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## Plant choice for oviposition in the phytophagous insect *Bemisia tabaci*: cytotype, including symbionts, knows best!

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1 **Plant choice for oviposition in the phytophagous insect *Bemisia***  
2 ***tabaci*: cytotype, including symbionts, knows best!**

3

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17

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## 20 **Abstract**

21 Most phytophagous insects harbour symbiotic microorganisms that may facilitate, at  
22 multiple levels, the exploitation of plants. Actually, very little is known about the role of these  
23 symbionts in insects' host plant choice. The whitefly *Bemisia tabaci* is a good model to  
24 explore these topics. It harbours a nutritional 'primary' endosymbiont allowing it to thrive on  
25 plant sap, and up to seven 'secondary' endosymbionts (S-symbionts) whose roles in plant  
26 utilization are currently under study. Here, we first investigated the influence of cytotype on  
27 females' oviposition rate on hibiscus and lantana, respectively a favourable and an  
28 unfavourable host plant for *B. tabaci*. We then addressed whether cytotype affects whiteflies'  
29 plant choice for oviposition. Using genetically homogeneous whiteflies harbouring different  
30 cytotypes, we showed that oviposition rate was significantly lower on lantana than on  
31 hibiscus, but that this reduction varied between cytotypes. Moreover, according to their  
32 cytotype, whiteflies preferred hibiscus over lantana, or showed no preference. Thus, cytotype  
33 influenced plant choice for oviposition. Altogether, our results indicate that, without a  
34 cytotype that facilitates the utilization of lantana, whiteflies may avoid this host plant. Since  
35 cytotypes harbour different S-symbionts' combinations, we argue that the influence of these  
36 symbionts on whitefly oviposition behaviour is very likely.

37 **Keywords:** *Bemisia tabaci*, cytotype, oviposition behaviour, plant choice, symbionts

38 **Highlights**

- 39 • Cytotype (including symbionts) affects whiteflies oviposition rate
- 40 • Cytotype determines plant choice for oviposition
- 41 • Different symbionts' combinations affect whitefly oviposition behaviour

## 42 Introduction

43 Microbial symbiosis is widespread in eukaryotes. Some symbionts are parasites with  
44 negative effects on their host. Other symbionts are mutualists with beneficial effects, or  
45 commensals with no apparent effects (Buchner, 1965; Ferrari & Vavre, 2011; Tipton et al.,  
46 2019). Infection by parasites often induces host behavioural changes. Some of these changes  
47 improve transmission and/or survival of the parasite at the expense of host fitness and are  
48 considered as ‘parasite’s manipulations’ (Heil, 2016; Lewis & Lize, 2015; Poulin, 2010; Vale  
49 et al., 2018). On the contrary, other behavioural changes benefit the host and participate to its  
50 defence strategies against parasites (Hart, 2011; Vale et al., 2018). While symbiont-driven  
51 behavioural alterations have been frequently observed in conflicting interactions, host  
52 behavioural modifications in mutualistic or commensal interactions have received less  
53 attention. However, recent discoveries indicate that these types of symbiotic interactions may  
54 have various effects on insect behaviours related to locomotion (Schretter et al., 2018),  
55 reproduction (Najarro et al., 2015; Sharon et al., 2010), foraging (Akami et al., 2019;  
56 Angelella et al., 2018; Leitão-Gonçalves et al., 2017; Leybourne et al., 2020; Qiao et al.,  
57 2019; Wong et al., 2017) or interactions with other organisms (Dion et al., 2011; Polin et al.,  
58 2014; Sochard, Bellec, et al., 2021) (for a review, see also Hosokawa & Fukatsu, 2020).

59 Most insect species are associated with microbial symbionts, which colonize their gut,  
60 body cavities or cells (Hansen & Moran, 2014). In phytophagous insects, mutualistic  
61 symbionts can facilitate the utilization of food sources that are unbalanced (*e.g.* phloem sap)  
62 or difficult to digest (*e.g.* wood) through the provisioning of essential and otherwise limiting  
63 nutrients, the detoxification of plant defence compounds or the breakdown of plant polymers,  
64 respectively (Frago et al., 2012; Hansen & Moran, 2014). Much less is known about the  
65 influence of symbionts in host plant selection. Recent works have shown that the gut

66 symbiotic bacteria can affect food choice and foraging decisions under laboratory conditions  
67 in the fruit fly *Drosophila melanogaster* (Leitão-Gonçalves et al., 2017; Qiao et al., 2019;  
68 Wong et al., 2017) and the oriental fruit fly *Bactrocera dorsalis* (Akami et al., 2019). Other  
69 studies on phloem sap-feeding hemipterans have demonstrated that infection by intracellular  
70 bacteria can affect their interaction with the plants by modifying plant probing behaviour, like  
71 in the cowpea aphid *Aphis craccivora* (Angelella et al., 2018) and the bird cherry oat aphid  
72 *Rhopalosiphum padi* (Leybourne et al., 2020). On the other hand, intracellular symbionts have  
73 no or only moderate influence on host plant selection in the pea aphid *Acyrtosiphon pisum*  
74 (Sochard, Dupont, et al., 2021; Sochard, le Floch, et al., 2021). Studies on a broader spectrum  
75 of host-symbiont associations are needed to better assess the role of symbionts in insect plant  
76 choice. This may also shed light on the potential impact of symbiosis on hosts' ecological  
77 diversification and speciation (Brucker & Bordenstein, 2012; Vavre & Kremer, 2014). Indeed,  
78 for phytophagous insects, being restricted to specific plants is likely to limit gene flow  
79 between populations (Bird et al., 2012; Schluter, 2001).

80 The tobacco whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae) constitutes an  
81 interesting model to address this question. It represents a highly diversified cryptic species  
82 complex and, to date, 42 putative species have been proposed in phylogenetic analyses based  
83 on mitochondrial cytochrome oxidase 1 (*mtCOI*) sequences (de Barro et al., 2011; Dinsdale et  
84 al., 2010; Firdaus et al., 2013; Roopa et al., 2015). Previous studies reported significant  
85 variation in plant preference and/or utilization capabilities between *B. tabaci* species. Some  
86 are 'generalist' species with a broad host plant range, while others can be considered as  
87 'specialist' species, with a restricted host plant range (Malka et al., 2018). Differences can  
88 also be seen within species: indeed, in some species, genetic mitochondrial groups can be  
89 identified, as in the case of the Mediterranean (MED) species, which can be divided into three  
90 groups, Q1, Q2 and Q3 (Mouton et al., 2015; Vyskočilová et al., 2018). While the Q1 and Q2

91 groups are relatively polyphagous (Vyskočilová et al., 2019), field observations and  
92 laboratory experiments indicate that the Q3 group, only identified in Burkina Faso to date, has  
93 a more restricted host range and seems specialized on lantana (*Lantana camara*) (Romba et  
94 al., 2018; Romba & Gnankiné, 2018), a host plant that is otherwise unfavourable to the MED  
95 species (Benhamou et al., 2021). Other comparative experiments revealed host range  
96 differences between Q1 and Q2, and among Q1 populations from different geographical areas  
97 (Vyskočilová et al., 2019).

98 As other phloem sap-feeding insects, *B. tabaci* harbours an obligate ‘primary’  
99 intracellular symbiont (P-symbiont) that provide essential amino acids which are not present  
100 in sufficient quantities in the phloem sap for whiteflies’ development, survival and  
101 reproduction (Baumann, 2005; Douglas, 2009). This  $\gamma$ -proteobacterium, *Portiera*  
102 *aleyrodidarum* (hereafter *Portiera*), is common to all members of the *B. tabaci* species  
103 complex (Thao & Baumann, 2004). *Portiera* resides within the cytoplasm of specialized host  
104 cells, the bacteriocytes, associated to form an organ, the bacteriome (Gottlieb et al., 2008).  
105 *Portiera* is vertically transmitted through a mechanism which is unique to whiteflies, with an  
106 entire bacteriocyte being transferred to the next generation (Buchner, 1965; Luan et al.,  
107 2016,2018). In addition to this P-symbiont, *B. tabaci* harbour facultative ‘secondary’  
108 symbionts (S-symbionts). Seven bacterial genera of S-symbionts have been reported to date:  
109 *Arsenophonus*, *Cardinium*, *Fritschea*, *Hamiltonella*, *Hemipteriphilus*, *Rickettsia* and  
110 *Wolbachia* (Bing et al., 2013; Everett et al., 2005; Gottlieb et al., 2006; H. Wang et al., 2020;  
111 Zchori-fein & Brown, 2002), with up to four present in the same insect body (Zchori-Fein et  
112 al., 2014). They all co-occur within the same bacteriocytes as *Portiera*, but some of them can  
113 also colonize other tissues of the host (Gottlieb et al., 2008). *B. tabaci* S-symbionts are  
114 predominantly vertically transmitted, but some of them can also be horizontally transmitted,  
115 for instance through the phloem when whiteflies feed upon the same plant (Caspi-Fluger et

116 al., 2012; S. Li et al., 2016; Y. Li et al., 2017). Analyses of *B. tabaci* S-symbionts suggest that  
117 some of them could contribute to their hosts' nutrition. Indeed, *Portiera*'s genome has  
118 undergone drastic reduction (Rao et al., 2015) as a consequence of its prolonged intracellular  
119 lifestyle (Mccutcheon & Moran, 2012; Moran et al., 2008). It has lost almost all genes  
120 involved in the synthesis of vitamins and cofactors, and several of its essential amino acid  
121 pathways are incomplete (Rao et al., 2015), functions that S-symbionts may replace or  
122 complement (Opatovsky et al., 2018; Rao et al., 2015; Ren et al., 2020; Y.-B. Wang et al.,  
123 2020). As an example, *Hamiltonella* can provide vitamins and cofactors (Rao et al., 2015;  
124 Ren et al., 2020; Y.-B. Wang et al., 2020), and could also complete the missing steps of the  
125 essential amino acid lysine biosynthesis pathway of *Portiera* (Rao et al., 2015). Interestingly,  
126 by producing metabolites able to interact with their hosts' neurons or sensory organs or that  
127 are precursors of neurotransmitters, S-symbionts may directly influence their hosts' behaviour  
128 (Engl & Kaltenpoth, 2018; Shropshire & Bordenstein, 2016). Importantly, S-symbiont  
129 composition differs between mitochondrial groups, both across (Zchori-Fein et al., 2014) and  
130 within (Gnankiné et al., 2013; Gueguen et al., 2010) species, raising the possibility that these  
131 symbionts may contribute to *B. tabaci* species complex ecological diversification.

132         Recently, we demonstrated that S-symbionts might affect the range of the host plants  
133 suitable for *B. tabaci*. Indeed, we have shown that cytotype (referring to the cytoplasmic  
134 characteristics of the insect line, including the mitochondria and intracellular symbionts)  
135 affects whitefly capability to feed and oviposit on lantana (*Lantana camara*), an unfavourable  
136 host plant to *B. tabaci* (Benhamou et al., 2021). The aims of the present study were to  
137 investigate whether whiteflies exhibit plant choice for oviposition and whether the S-symbiont  
138 community may influence their oviposition behaviour. To fulfil these objectives, we  
139 performed choice experiments between a plant known to be favourable for *B. tabaci*, hibiscus



140 (*Hibiscus moscheutos*), and the unfavourable lantana, using genetically homogeneous  
141 whiteflies harbouring different cytotypes (and, hence, different S-symbionts).

## 142 **Material and Methods**

### 143 *Insects*

144 Three *B. tabaci* parental lines (F0) from the Mediterranean (MED) species were used  
145 in this study: AA(Q1-HW), BB(Q1-HR) and CC(Q2-ARW) that belong to the mitochondrial  
146 groups Q1 or Q2, and that are associated with different S-symbionts (**Table 1**). The first  
147 uppercase double letters indicate females' diploid nuclear genotype (AA, BB or CC) (males  
148 are haploid as *B. tabaci* reproduces by arrhenotoky). Characters within **parenthesis** refer to  
149 their cytotype, including their mitochondrial group (Q1 or Q2) and S-symbionts (HW, HR or  
150 ARW; A: *Arsenophonus*, H: *Hamiltonella*, R: *Rickettsia*, W: *Wolbachia*). Insect lines were  
151 reared on hibiscus plants in mesh cages in climate-controlled rooms at 26°C ± 1°C and 70%  
152 relative humidity with a 14L:10D photoperiod. The same climate-controlled conditions have  
153 been used for the whole study.

154 **Table 1. *Bemisia tabaci* laboratory lines used in this study.**

Line	Nuclear Genotype	Cytotype		Collection information		
		Mitochondrial group	S-Symbionts <sup>a</sup>	Year	Location (Country)	Plant
AA(Q1-HW)	AA	Q1	HW	2012	Tympaki (Greece)	Eggplant <i>Solanum</i> sp.
BB(Q1-HR)	BB	Q1	HR	2012	Les Ponts-de-Cé (France)	Mandevilla <i>Mandevilla</i> sp.
CC(Q2-ARW)	CC	Q2	ARW	2018	Lyon (France)	Lantana <i>Lantana camara</i>

<sup>a</sup> A: *Arsenophonus*, H: *Hamiltonella*, R: *Rickettsia*, W: *Wolbachia*.

## 156 *Collection of F1 females*

157 To separate cytotype-related and genotype-related effects, experiments were  
158 performed on F1 females obtained from the 9 possible crosses between the F0 parental lines  
159 (**Table 2**, experimental design shown in **Fig. S1**), based on the procedure described in  
160 Benhamou *et al.* (Benhamou et al., 2021). These crosses produced **either** F1 females with  
161 identical nuclear genotypes **(the two letters refer to the maternally (first) and paternally**  
162 **(second) inherited nuclear genotype)** but different cytotypes [*e.g.* AB(Q1-HW) and BA(Q1-  
163 HR)], or the opposite, *i.e.* females with the same cytotype but different genotypes [*e.g.*  
164 AA(Q1-HW), AB(Q1-HW) and AC(Q1-HW)]. The three lines were synchronized as follows:  
165 adults from the hibiscus stock cages were allowed to mate and oviposit for 7 days on cotton  
166 leaves. To keep them fresh, leaves were fixed on their adaxial side on a 1cm layer of 2% Agar  
167 (Sigma-Aldrich®) in plastic Petri dishes (90mm in diameter). Petri dishes were placed upside-  
168 down to simulate the situation of leaves attached to a plant with the abaxial surface down.  
169 Cotton was used as it is not involved in the subsequent experiments, thus avoiding possible  
170 effect of the F0 individuals' plant on the traits assessed on the following F1 generation (**Fig.**  
171 **S1**). We chose cotton because it is a known favourable plant for the *B. tabaci* MED species  
172 groups Q1 and Q2 (Romba & Gnankiné, 2018; Vyskočilová et al., 2018). F0 females were  
173 collected within 5 hours after emergence. Individuals' sex was determined based on their  
174 genitalia, by observation under a stereomicroscope (Leica EZ4, Leica Microsystems GmbH,  
175 Wetzlar, Germany). F0 females (<5-h-old) were considered virgin as newly emerged adults  
176 do not immediately mate (Li et al., 1989). As *B. tabaci* reproduces by arrhenotoky, which  
177 means that unmated females produce only haploid eggs that develop into males, this was  
178 confirmed by the absence of females in their offspring. Each cross was made on cotton  
179 (90mm in diameter Petri dishes) using groups of 15 F0 males and 15 F0 females (3 replicates  
180 for each). These 30 individuals were left for 1 week on the same cotton leaf to mate and

181 oviposit. Upon emergence, F1 virgin females (<5-h-old) were collected for further  
 182 experiments as described hereafter. The whole procedure (crosses and experiments) was  
 183 independently performed three times, treated as “experimental blocks” in the statistical  
 184 analyses.

		Mother (F0) <sup>a</sup>		
		AA(Q1-HW)	BB(Q1-HR)	CC(Q2-ARW)
Father (F0) <sup>b</sup>	A(Q1-HW)	AA(Q1-HW)	BA(Q1-HR)	CA(Q2-ARW)
	B(Q1-HR)	AB(Q1-HW)	BB(Q1-HR)	CB(Q2-ARW)
	C(Q2-ARW)	AC(Q1-HW)	BC(Q1-HR)	CC(Q2-ARW)

<sup>a</sup> F0 and F1 Females identification: Nuclear genotype(Cytotype); Nuclear genotype: letters indicate the maternally (first) and the paternally (second) inherited nuclear genotype; Cytotype: Mitochondrial group (Q1 or Q2) + S-symbionts; S-symbionts: A: *Arsenophonus*; H: *Hamiltonella*; R: *Rickettsia*; W: *Wolbachia*.

<sup>b</sup>F0 Fathers' genotypes (A, B or C) are indicated by only one letter as males are haploid.

185 **Table 2. Nuclear genotypes and cytotypes of *B. tabaci* F1 females.**

### 186 *Cytotype determination*

187 For each parental line (**Table 1**) and F1 cross (**Table 2**), mitochondrial group (Q1 or  
 188 Q2) and symbiont infection status (*Portiera*, *Arsenophonus*, *Hamiltonella*, *Rickettsia*,  
 189 *Wolbachia*) were checked on 8 females to ensure that the expected cytotype was correct. Total  
 190 DNA was extracted from individual whiteflies using the NucleoSpin 95 Tissue kit (Macherey  
 191 Nagel GmbH, Düren, Germany) following the manufacturer's instructions. Samples were  
 192 crushed in a mix of 60µL of lysis buffer and 8µL of protein K (22mg/mL) with 1.4mm sterile  
 193 stainless-steel beads using a TissueLyser (Qiagen, Hilden, Germany). Elution was done in  
 194 100µL of buffer and DNA was then stored at -20°C. The mitochondrial haplotype was  
 195 checked by PCR-RFLP according to the method described in Henri *et al.* (Henri et al., 2013),  
 196 allowing to differentiate between the Q1 and Q2 groups. The infection status was determined  
 197 using quantitative PCR (qPCR) using the following genes: *16S* rRNA for *Arsenophonus*,

198 *dnaK* for *Hamiltonella*, *16S* rRNA for *Portiera*, *gltA* for *Rickettsia* and *ftsZ* for *Wolbachia*  
 199 (Table 3). The  $\beta$ -actin gene from *B. tabaci* (Table 3) was used as a DNA extraction control.  
 200 The PCR amplifications were performed on a CFX-96 Real Time PCR machine (Bio-Rad,  
 201 Hercules, USA). Each reaction consisted of 5 $\mu$ L of SYBR® Green 2x Supermix (Bio-rad) in  
 202 addition to 2 $\mu$ L of DNA sample, 2 $\mu$ L of nuclease-free water, and 0.5 $\mu$ L of forward and  
 203 reverse primers (500nM).

204 **Table 3. qPCR primers used in this study.**

Organism	Gene	Primers	Primer sequence	Fragment size (bp)	Hybridization T° (°C)	Reference
<i>Bemisia tabaci</i>	<i><math>\beta</math>-actin</i>	wf-Bactin-F	5'-TCTTCCAGCCATCCTTCTTG-3'	130	63	(Sinisterra et al., 2005)
		wf-Bactin-R	5'-CGGTGATTTCCTTCTGCATT-3'			
<i>Portiera</i>	<i>16S</i>	Port73-F	5'-GTGGGGAATAACGTACGG-3'	193	60	(Caspi-Fluger et al., 2011)
		Port266-R	5'-CTCAGTCCCAGTGTGGCTG-3'			
<i>Arsenophonus</i>	<i>16S</i>	ArsF3	5'-GTCGTGAGGAARGTGTARGGTT-3'	765	63	(Duron et al., 2008)
		ArsR3	5'-CCTYTATCTCTAAAGGMTCGCTGGATG-3'			
<i>Hamiltonella</i>	<i>dnaK</i>	dnaK-F	5'-GGTTCAGAAAAAAGTGGCAG-3'	155	60	(Moran et al., 2005)
		dnaK-R	5'-CGAGCGAAAGAGGAGTGAC-3'			
<i>Rickettsia</i>	<i>gltA</i>	glt375-F	5'-TGGTATTGCATCGCTTTGGG-3'	199	60	(Caspi-Fluger et al., 2011)
		glt574-R	5'-TTTCTTTAAGCACTGCAGCAGC-3'			
<i>Wolbachia</i>	<i>ftsZ</i>	F2	5'-TTGCAGAGCTTGGACTTGAA-3'	400	55	(Vavre et al., 1999)
		R2	5'-CATATCTCCGCCACCAGTAA-3'			

## 205 **Plants**

206 Plants were grown in the same climate-controlled conditions as the ones used for  
 207 rearing lines, in insect-free rooms. Cotton, *Gossypium hirsutum* L. (Malvaceae) cv. 'Elpida',  
 208 and hibiscus, *Hibiscus moscheutos* L. (Malvaceae) cv. 'Honeymoon', were grown from seeds  
 209 while lantana, *Lantana camara* L. (Verbenaceae) was vegetatively propagated from cuttings  
 210 in pots using a 75:25 (v/v) mix of potting soil and vermiculite. For all experiments performed  
 211 in this study, fully developed leaves, randomly collected from 2-month-old plants, have been  
 212 used.

### 213 *No-choice oviposition and egg hatching rate*

214 The influence of whitefly cytotype on females' oviposition and egg hatching rate on  
215 hibiscus and lantana was investigated using no-choice oviposition tests. F1 virgin females  
216 (<5-h-old), which developed on cotton, were put individually on hibiscus or lantana leaf disks  
217 (20mm in diameter, to standardize the leaf area) fixed on an agar layer in Petri dishes (55mm  
218 in diameter), and placed upside down. After 7 days, females were removed and the number of  
219 eggs laid (oviposition) was recorded under a stereomicroscope. Ten days later, the number of  
220 eggs that hatched was estimated by counting the number of larvae (including both live and  
221 dead larvae). This method was used because the larvae, even dead, are easier to identify than  
222 the empty eggs. We also calculated the number of eggs that did not hatch (number of eggs  
223 laid – number of eggs hatched). Thirteen to 17 individual measures were obtained per  
224 cytotype/genotype combination and per plant.

### 225 *Plant choice for oviposition*

226 Plant choice for oviposition was investigated in binary choice experiments between  
227 hibiscus and lantana. The experimental setup used was inspired from the one developed by  
228 Shah and Liu (Shah & Liu, 2013). Choice arenas (produced 1 hour before use) consisted of  
229 one lantana and one hibiscus leaf disk (20mm in diameter), fixed on their adaxial side on an  
230 agar layer in a Petri dish (90mm in diameter). Disks were arranged opposite and at equal  
231 distance (20mm) from the center of the arena (**Fig. S1**). For this experiment, we used 2-d-old  
232 females to ensure they were old enough to oviposit from the very beginning of the tests, at it  
233 lasted less time than the previous no choice experiments. Newly emerged virgin females (<5-  
234 h-old), which developed on cotton, were transferred on fresh cotton leaves (55mm in diameter  
235 Petri dishes) for 2 days. Tests were initiated every day in the morning at the same hour with  
236 the introduction of one F1 female (2-d-old) into the center of each arena, which were then

237 placed upside down. Thirty-two hours later, the female's location was recorded and the  
238 number of eggs laid on each leaf disk was counted under a stereomicroscope. As far as  
239 possible, experiments were run every day for all nine cytotype/genotype combination  
240 simultaneously. Measures were considered to be valid when females were found alive on a  
241 leaf disk and if they laid at least one egg at the end of the tests. Thereby, 31 to 37 valid  
242 measures were obtained per cytotype/genotype combinations.

### 243 *Statistical analyses*

244 For no-choice experiments, oviposition and egg average hatching rate were analysed  
245 by a generalized linear model (GLM) (with a log link and a negative binomial or a quasi-  
246 binomial error structure, respectively) with the plant species, the insect cytotype, the insect  
247 nuclear genotype (as a nested effect within the cytotype) and the experimental block set as  
248 explanatory variables. The average hatching rate was calculated according to the formula (a),  
249 where  $i$  is the replicate number and  $N$  is the total number of replicates. Eggs that hatched were  
250 considered as 'successes' ('No.successes'), and eggs that did not hatch as 'failures'  
251 ('No.failures').

$$252 \quad (a) \text{ average proportion of successes} = \frac{\sum_{i=1}^N (\text{No.successes})}{\sum_{i=1}^N (\text{No.successes} + \text{No.failures})}$$

253 For the plant choice experiment, oviposition was analysed by a GLM (with a quasi-  
254 binomial error structure) with the insect cytotype, the insect nuclear genotype (integrated into  
255 the model as a nested effect within the cytotype) and the experimental block set as  
256 explanatory variables. The response variable is expressed as the average proportion of eggs  
257 laid on lantana compared to the total number of eggs laid on lantana (accounted as  
258 'successes') plus hibiscus (accounted as 'failures'), given by the formula (a). The number of  
259 eggs laid on hibiscus or lantana according to females cytotype and genotype in the plant

260 choice experiment was analysed using a GLM (with a negative binomial error structure).  
261 From the complete models, we performed a model simplification through a backward  
262 procedure (Crawley, 2013). Multiple comparison analyses were carried out by Tukey's test  
263 (Tukey, 1949) to investigate statistical relationships between explanatory variables levels  
264 using the *emmeans* R package (Russell, 2020). The *emmeans* R package was also used to  
265 extract means, average proportions and 95% confidence intervals (95%CI) from the models.  
266 All data analyses were performed using the R software (R Development Core Team 2011;  
267 <http://www.R-project.org>).

## 268 ***Data accessibility***

269 The datasets generated and analysed in this study can be obtained from the Zenodo  
270 online repository at: <https://zenodo.org/record/6414033>.

## 271 ***Ethical note***

272 This research adheres to the ASAB/ABS Guidelines for the Use of Animals in  
273 Research, the legal requirements of France and the institutional guidelines of the University of  
274 Lyon.

## 275 **Results**

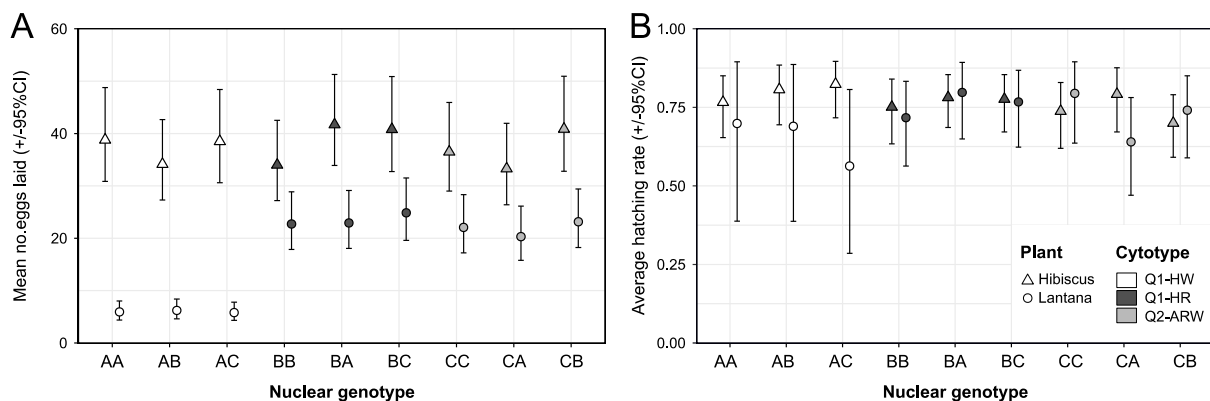
### 276 ***No-choice oviposition and hatching rate***

277 The influence of whitefly cytotype on females' ability to feed and produce offspring  
278 on favourable and non-favourable plants were investigated by measuring females' oviposition  
279 and egg hatching rate on hibiscus or lantana in no-choice experiments (**Fig. 1**). For the  
280 number of eggs laid, there was no difference between the three experimental blocks [ $\chi^2(2) =$



281 1.60,  $P = 0.45$ ]. For a given cytotyp e, there was no difference between genotypes [ $\chi^2(6) =$   
282 3.57,  $P = 0.74$ ]. There was also no tripartite interaction between plant, cytotyp e and genotype  
283 [ $\chi^2(6) = 1.43$ ,  $P = 0.96$ ]. However, there was a significant interaction between the plant  
284 species and the insect cytotyp e [ $\chi^2(2) = 103.20$ ,  $P < 0.001$ ]. This interaction results from the  
285 fact that, while the number of eggs laid was homogeneous among cytotyp es on hibiscus  
286 (mean, 37.71; standard error [SE]: 1.31) ( $P > 0.99$ ), it was significantly reduced on lantana for  
287 all cytotyp e/genotype combinations ( $P < 0.001$ ), but to different extents between cytotyp es.  
288 Indeed, females with the cytotyp e Q1-HW consistently laid a lower number of eggs on  
289 lantana (mean, 5.98; SE: 0.74) than females with cytotyp es Q1-HR (mean, 23.50; SE: 1.40) ( $P$   
290  $< 0.001$ ) or Q2-ARW (mean: 21.88; SE: 1.41) ( $P < 0.001$ ) that laid a similar number of eggs  
291 on this plant ( $P = 0.98$ ) (**Fig. 1A**). These results confirm our previous data (Benhamou et al.,  
292 2021) showing that lantana is globally a less favourable host plant than hibiscus, but also  
293 highlight that some cytotyp es mitigate this effect.

294 Regarding the average egg hatching rate (**Fig. 1B**), there was no difference between  
295 experimental blocks [ $F(2,202) = 1.91$ ,  $P = 0.15$ ]. We also did not detect any influence of the  
296 plant species [ $F(1,238) = 1.35$ ,  $P = 0.25$ ] or insect cytotyp e [ $F(2,238) = 0.65$ ,  $P = 0.52$ ], and  
297 no interaction between these two factors [ $F(2,238) = 1.26$ ,  $P = 0.29$ ]. There was no difference  
298 between genotypes for each cytotyp e [ $F(6,238) = 0.27$ ,  $P = 0.95$ ], and no interaction between  
299 plant, cytotyp e and genotype [ $F(6,238) = 0.72$ ,  $P = 0.63$ ].

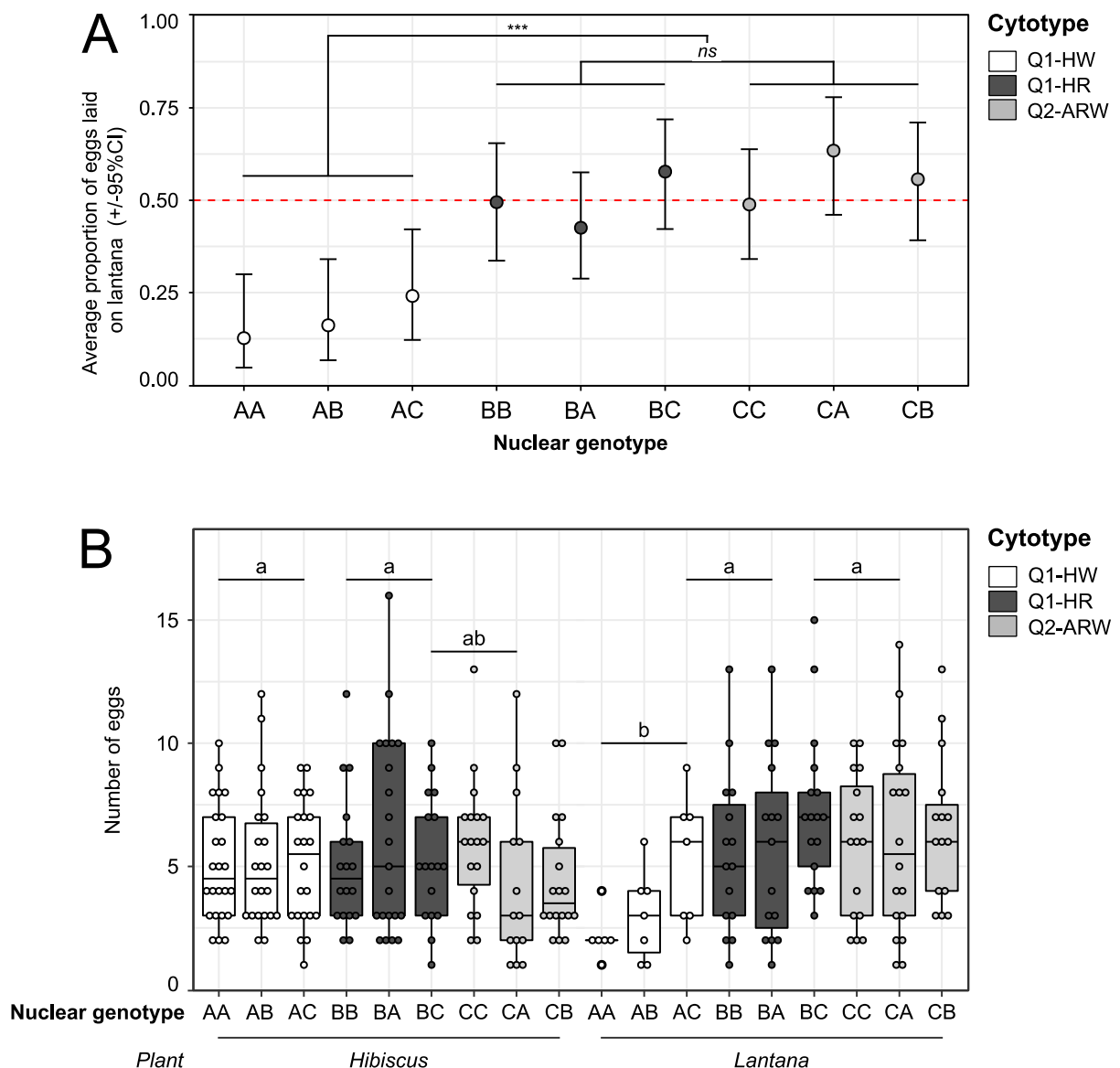


300 **Figure 1. Effect of the insects' genotype and cytotype on *B. tabaci* females' oviposition**  
301 **and egg hatching rate on hibiscus and lantana (no choice experiment).** (A) Mean number  
302 of eggs laid per female [ $\pm$  95% confidence interval (CI)] over 7 days. (B) Average egg  
303 hatching rate ( $\pm$  95% CI) after 10 days. All individuals are F1 females obtained from crosses  
304 of laboratory lines: AA(Q1-HW), BB(Q1-HR), or CC(Q2-ARW). F1 female legend key:  
305 Nuclear genotype: letters indicate the maternally (first) and the paternally (second) inherited  
306 nuclear genotype; Cytotype: mitochondrial group+S-symbionts (A: *Arsenophonus*, H:  
307 *Hamiltonella*, R: *Rickettsia*, W: *Wolbachia*). Thirteen to 17 individual measures were  
308 obtained per type of F1 female and per plant.

### 309 *Oviposition choice according to the insect cytotype*

310 We then investigated the influence of the whiteflies' cytotype on female plant choice  
311 for oviposition between hibiscus and lantana (**Fig. 2**). Oviposition choice is expressed here as  
312 the mean proportion of eggs laid on lantana compared to the total number of eggs laid on the  
313 two plants (**Fig. 2A**). There was no effect of the experimental block factor [ $F(2,278) = 0.13$ ,  $P$   
314  $= 0.88$ ] and no difference between genotypes for a given cytotype [ $F(6,296) = 0.82$ ,  $P = 0.56$ ].  
315 In contrast, there was a significant effect of the insect cytotype on oviposition plant choice  
316 [ $F(2,296) = 17.46$ ,  $P < 0.001$ ]: females with the cytotype Q1-HW laid a greater proportion of  
317 eggs on hibiscus (around 80%) than on lantana (around 20%), while females with the cytotype  
318 Q1-HR or Q2-ARW showed no oviposition preference, *i.e.* the average proportion of eggs  
319 laid on hibiscus and lantana was merely 50% (**Fig. 2A**). Most females (95%) laid eggs on a  
320 single leaf disk: the one they were on at the end of the experiment. Only a few of them (5%)  
321 laid eggs on both leaf disks (**Fig. S2**). During this short-term time period (32h), females that  
322 have chosen a single leaf disk laid a similar amount of eggs, about 5, whatever their choice  
323 (hibiscus or lantana), and whatever their cytotype or genotype, with one exception: females

324 with the cytotype Q1-HW not only chose lantana less often than hibiscus but, when they did,  
 325 they laid a lower number of eggs (mean, 3.55; SE, 0.52) than the ones who chose hibiscus  
 326 (mean, 5.16; SE, 0.30) [effect of the interaction between the plant species and the insect  
 327 cytotype:  $\chi^2(2) = 11.72$ ,  $P = 0.0028$ ; effect of the insect's nuclear genotype :  $\chi^2(6) = 3.62$ ,  $P =$   
 328 0.73] (**Fig. 2B**). A similar number of eggs, about 5, was laid by females that oviposited on  
 329 both leaf disks (**Fig. S3**).



330 **Figure 2. Effect of the insects' genotype and cytotype on *B. tabaci* females' oviposition**  
 331 **plant choice of hibiscus vs lantana. (A) Average proportion of eggs laid on lantana [ $\pm 95\%$**   
 332 **confidence interval (CI)] compared to the total number of eggs laid on the two plants over the**

333 course of a 32h trial. The oviposition choice was investigated from 31 to 37 individuals per  
334 cytotype/genotype combinations. Significance:  $p < 0.001$ : \*\*\*,  $p > 0.05$ : *ns* (Tukey's test). **(B)**  
335 Number of eggs laid by females laying eggs exclusively on hibiscus or lantana (which  
336 correspond to 95% of the females). Each dot represents one measure for one female; box  
337 length represents the interquartile range; whiskers indicate the lowest and largest data points,  
338 excluding outliers. Black horizontal bars correspond to the median. To decipher the plant x  
339 cytotype interaction, letters above the boxes indicate statistical groups determined by Tukey's  
340 multiple comparison test ( $P < 0.05$ ). Measures were performed on individual F1 females  
341 obtained from crosses of laboratory lines: AA(Q1-HW), BB(Q1-HR), or CC(Q2-ARW). F1  
342 females legend key: Nuclear genotype: letters indicate the maternally (first) and the paternally  
343 (second) inherited nuclear genotype; Cytotype: mitochondrial group + S-symbionts (A:  
344 *Arsenophonus*, H: *Hamiltonella*, R: *Rickettsia*, W: *Wolbachia*).

## 345 **Discussion**

346 In the present study, we demonstrate that whitefly cytotype is a major determinant of  
347 both females' oviposition rate in no-choice experiments and oviposition behaviour in choice  
348 experiments, while we did not find any influence of the insects' genotype on those traits. We  
349 acknowledge the possibility that these observations could result from genetic maternal effects,  
350 such as the mother transmitting epigenetic states like DNA methylation or supplying eggs  
351 with mRNA or proteins (English et al., 2015). The cytotype is composed of several  
352 components but differences due to potential genetic and/or gene expression variability of the  
353 mitochondria or the P-symbiont between cytotypes seem unlikely due to (i) the extremely low  
354 mitochondrial DNA divergence between Q1 and Q2 populations (Vyskočilová et al., 2018),  
355 and (ii) the similar genomic features and metabolic capabilities of *Portiera* across the *B.*  
356 *tabaci* species complex (Santos-Garcia et al., 2020; Zhu et al., 2019, 2021). In contrast,

357 cytotypes differ in their S-symbiont composition, harbouring either *Hamiltonella* and  
358 *Wolbachia* (Q1-HW), *Hamiltonella* and *Rickettsia* (Q1-HR) or *Arsenophonus*, *Rickettsia* and  
359 *Wolbachia* (Q2-ARW). Therefore, it is likely that differences in traits and behaviours between  
360 cytotypes result from this composition.

361         In this study, we also show that, in no-choice experiments, oviposition is lower on  
362 lantana compared to hibiscus. Similarly to what we observed in a previous study, this could be  
363 partially explained by the lower amount of the essential amino acids (EAAs) isoleucine,  
364 leucine, phenylalanine and valine available in this plant compared to more favourable plants  
365 (Benhamou et al., 2021). We also confirm that some cytotypes attenuate this effect: females  
366 with cytotypes Q1-HR or Q2-ARW laid more eggs on lantana than females with cytotpe Q1-  
367 HW, which could be due to the influence of the S-symbionts on their hosts' free amino acid  
368 (AA) metabolism (Benhamou et al., 2021; Opatovsky et al., 2018; Rao et al., 2015). We  
369 demonstrate here that this effect is dependent on the host plant species since oviposition is  
370 homogeneous on hibiscus among cytotypes.

371         In choice experiments, females with cytotpe Q1-HW oviposited more frequently on  
372 hibiscus than on lantana, while other females did not show plant preference. Behavioural  
373 changes associated to symbionts may be attributable to the host's adaptive response to  
374 symbiont infection or to the direct modification by the symbiont of the host behaviour. Here,  
375 the choice looks adaptive: the oviposition preference of females with cytotpe Q1-HW  
376 towards hibiscus could be a response of the whitefly, driven by the lack of a cytotpe  
377 facilitating the utilization of lantana. Conversely, females with cytotpes Q1-HR and Q2-  
378 ARW, with no apparent plant preference, may be less selective considering their relatively  
379 advantageous cytotpe on lantana. Similar observations have been made in the olive fruit fly  
380 *B. oleae*, in which experimental manipulation of the gut bacterial consortium resulted in  
381 altered oviposition behaviour (Jose et al., 2019). Uninfected *B. oleae* showed less frequent

382 oviposition on fruits, which may benefit the insect by avoiding oviposition on food sources  
383 that are difficult to use in the absence of the symbionts. It cannot be completely excluded that  
384 these observations are not an adaptive response of the host to S-symbiont infection. Indeed,  
385 the fact that half of the individuals of the cytotypes Q1-HR and Q2-ARW made non-optimal  
386 choices by choosing lantana could be due to behavioural manipulation (driven by the  
387 symbiont benefit), but the presumed benefit for the symbiont remains unknown.

388         The overall effect of the cytotype on whitefly oviposition behaviour may result as the  
389 net effect of the entire symbiotic community or may depend on the infection by a single S-  
390 symbiont species. Consistent with this second hypothesis, the avoidance/acceptance of lantana  
391 for oviposition can be correlated to the absence/presence of the S-symbiont *Rickettsia*, as  
392 whiteflies with *Rickettsia*-associated cytotypes (Q1-HR and Q2-ARW) show the same  
393 phenotype. Interestingly, *Rickettsia* has been associated to various phenotypic modifications  
394 in *B. tabaci*, such as an increase of the fitness in some environments (Cass et al., 2016; Himler  
395 et al., 2011), heat tolerance (Brumin et al., 2011) or resistance to entomopathogenic  
396 *Pseudomonas syringae* strains (Hendry et al., 2014) (for a review see also Milenovic et al.,  
397 2022). Moreover, *Rickettsia* was recently found to increase *B. tabaci* attraction towards  
398 tomato plants infected with the Tomato yellow leaf curl virus (Kliot et al., 2019), supporting  
399 the hypothesis that this symbiont affects its host behaviour. Alternatively, it cannot be  
400 excluded that whiteflies do not have any preference but that the combination of *Hamiltonella*  
401 and *Wolbachia* in females with cytotype Q1-HW decreases the preference for lantana.  
402 However, less is known about the impact of this particular S-symbionts combination on their  
403 hosts.

404         Mechanisms by which *Rickettsia* or any other S-symbiont may influence *B. tabaci*  
405 oviposition behaviour are unknown to date. Studies on a broad spectrum of microorganisms  
406 suggest that symbionts may influence their host behaviour directly, through the production of

407 a microbial signal (e.g. some EAAs) able to interact with their hosts' neurons or sensory  
408 organs or that are precursors of neurotransmitters (Engl & Kaltenpoth, 2018; Shropshire &  
409 Bordenstein, 2016). Symbionts could also influence their host behaviour indirectly, through  
410 their effects on host physiological functions (e.g. metabolism, immunity, endocrine system  
411 and pheromone production) that ultimately influence the host nervous system (Engl &  
412 Kaltenpoth, 2018; Lynch & Hsiao, 2019; Shropshire & Bordenstein, 2016). In *D.*  
413 *melanogaster* deprived of their gut bacteria, feeding on a diet depleted in EAAs elicits  
414 preference for AA-rich food, while this behaviour can be rescued in flies inoculated with gut  
415 bacteria (Leitão-Gonçalves et al., 2017). Therefore, it was proposed that flies are able to  
416 detect changes in their inner free EAA concentrations, modulating their preference for AA-  
417 rich food. It was also proposed that *D. melanogaster* gut bacteria could provide their host with  
418 EAAs, thereby modulating the nutritional status and subsequent food preference for this insect  
419 (Leitão-Gonçalves et al., 2017). Similarly, S-symbionts may influence *B. tabaci* oviposition  
420 behaviour through their impact on their hosts' amino acid metabolism and nutritional status  
421 (Benhamou et al., 2021; Opatovsky et al., 2018; Rao et al., 2015; Ren et al., 2020; Y.-B.  
422 Wang et al., 2020). Regarding more specifically *Rickettsia*, genomic and experimental studies  
423 in *B. tabaci* MEAM1 (Middle-East Asia Minor 1) species suggest that this S-Symbiont could  
424 complement the P-Symbiont and directly contribute to the biosynthesis of several EAAs,  
425 including lysine (Bao et al., 2021) and the branched-chain amino acids isoleucine, leucine and  
426 valine (Opatovsky et al., 2018). According to this hypothesis, the apparent increase  
427 production of EAAs previously reported in *Rickettsia*-associated cytotypes may explain why  
428 they show no preference between plants with high (i.e. hibiscus) and low (i.e. lantana)  
429 amounts of these specific EAAs (Benhamou et al., 2021). Conversely, the lower level of  
430 EAAs production in Q1-HW females may elicit preference for hibiscus. However, the

431 mechanisms by which insects could detect changes in internal free EAAs availability and  
432 subsequent changes in behaviour are not known.

433 In conclusion, this work shows that the host plant choice of *B. tabaci* for oviposition is  
434 determined by the insect cytotype, most likely by the S-symbiont community. Whether these  
435 effects depend on single or multiple S-symbiont species is unknown to date, and further  
436 studies should investigate the respective contribution of each S-symbiont, including *Rickettsia*  
437 as promising candidate, to host behaviour. This will require separation of S-symbionts from  
438 other components of the cytotype, *i.e.*, selective elimination or transfer of symbionts to  
439 whiteflies of identical genetic background. In this perspective, recent studies have made  
440 encouraging advances in manipulating *B. tabaci* symbiotic communities by selectively  
441 eliminating S-symbionts using heat (Shan et al., 2019) or antibiotic treatments (Ren et al.,  
442 2020; Shan et al., 2019; Y.-B. Wang et al., 2020). Mechanisms by which S-symbionts mediate  
443 the insect behaviour also remain to be determined. Future investigations will help in  
444 dissecting the molecular bases of whitefly behaviour to accurately determine the influence of  
445 S-symbionts during each host plant selection step (*e.g.* olfaction or probing). Importantly,  
446 acting on their hosts' niche choice, S-symbionts could contribute to build-up reproductive  
447 isolation between whitefly populations. However, in our framework, reproductive isolation is  
448 not complete, as the choice of hibiscus is common to all cytotypes. Future work should  
449 explore additional plant combinations to determine whether S-symbionts can lead to complete  
450 reproductive isolation through differential host plant choice. Such directions would help to  
451 better encompass the influence of symbionts on insects' ecological diversification and  
452 speciation.

## 453 **Declarations of interest**

454 Declarations of interest: none



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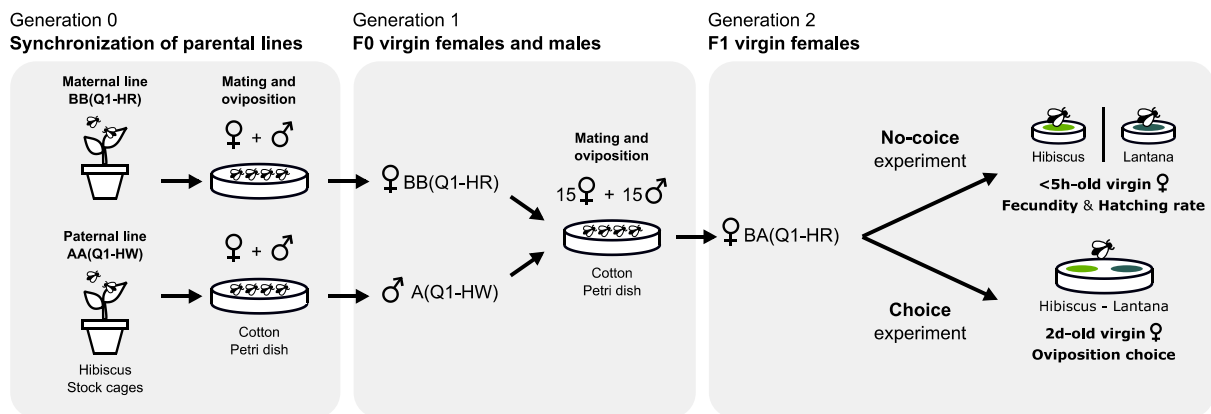
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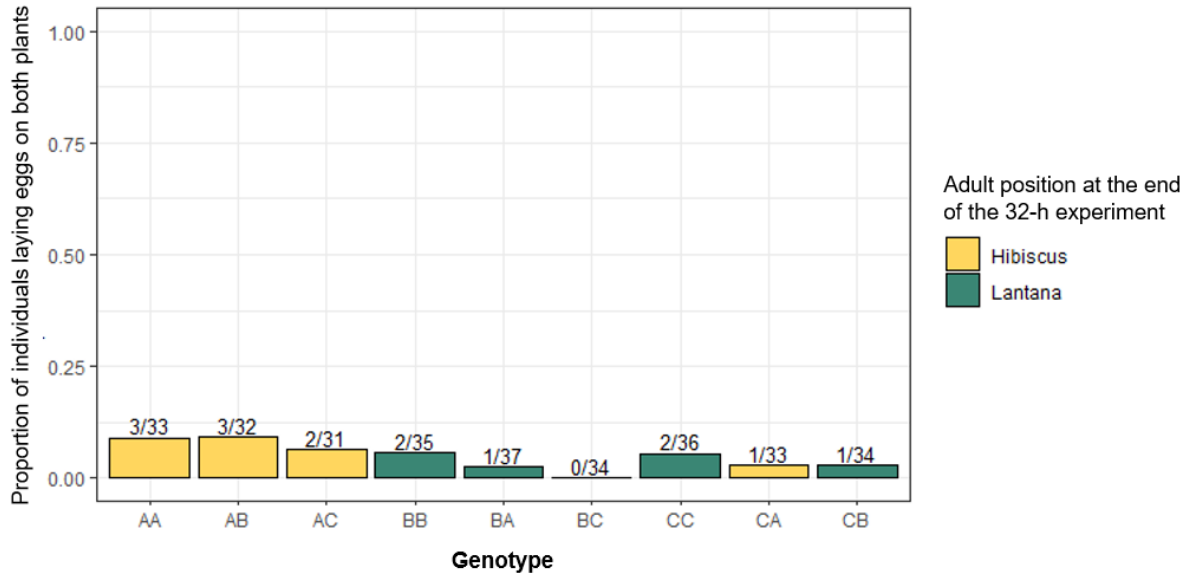
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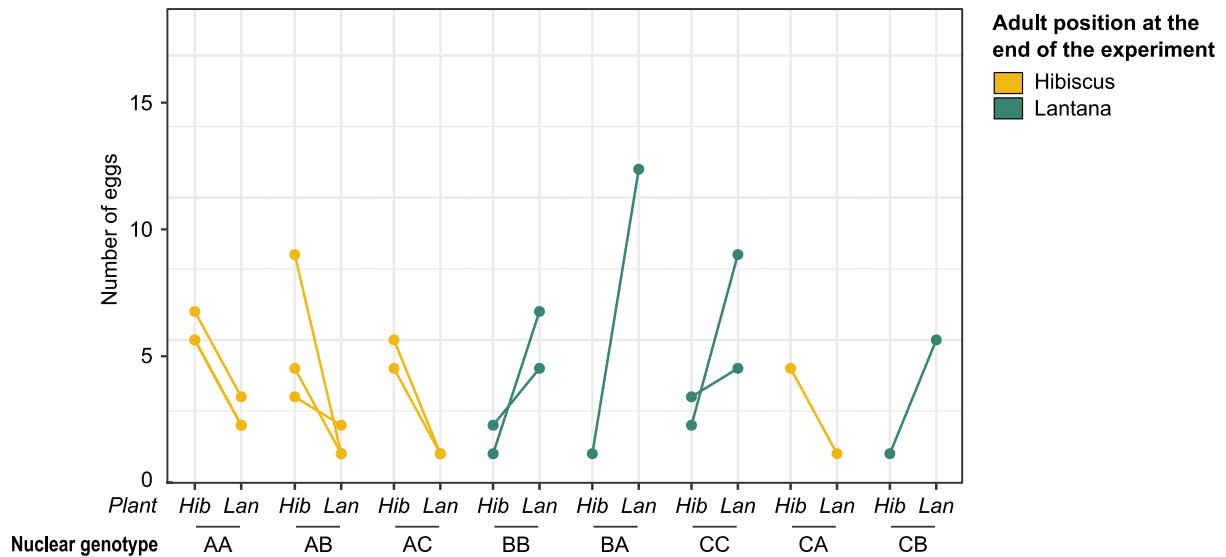
748 **Supplementary material**



749 **Figure S1. Experimental procedure used for no-choice and choice experiments on F1**  
 750 **females**, using BA(Q1-HR) F1 females as an example. All experiments were performed on  
 751 individual F1 females. Oviposition choice was assessed by counting the number of eggs laid  
 752 per female after 32 h on each plant (n=31-27). Fecundity (number of eggs laid) was assessed  
 753 over 7 days per F1 female after which the female was removed from the Petri dish. The  
 754 hatching rate was calculated as the ratio of larvae (observed 10 days after removing the  
 755 female), over the total number of eggs laid per F1 female (see formula (a) from main text)  
 756 (n=13-17).



757 **Figure S2. Proportion of *B. tabaci* females laying eggs on both hibiscus and lantana**  
 758 **according to their genotype in choice experiments.** Most of females laid eggs on a single  
 759 plant species. Colors indicate the female's position at the end of the experiment. Numbers  
 760 above bars indicate absolute values (number of females laying eggs on both plants / total  
 761 number of females analyzed).



762 **Figure S3. Number of eggs laid by whiteflies ovipositing on both plants in hibiscus vs**  
 763 **lantana plant choice for oviposition experiments, according to their nuclear genotype.**  
 764 There was no data for genotype BC, as no BC(Q1-HR) female oviposited on both plants. Each  
 765 dot pair corresponds to an individual females' oviposition on hibiscus (Hib) and lantana (Lan).  
 766 Colors indicate the female's position at the end of the experiment.