. vitrata* caterpillars. Parasitized caterpillars
92 were subsequently transferred to large cylindrical plastic containers (11 cm height x 16.5 cm
93 diameter) containing sprouting cowpea seeds and reared until obtaining pupae of the parasitoid.

94 **2.2 Host plants**

95 Cowpea flowers and pods (at pod filling stage) were collected from unsprayed fields planted with
96 the Benin local variety ‘Kpodji-guêguê’ at IITA-Benin ($6^{\circ}25'7.262''N$ $2^{\circ}19'37.657''E$). The
97 flowers of the main wild host plants of *M. vitrata* (*S. rostrata*; *L. sericeus* and *T. platycarpa*) were
98 collected from natural populations in the Zou Department in Benin, North of Cotonou
99 ($7^{\circ}20'48.937''N$ $2^{\circ}3'59.472''E$).

100 **2.3 Olfactometer setup**

101 The response of *T. javanus* females to plant volatiles was tested using a glass Y-tube olfactometer
102 (Serbatoi Autoclavi, Type Elto, Vol. 50) as described by Dannon et al., (2010). The internal
103 diameter of the Y-tube measured 3.5 cm with an approximate wind speed in the olfactometer arms
104 of 4 L/min. Each female parasitoid was transferred individually to the Y-tube, and the behavior of
105 each individual was observed for 10 minutes as soon as it started moving. Females unable to move

106 for more than 5 minutes at the release point, those moving but not entering in one of the Y-tube
107 arms, as well as those not reaching the end of the arm were considered as non-responding. The
108 positions of the odors sources were exchanged after testing five parasitoids to avoid bias by
109 accidental asymmetry in the experimental setup.

110 *2.3.1 Response of T. javanus female to volatiles produced by M. vitrata-infested cowpea plant*
111 *organs*

112 Both *M. vitrata*-infested and uninfested cowpea flowers and pods were collected early in the
113 morning (07:00 to 09:00 h). Flower were cut and kept separately in kraft paper bags to avoid odors
114 contaminations. In order to standardize the infestation conditions, infested organs were considered
115 as flowers and pods infested only by *M. vitrata* caterpillar second (L2) and third (L3) larval instars,
116 respectively. Subsequently, we selected flowers or pods infested at the rate of two caterpillars per
117 organ. For each odors source, we tested the effect induced by ten organs pooled together in glass
118 jars connected to the olfactometer's arms.

119 Each of the following ten odors sources combinations were tested:

120 *Flowers:* (1) clean air versus uninfested flowers (80 females tested), (2) clean air versus
121 caterpillar-infested flowers (160 females tested), (3) uninfested flowers versus caterpillar-infested
122 flowers (160 females tested).

123 *Pods:* (4) clean air versus uninfested pods (80 females tested), (5) clean air versus
124 caterpillar-infested pods (160 females tested), (6) uninfested pods versus caterpillar-infested pods
125 (160 females tested).

126 *Both:* (7) uninfested pods versus uninfested flowers (80 females tested), (8) caterpillar-
127 infested pods versus uninfested flowers (80 females tested), (9) uninfested pods versus caterpillar-

128 infested flowers (80 females tested), and (10) caterpillar-infested pods versus caterpillar-infested
129 flowers (80 females tested).

130 2.3.2 *Response of T. javanus females to volatiles produced by M. vitrata-infested wild host* 131 *plants*

132 Whole flower racemes were collected in early morning (07:00 to 09:00 h) from patches of wild
133 host plants. The racemes of *S. rostrata*, *L. sericeus* and *T. platycarpa* were collected from Passagon
134 (125 km, 2h 30 minutes driving time), Massi (88 km, 1h 50 minutes driving time), and Djidja (142
135 km, 3h 35 minutes driving time) from the IITA-Benin station, respectively. Each fresh-cut healthy
136 raceme was kept separately in kraft paper bags to avoid odors contaminations. To obtain infested
137 flowers, two racemes of *S. rostrata*, *L. sericeus* and *T. platycarpa*, respectively, were placed
138 separately in cylindrical plastic containers (9 cm diameter x 4.5 cm height) and artificially infested
139 by introducing ten 3-day-old *M. vitrata* caterpillars in the containers for 24 hours.

140 The attraction of *T. javanus* female parasitoids to (1) clean air versus uninfested flowers, (2) clean
141 air versus caterpillar-infested flowers, and (3) uninfested flowers versus caterpillar-infested
142 flowers were examined for each of the wild host plants. A total of sixty replicates (individual *T.*
143 *javanus*) were assayed for each of the odors source combinations.

144 **2.4 Statistical analysis**

145 Adult female parasitoid choices were compared using a χ^2 test to determine whether the observed
146 distribution of responding wasps significantly diverged from a 50:50 distribution, which is
147 expected if the wasps do not display any attraction toward the tested odors. The number of no-
148 choice wasps was recorded but not included in the statistical analysis. The statistical software
149 package R 3.3.2 (R Core Team, 2016) was used for all statistical analyses.

150 **3. Results**

151 **3.1 Cowpea flower volatiles attraction**

152 The parasitoid did not discriminate between clean air and uninfested flowers ($\chi^2= 3$, $df=1$, $p =$
153 0.08). However, preference was displayed for caterpillar-infested flowers over clean air ($\chi^2=10.39$,
154 $df=1$, $p < 0.001$). Moreover, caterpillar-infested flowers were preferred over uninfested flowers
155 ($\chi^2=8.01$, $df=1$, $p < 0.01$) (Fig 1).

156 **3.2 Cowpea pod volatiles attraction**

157 The parasitoids showed significant preference to both uninfested pods ($\chi^2=18$, $df=1$, $p < 0.001$) and
158 infested pods ($\chi^2=41.46$, $df=1$, $p < 0.001$) over clean air. They significantly preferred caterpillar-
159 infested pods to uninfested pods ($\chi^2=4.83$, $df=1$, $p = 0.03$) (Fig 2).

160 **3.3 Discrimination of cowpea pod and cowpea flower volatiles**

161 The wasps displayed a significant preference for uninfested cowpea pods over uninfested cowpea
162 flowers ($\chi^2=9.65$, $df=1$, $p = 0.002$) or caterpillar-infested flowers ($\chi^2=8.45$, $df=1$, $p = 0.004$).
163 Similarly, significant attraction to caterpillar-infested pods was observed over uninfested cowpea
164 flowers ($\chi^2=5.23$, $df=1$, $p = 0.022$) or caterpillar-infested flowers ($\chi^2=5.40$, $df=1$, $p = 0.02$) (Fig
165 3).

166 **3.4 Wild host plant flowers volatiles attraction**

167 Generally, flowers were more attractive to the female *T. javanus* than clean air, although *L.*
168 *sericeus* uninfested flowers were less preferred (Fig 4). However, parasitoids did not display any
169 significant preference when offered combination of odors sources from the same plant species,
170 neither for flowers of *L. sericeus* (Fig 4) nor for *S. rostrata* (Fig 5). Uninfested flowers of *T.*

171 *platycarpa* were less attractive than infested flowers of *T. platycarpa* ($\chi^2=11.79$, $df=1$, $p < 0.001$)
172 (Fig 6).

173 **4. Discussion**

174 The present work has demonstrated that *T. javanus* females were able to distinguish *M.*
175 *vitrata*-infested organs from non-infested organs of cowpea and *T. platycarpa*. Odors can be
176 produced by plants following herbivore damage for attracting natural enemies (Turlings and
177 Wäckers, 2004; Arimura et al., 2009). Cowpea fully expanded trifoliolate leaves are known to release
178 novel odors compounds in response to herbivore infestation (Van Den Boom et al., 2004).
179 Subsequent studies have reported that *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae)
180 caterpillar infested cowpea plant released specific volatiles attracting females of the parasitoids
181 *Campoletis sonorensis* (Cameron) (Hymenoptera, Ichneumonidae), *Microplitis rufiventris*
182 Kokujev (Hymenoptera: Braconidae) and *Cotesia marginiventris* (Cresson) (Hymenoptera:
183 Braconidae) (D'Alessandro and Turlings, 2005; Sobhy et al., 2018). However, there have been
184 only a few studies investigating *M. vitrata*-infested cowpea flowers releasing odors to attract
185 parasitoids (Dannon et al., 2010). In our work, *T. javanus* females were attracted both by odors of
186 infested cowpea flowers and infested pods. However, the parasitoid preferred caterpillar-infested
187 cowpea pods over caterpillar-infested flowers, suggesting that odors released from cowpea pods
188 may be more detectable to the female parasitoids. According to Turlings et al. (1993), the quality
189 of odors released by the plant attacked by the same caterpillar species can vary depending on the
190 organs infested. Therefore, the discrimination of the pod odors observed in the wasps could be due
191 to difference in herbivore-induced plant volatile composition.

192 We observed that the female parasitoids were able to distinguish undamaged cowpea pods
193 from infested cowpea flowers. Therefore, we cannot completely discard the hypothesis that even

194 undamaged cowpea pods may release odors that can be used as an attractive signal cue for the
195 female *T. javanus*. For example, Kigathi et al. (2009), identified several herbivore-induced
196 volatiles released at low level from undamaged forage legume plants, *Trifolium pratense* L.,
197 (Leguminosae). The fact the female parasitoid discriminated undamaged cowpea pods also might
198 be attributed to the odors composition variability between infested cowpea flowers and undamaged
199 pods. To date, several studies have identified whole cowpea plant (Lwande et al., 1989; Benders
200 et al., 2015; Zhou et al., 2015; Sobhy et al., 2018), leaf (Van Den Boom et al., 2004) and floral
201 volatiles (Andargie et al., 2014; Wang et al., 2014; Feng et al., 2017), but none has ever
202 investigated cowpea pod volatiles. However, it has been shown that volatiles varied quantitatively
203 at different phenological stages of another leguminous crop, pea (*Pisum sativum* L.). The pea pod
204 releases volatiles which are more attractive to the pea weevil (*Bruchus pisorum* L.) (Coleoptera:
205 Bruchidae) than flower volatiles or volatiles from whole plants (Ceballos et al., 2015). But why
206 would *T. javanus* be more attracted to pod volatiles? Female *T. javanus* may be able to adjust host
207 localization strategies and choose host microhabitat that can enhance her offspring survival
208 probability. Phytophagous insects have developed different feeding strategies to escape natural
209 enemies (Connor and Taverner, 1997), including concealed feeding habitat that may limit
210 predation and parasitism risks (Tschanz et al., 2005). *M. vitrata* caterpillars predominantly feeds
211 inside plant organs. Feeding starts from the green, unopened flowers, with growing caterpillars
212 moving to older flowers and ultimately pods where it completes its development (Bailey, 2007;
213 Jayasinghe et al., 2015). Feeding inside growing cowpea pods might incur less mortality risks (e.g.
214 by predation) than if moving between two flowers or from flower to pods. The higher protection
215 conferred by a concealed feeding habitat applies to both non-parasitized and parasitized hosts.
216 Mortality of parasitoid offspring is closely related to the parasitized host mortality (Fritz, 1982).

217 Hence, foraging parasitoids have adopted strategies such as the innate preference for odors
218 released from host microhabitat, to enable them to choose suitable hosts that minimize offspring
219 mortality during immature stages development (Vet and Dicke, 1992; Hedlund et al., 1996) or
220 developed long ovipositors to probe and parasitize concealed host (Sharkey, 1992). We can,
221 therefore, hypothesize that *T. javanus* may be attracted to volatiles released from caterpillar-
222 infested pods as host microhabitat, as a strategy to minimize mortality risk of its offspring.

223 Floral odors compositions generally vary between closely related species (Knudsen et al.,
224 2006). Undamaged leaves and flowers of the peabush *S. cannabina* were reported to release odors
225 attracting the female parasitoid *A. taragamae* females when tested against clean air (Dannon et al.,
226 2010). In our work, among the three plant species tested (*L. sericeus*, *S. rostrata*, and *T.*
227 *platycarpa*.), only infested flowers of *T. platycarpa* exhibited significant attraction to female
228 parasitoids when tested against uninfested flowers of the same plant. These observations are in
229 agreement with previous studies indicating that different host plants can emit specific volatiles
230 signaling the presence of herbivores (Dicke et al., 2003; Turlings and Wäckers, 2004). The
231 discrimination of infested vs. uninfested flowers of *T. platycarpa* may be due to specific volatiles
232 released by the plant in response to herbivore infestation.

233 The long-term goal of this research was to determine the parasitism competence of the
234 exotic wasp *T. javanus* foraging for the pod borer *M. vitrata* in a new environment in Africa. Our
235 studies have showed that cowpea pods fed upon by the pod borer caterpillars are attractive to the
236 parasitoid and these are encouraging news. However, we also observed that not all *M. vitrata* wild
237 host plants detached flowers were able to emit volatiles attracting the foraging parasitoids, calling
238 for future bioassays to be carried out in more natural settings (Ballhorn and Kautz, 2013). In fact,
239 several factors can influence odors compositions and releasing intensity in plants (Paré and

240 Tumlinson, 1999): the degree of the biotic stresses such as herbivores damage (Niinemets et al.,
241 2013), and abiotic stress such as light intensity, time of year, water stress, and nutrient availability
242 (Takabayashi et al., 1994; Becker et al., 2015). Therefore, complementary investigations of the
243 parasitoid attraction to different host plants (focusing on flowers and pods) in natural environments
244 could lead to a more consistent assessment of the host finding behavior of foraging parasitoids
245 (Wäschke et al., 2014). On the other hand, the ability of a parasitoid to find the appropriate host
246 habitat can be influenced by varying quantities and/or qualities of released volatiles, which can
247 differ among plants species exposed to the feeding activity of the same polyphagous herbivore
248 (Veterans, 1992; Becker et al., 2015), such as the cowpea pod borer. To overcome these obstacles
249 in host habitat recognition, and enhance the host finding efficiency of foraging parasitoids, novel
250 approaches are targeting the biosynthesis of specific and effective HIPVs (Peñaflor and Bento,
251 2013; Sobhy et al., 2018) that can be applied on the target crop for enhancing parasitoid recruitment
252 (James et al., 2005). Hence, further investigations should attempt to identify specific volatile
253 compounds emitted by cowpea and other wild host plants, and their different organs attacked by
254 caterpillars of the pod borer, in order to assess the quantitative and qualitative responses of
255 candidate biological control agents such as *T. javanus* to these HIPVs, with the long-term goal to
256 re-engineer the chemical ecology dominating the complex tritrophic interactions between the crop,
257 herbivores and their natural enemies, and make the latter more competitive.

258

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266

267 **Disclosure**

268 All authors declare that they have no conflict of interests.

269

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421

422 **Figure captions**

423 **Fig. 1.** Response of female *T. javanus* when offered volatiles sources from cowpea flower in a Y-
424 tube olfactometer. Numbers in the bars represent the total number of parasitoids that chose either
425 olfactometer arm. Probabilities given to the right of bars are for the Chi-square test ($p < 0.05$)

426

427 **Fig. 2.** Response of female *T. javanus* when offered volatiles sources from cowpea pod in a Y-
428 tube olfactometer. Numbers in the bars represent the total number of parasitoids that chose either
429 olfactometer arm. Probabilities given to the right of bars are for the Chi-square test ($p < 0.05$)

430

431 **Fig. 3.** Response of female *T. javanus* when offered choices between cowpea flower and cowpea
432 pod volatiles sources in a Y-tube olfactometer. Numbers in the bars represent the total number of
433 parasitoids that chose either olfactometer arm. Probabilities given to the right of bars are for the
434 Chi-square test ($p < 0.05$)

435

436 **Fig. 4.** Response of female *T. javanus* when offered volatiles sources from *L. sericeus* flower in a
437 Y-tube olfactometer. Numbers in the bars represent the total number of parasitoids that chose either
438 olfactometer arm. Probabilities given to the right of bars are for the Chi-square test ($p < 0.05$)

439

440 **Fig. 5.** Response of female *T. javanus* when offered volatiles sources from *S. rostrata* flower in a
441 Y-tube olfactometer. Numbers in the bars represent the total number of parasitoids that chose either
442 olfactometer arm. Probabilities given to the right of bars are for the Chi-square test ($p < 0.05$)

443

444 **Fig. 6.** Response of female *T. javanus* when offered volatiles sources from *T. platycarpa* flower in
445 a Y-tube olfactometer. Numbers in the bars represent the total number of parasitoids that chose
446 either olfactometer arm. Probabilities given to the right of bars are for the Chi-square test ($p < 0.05$)

447

448

449

Figure 1

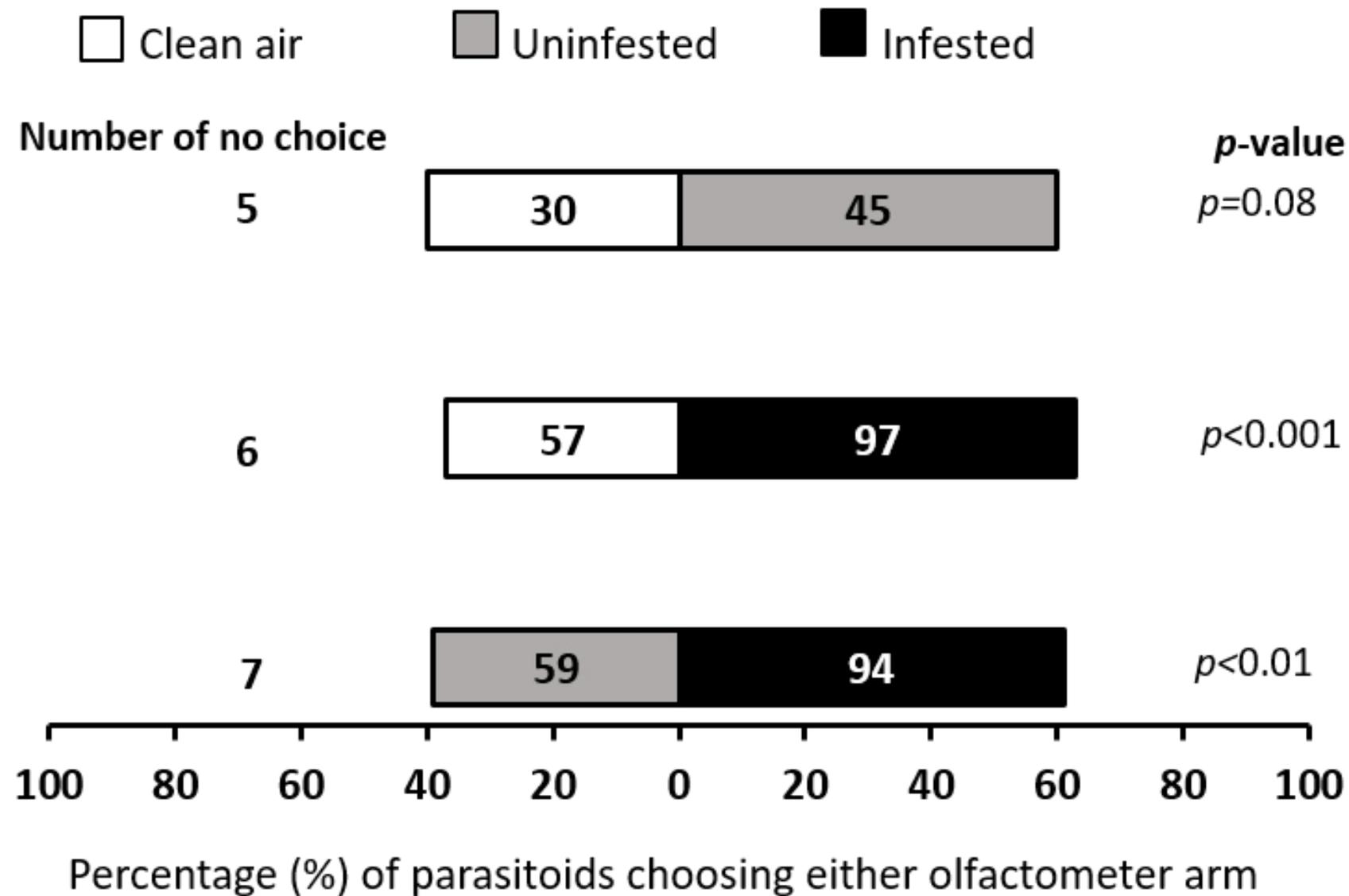


Figure 2

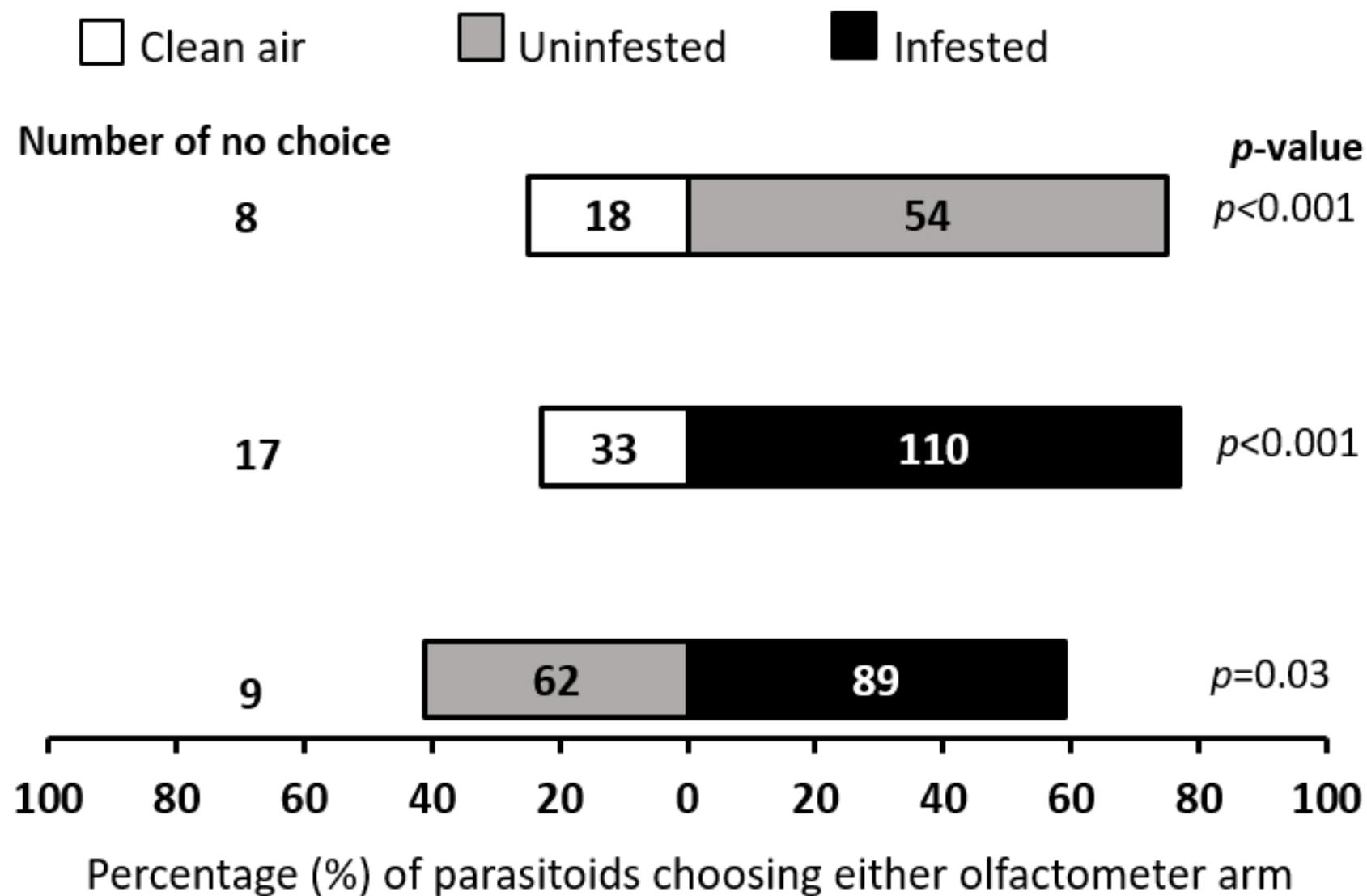


Figure 3

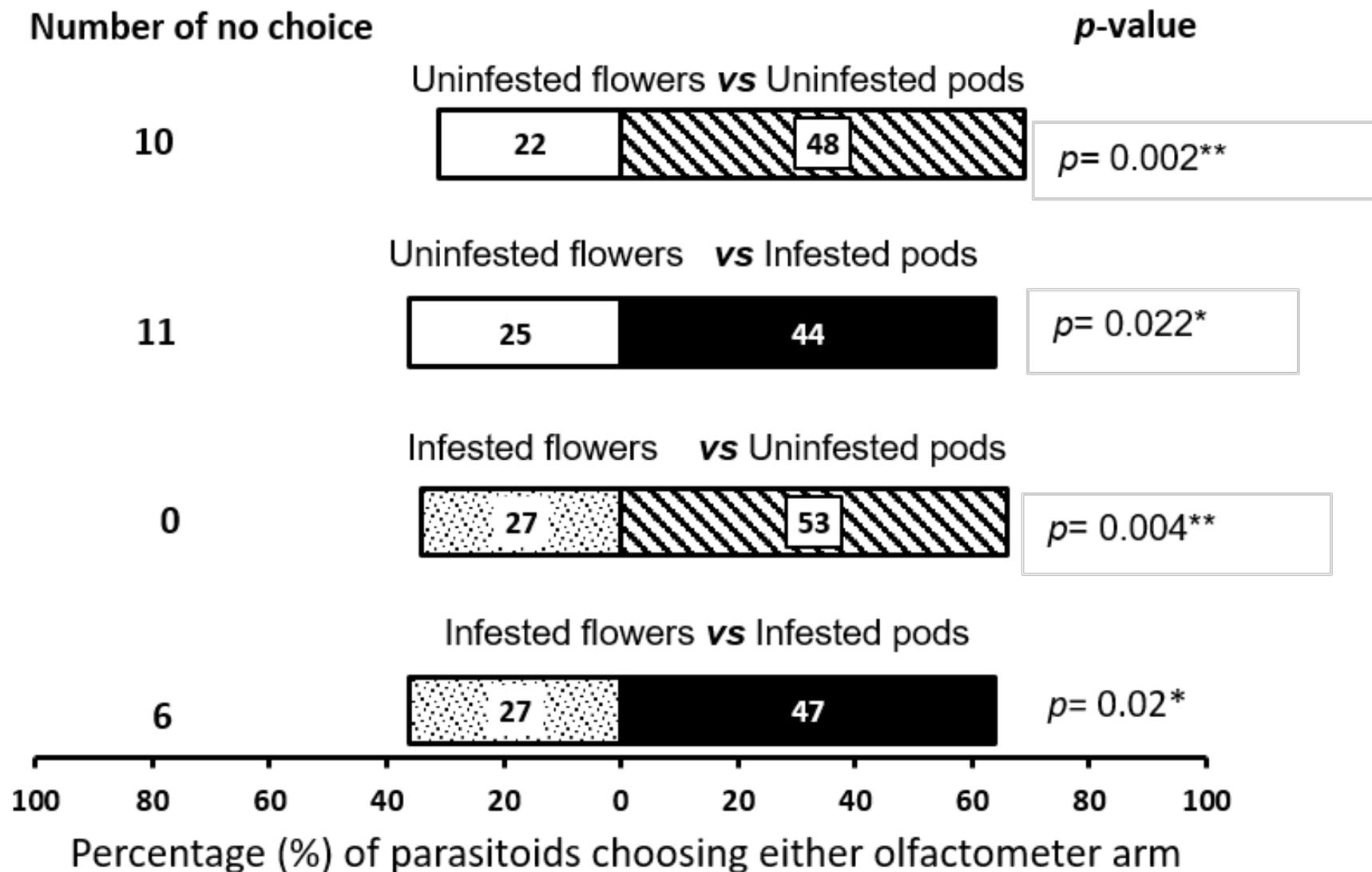


Figure 4

□ Clean air

■ Uninfested

■ Infested

Number of no choice

p-value

18



p=0.13

10



p<0.01

3



p=0.691

100 80 60 40 20 0 20 40 60 80 100

Percentage (%) of parasitoids choosing either olfactometer arm

Figure 5

□ Clean air

■ Uninfested

■ Infested

Number of no choice

6



p-value
 $p < 0.01$

7



p-value
 $p < 0.001$

8



p-value
 $p = 0.16$

100 80 60 40 20 0 20 40 60 80 100

Percentage (%) of parasitoids choosing either olfactometer arm

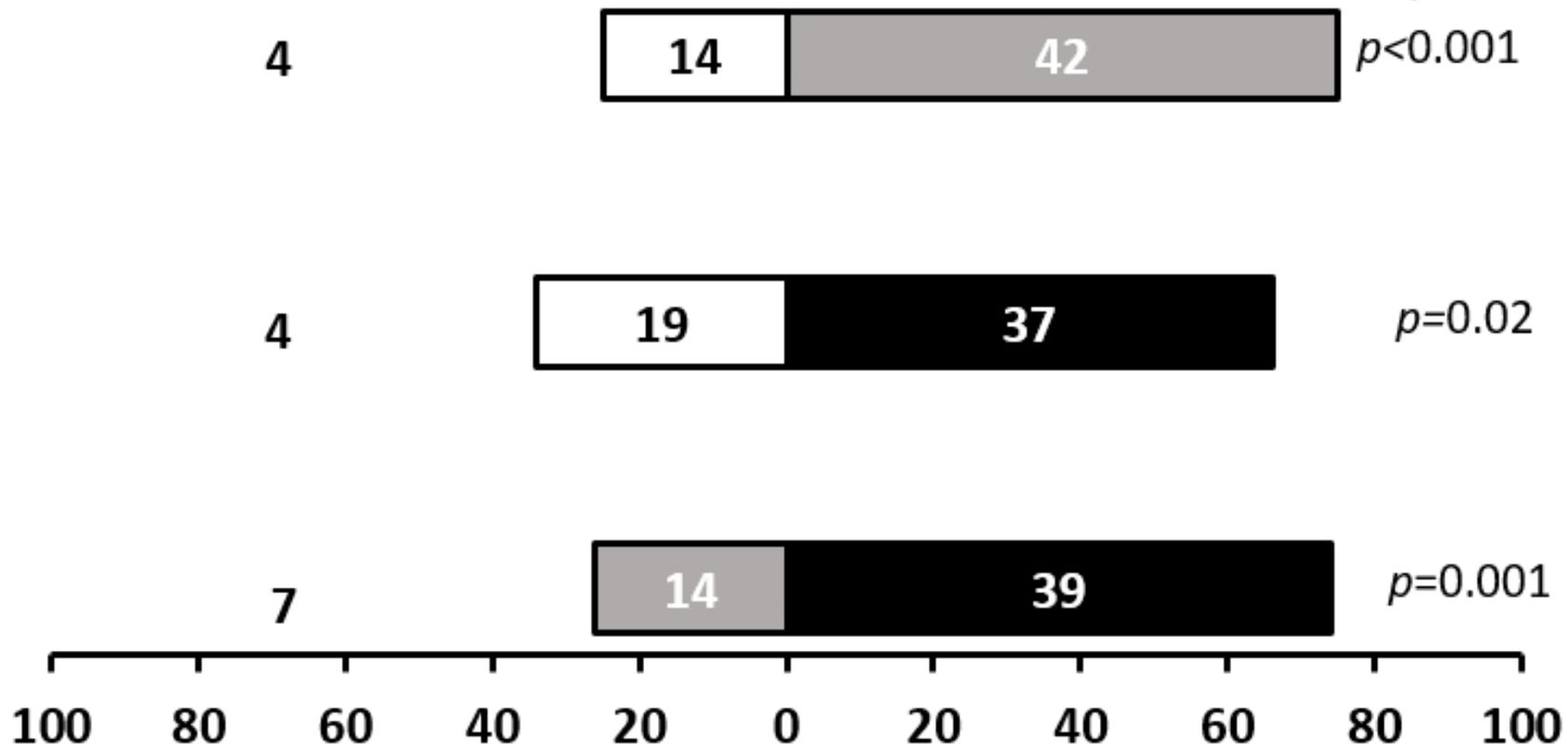
Figure 6

□ Clean air

■ Uninfested

■ Infested

Number of no choice



Percentage (%) of parasitoids choosing either olfactometer arm

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