Size and shape variation of *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae) in two hosts: A morphometric approach

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ARTICLE INFO

ABSTRACT

The mahogany shoot borer (*Hypsipyla grandella*) attacks different Meliaceae species and impedes its plantation. Its biology is poorly known, but some results show a preference for *Cedrela odorata* L. over *Swietenia macrophylla* King, which could generate intraspecific variations. We studied the effect of these hosts on *H. grandella* right-forewing size and shape variation, using a geometric morphometry approach. We collected larvae in plantations of each host, rose them in seedlings of the same original host and set 13 landmarks on 63 right-forewings. Sexual-shape dimorphism was present and the right-forewings of individuals collected in *C. odorata* were larger. Removing the allometric effect and comparing magnitude and direction in the plastic responses of the sexual-shape dimorphism, we only found differences in the direction. Differences in the right-forewing shape within sexes were present when comparing hosts and removing the allometric effects. Only the right-forewing of males differs between hosts in terms of shape. The differences found could influence the species' flying system. Individuals with the larger right-forewings could be more frequent in *C. odorata* plated areas, with an increased ability for long-distance flights, which is undesired in integrated pest management systems.

1. Introduction

Commonly, the mahogany shoot borers (*Hypsipyla* spp. Lepidoptera: Pyralidae) are related to a nuisance moth in tropical forestry, attacking mahoganies (Meliaceae: *Cedrela* spp., *Swietenia* spp., *Kaya* spp., *Toona* spp. and others). This happens because its attacks on leading shoots could affect all plants in a stand resulting in trees with poor form and multiple shoots, and destroying future revenues. Strikingly, methods that reduce its attacks to financially acceptable levels are unavailable, their impact. Some researchers' proposals include resistant genotypes (Newton et al., 1993) management of shade, the use of repellent species and its natural enemies (Ruiz et al., 2016).

Given the importance of the mahogany shoot borers in the silviculture of some tropical forest species, one could expect that it was a well-studied insect, but its biology is poorly known. This lack of knowledge

limits the possibility to develop effective control methods based on their biology. The most relevant mahogany shoot borer in Colombia is *Hypsipyla grandella* Zeller. *H. grandella* is distributed in locations where its hosts occur: from South USA (Florida) to Paraguay (Heinrich, 1956). Also, *Hypsipyla ferrealis* (Hampson) is the other species of the genus reported in Colombia, distributed from Brazil to Costa Rica (Heinrich, 1956). Within this genus, the wing venation is slightly variable (changing in stalking, origin, and distribution within the wing), but not within *H. grandella*—there are no distinguishable wing features between males and females of *H. grandella* (Heinrich 1956). When comparing *H. grandella* with non-migrants Pyralidae, this moth is capable of medium-distance flights, but when contrasted with migrants, *H. grandella* has a low-flight ability (Table 1). *H. grandella* wing (Fig. 1) exhibits some shape characteristics that long-distance Lepidoptera share in the forewing, such as a straight costal margin, with C, SC and R

Table 1
Total distance flown of different Pyralidae (Lepidoptera) species under laboratory flight mills.

Species & authors	Age (days-old) & sex	Mean (SE) of total distance (km) of all flights combined
Amyelois transitella (Walker)	1 & ♀ ♂	12.2 (0.92) [a]
Sappington and Burks (2014)	3 & ♀ ♂	10.2 (0.93)
Cactoblastis cactorum (Berg)	1 & ♂	1.04 (0.14)
Sarvary et al. (2008)	1 & ♀	2.02 (0.26)
Cnaphalocrocis medinalis (Guenée)	3 & ♀ ♂	33.26 (0.25) – 44.39 (0.27)
(Li et al., 2013)[b]		
Hypsipyla grandella Zeller (Fasoranti et al., 1982)	1 & ♂	21.8 (4.5)
	1 & ♀	23.7 (5.1)
	3 & ♂	40.0 (2.8)
	3 & ♀	16.9 (2.5)
Loxostege sticticalis (Linnaeus, 1761)	3 & ♂	27.14 (3.14)
(Xie et al., 2012)[b]	3 & ♀	27.09 (3.16)

[a] Observations exclude individuals without at least one flight of 3 min. ND: no data.
[b] Migrant species *C. medinalis* (Li et al., 2013) and *L. sticticalis* (Qing and Zhang, 2001).

parallel and close together (Qing and Zhang, 2001. These introduce the idea that our studied moth is a long-distance flier.

One remarkable aspect of *H. grandella* biology is its preference for *Cedrela odorata* L. over *Swietenia macrophylla* King (Grijpma, 1970)—which are sympatric species. This exposes *H. grandella* to different conditions within each host, mostly related to the host's phytochemicals, but also to specific natural enemies, leading to a possible host-associated differentiation (Pfennig et al., 2010). It is common to find that the larvae's host influence the size of adults, as in the case of *Heliconisu erato* (L.) (Lepidoptera: Nymphalidae) (Rodrigues and Moreira, 2004; 2002). Also, the food source during immature stages influence adults shape, as in *Macaria mirthae* Vargas (Lepidoptera: Geometridae) (Benítez et al., 2015). In addition, larvae feeding on a particular plant could develop morphological differences that later influence its development (Jorge et al., 2011).

With this background, an immediate question appears: do *C. odorata* or *S. macrophylla* affect the size and shape of the right-forewing of *H. grandella*? To answer this, we evaluated the hypothesis that these hosts produce size and shape variation in *H. grandella* using geometric morphometry applied to the right-forewing. We used wings because of their significance for migration, territorialism, courtship and escape from natural enemies (DeVries et al., 2010; Wootton, 1992). In this, forewing size and shape for different Lepidoptera, indicate several aspects related to fly behaviour as an influence in flight distance: being long wings better for long-distance flights (DeVries et al., 2010) and narrow wings for controlled flights (Betts and Wootton, 1988; DeVries et al., 2010). On the other side, geometric morphometry describes differences within and between populations (Bookstein, 1991) taking advantage of the high heritability of wing morphology (Bitner-Mathé and Klaczko, 1999). This method helped to find morphological

variability in insects related to a different host, as in *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) (Cañas-Hoyos et al., 2016), *Ectomyelois ceratoniae* (Zeller) (Lepidoptera: Pyralidae) (Mozaffarian et al., 2007) and *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) (Khiaban et al., 2010).

2. Materials and methods

2.1. Study site and insects

This study was conducted from December 2017–April 2018 in experimental plots of *C. odorata* and *S. macrophylla*, 1.4–4.6 years old and 1–3 m in height, in El Nus Research Center -AGROSAVIA (06°29′07,1″ N, 074°50′43,2″ W, Colombia, Northwest South America). The area is at the Magdalena River basin with broken hills, narrow valleys and dendritic drainage, at 850 m above sea level and with a mean annual rainfall of 2223 mm, mean temperature of 23°C and 82.9% relative humidity. This area is a tropical rainforest according to the Holdridge life zone system.

We collected *H. grandella* larvae in different instars and put them on the top-leaves of seedlings of the original host within nylon mesh cages (60 × 40 × 40 cm) of one larva/plant. Seedlings were two months old and about 30–40 cm high, planted in plastic bags and watered twice a day (07:30 and 16:00) at field capacity approximately. We collected the emerged adults daily and placed them in glass containers with ethyl acetate. We initially identified *H. grandella* based on the internal genitalia of 20 adults randomly selected from the total of collected specimens and sexed the adults based on their external genitalia, as pictured by Heinrich (1956). For studying the internal genitalia, we extracted them, water-bathed them with KOH 10% for 10 min, rinsed them with
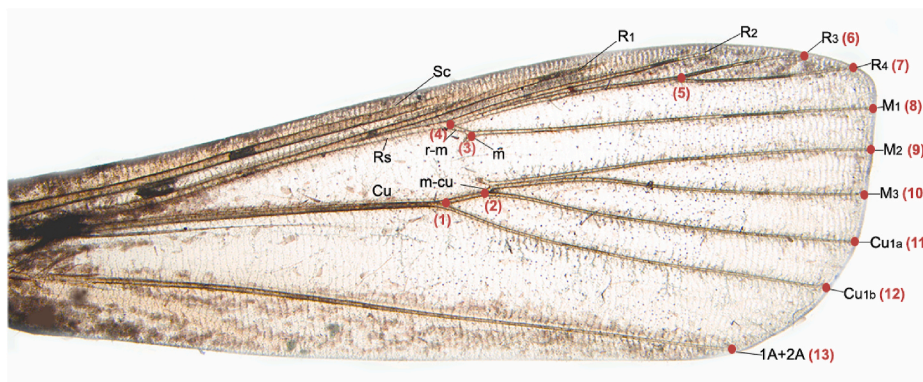

Fig. 1. Right-forewing of *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae) used to assess its size and shape variation with morphometric analysis. Dots with numbers on parentheses correspond to the used landmarks. Letter and numbers are names of the wing veins (Sc: subcostal, R: radius, Rs: radial sector, Cu: cubitus, M: media, A: anal, m-cu: medio-cubital, r–m: radio-medial).

70% ethanol and stored them in microvials with 1:1 glycerine and 70% ethanol. We confirmed the identification of all individuals when assigning landmarks following Heinrich (1956) (see geometric morphometry section).

2.2. Geometric morphometry

We dissected 63 adults of *H. grandella*, 20 females and 13 males collected from *C. odorata* and 15 females and 15 males on *S. macrophylla*. We soaked their right-forewings in 70% ethanol for 2 h and removed their scales with a brush when dried. Subsequently, we mounted the wings on a glass slide and, using the same distance for all specimens, photographed them with a camera Nikon D700 attached to a stereoscope Zeiss Stemi dv4. The specimens and their wings rest in the National Taxonomic Collection of Insects Luis María Murillo CTNI with catalogue number 6145.

We identified 13 type I landmarks (Bookstein, 1991) on the right-forewings and digitalized the coordinates in CLIC V.70 (Dujardin, 2013). These landmarks are the intersection between veins or with the wing margin, as follows (Fig. 1): 1. Cubitus (Cu) – Cu_{1b}, 2. medio-cubital (m-cu) - Cu_{1a}, 3. radio-medial (r-m) - media (M), 4. radial sector Rs) - radio-medial (r-m), 5. radius (R_3) - R_4, 6. R_3 - wing margin (wm), 7. R_4 - wm, 8. M_1 - wm, 9. M_2 - wm, 10. M_3 - wm, 11. Cu_{1a} - wm, 12. Cu_{1b} - wm, 13. Anal 1 A + 2 A (A) - wm.

We estimated the accuracy of the landmarks' location process by digitizing twice the coordinates in all individuals. Then, we did a repeatability (R) analysis (individual variance/total variance) for size (Centroid Size) and the shape (relative warps) on a one-way ANOVA, model II on repeated measures (Arnqvist and Mårtensson, 1998). In this, R varies from 0-1, 0 will indicate that all variance is within individuals and 1 between them in the CLIC V.70 package (Dujardin, 2013). A generalized analysis of Procrustes to the raw coordinates helped to remove the effect of scale and position and produce partial warps and uniform components (Rohlf, 1990; Rohlf and Slice 1990). Finally, we verified the differences in wing shape between sexes to prevent sexual dimorphism from hiding host-induced variation.

2.3. Size variation

Shapiro-Wilk test was used to check normality, and the Barlett test to check homogeneity of variance. We used the isometric estimator of the centroid size for size comparisons (Klingenberg et al., 2002) and evaluated the effects that host, sex, and their interaction have on wing size with a two-way ANOVA after verifying assumptions using RStudio ver. 2.8.1 (RStudio Team, 2008).

2.4. Shape variation

As the first exploration, we analysed the shape variables with a principal component analysis (PCA) using the CLIC V.70 package (Dujardin, 2013), which in the language of geometric morphometry is called relative-warp analysis (Rohlf, 1993). This analysis is a linear combination of the shape variables to obtain new variables that are progressively decreasing portions of the original variation. PCA was performed to produce a scatter plot of specimens along the first two component axes, producing maximal and second-to-maximal separation between groups. After the PCA, we compared the effects of host and sex on the right-forewing shape evaluating the Euclidean distances as described below. We used 1000 permutations to test the statistical differences between the compared groups and multiple comparisons adjusted by Bonferroni (Rice, 1989). We employed a multivariate regression analysis and a permutation test to check the allometry effect with the centroid size as the dependent variable and shape as the independent (Good, 2000). In addition, we verified the presence of a common allometric model between specimens of the two hosts and between sexes with a multivariate analysis of covariance (MANCOVA) and

evaluated its statistical significance differences using λ Wilks. In cases where the allometric effect was relevant, we calculated its statistical differences after the correction for size. The allometric effect was evaluated with a multivariate regression (Dujardin et al., 2010). When the allometric effect was significant, the common allometric slope hypothesis was contrasted by using a covariance analysis (multivariate analysis of covariance MANCOVA). When the model was not rejected (groups showed common allometric slopes), an adjustment was performed for the size to determine if the data continued showing differences in shape without the effect produced by the wing size, using the CLIC V.70 package (Dujardin, 2013).

Finally, we assessed the magnitude and direction of the changes by evaluating the multivariate-phenotypic changes of two states, where multivariate vectors of phenotypic change are calculated using the least squares means procedure described by Adams and Collyer (2009). For this procedure, we calculated the Euclidean distance between each pair of consensus configurations of each factor (sex and host) after a generalized analysis of Procrustes on the CLIC V.70 package (Dujardin, 2013). Emerging differences define vectors with length and direction, which are useful to estimate the magnitude and direction of the plastic responses. As a test of whether the vectors' directions were statistically different, the angles between them were calculated with arc sine-cosine, and the statistical significance of the differences in the magnitude and direction were verified using 1000 permutations (Adams and Collyer, 2009).

3. Results

For both sexes, repeatability in the measurement of the 63 wings of *H. grandella* was high for the aligned coordinates (R =0.960) and size (R =0.999), indicating that most of the variance we measured was between individuals. Repeatability of the highest eight principal components (relative warps—RW) accounts for 84% of the shape variation (RW1 R =0.993, RW2 R =0.982, RW3 R =0.958, RW4 R =0.969, RW5 R =0.955, RW6 R =0.935, RW7 R =0.923 and RW8 R =0.933).

3.1. Size variation

Centroid size presented normal distribution (Shapiro-Wilk: 0.980, *p* =0.405) and homogeneous variance (Bartlett test: 0.791, *p* =0.851). What was surprising, was that hosts had a significant effect on the right-forewing size, with larger specimens in *C. odorata* than in *S. macrophylla* (Fig. 2). We didn't detect sex or host–sex interaction effects on centroid size (Table 2).
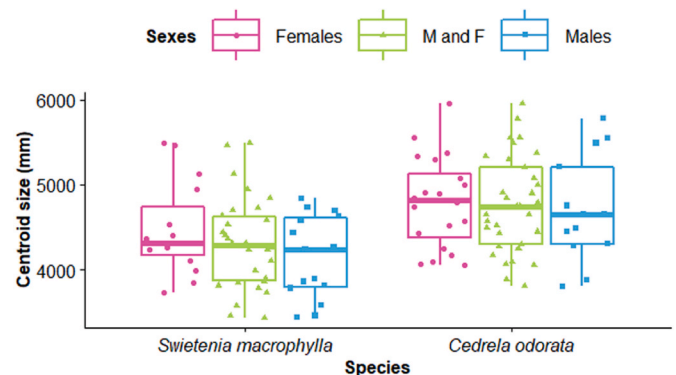
Fig. 2. Right-forewing centroid size variation of *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae) according to the hosts *Cedrela odorata* and *Swietenia macrophylla*. Boxplots contain the median value, Q1 and Q3.

Table 2
Two-way ANOVA to evaluate the null hypothesis of common right-forewing size of *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae) according to sexes and two host (*Cedrela odorata* and *Swietenia macrophylla*).

Effects	Sums of squares	d.f.	F-value	*p*-value
Host	3214379	1	10.723	0.002*
Sex	616318	1	2.056	0.157
Host x Sex	226507	1	0.756	0.388
Residuals	17686548	59		

*Statistically significant differences $p < 0.05$.

3.2. Shape variation

When we evaluated the right-forewing shape variation using the multivariate regression analysis, we found an allometric effect on the wing shape in males and females (*C. odorata* $p = 0.024$ and *S. macrophylla* $p = 0.006$). Also, we found common allometric slopes in those comparisons and the MANCOVA. But after correction for size differences in wing shape persisted between the sexes within-host (Table 3). According

to the principal component analysis, the two main axes of variation accounted for 44% of the total variation in right-forewing shape, dismissing the use of the other axes (Fig. 3). The comparison of consensus shapes between males and females within hosts showed spatial separation and indicated a remarkable sexual-shape dimorphism in *H. grandella*. Consequently, we only compared individuals of the same sex within hosts (Table 3).

Differences in Euclidean distances (ED) between subgroups and their angle were non-significant (ED $=0.001$, $p = 0.912$; $\theta = 62.286$, $p = 0.509$) when evaluating the magnitude and direction of the plastic responses of sexual dimorphism within hosts. Significant differences in the ED between subgroups were absent but were present in the change's direction (ED $=0.003$, $p = 0.677$; $\theta = 107.354$, $p = 0.038$) when excluding the allometric effect. Attractively, most of the landmarks were displaced when comparing right-forewing shape between sexes and within-host (Fig. 4)) revealing changes in some veins. Moreover, the males' right-forewing are narrower and more curved than the females'; in addition, the females' right-forewings are wider in the radial and the cubitus-anal area (Fig. 4).

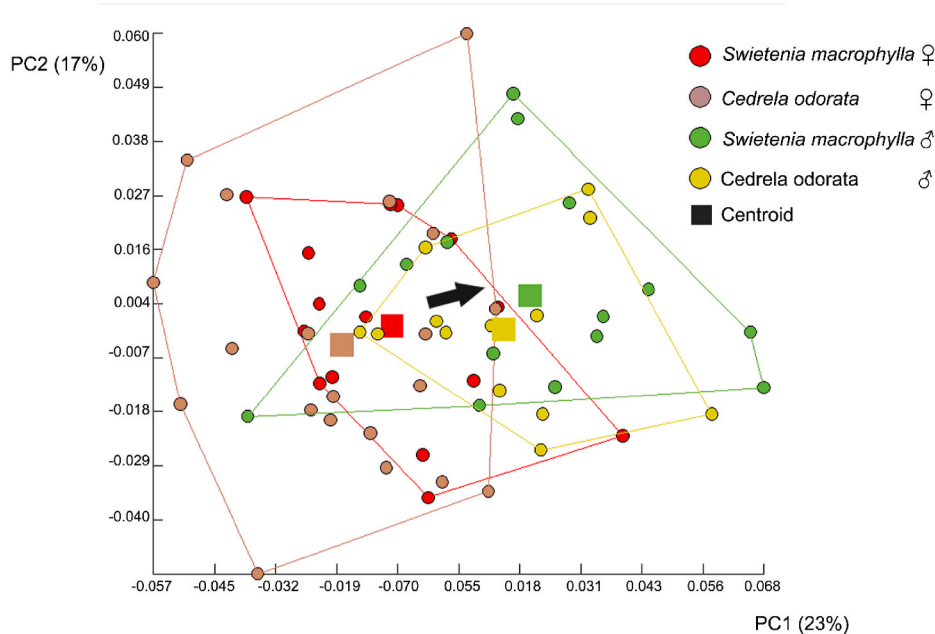When we compared sexes between hosts, we found allometric effects

Table 3
MANCOVA to evaluate the null hypothesis of a common allometric model between sexes of *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae) and two hosts (*Cedrela odorata* and *Swietenia macrophylla*) and Euclidean distances (ED) and statistical significance differences (*p*) of right-forewing shape between sexes and host, with and without allometric effect.

		Sex		Host	
		C. odorata ♀ over ♂	*S. macrophylla* ♀ over ♂	♀ *C. odorata* over *S. macrophylla*	♂ *C. odorata* over *S. macrophylla*
MANCOVA	Wilks λ	0.322	0.256	0.248	0.182
	F	0.764	0.658	1.376	0.609
	d.f. 1	22	22	22	22
	d.f. 2	8	5	10	3
	p	0.709	0.775	0.307	0.791
With allometric effect	ED	0.034	0.036	0.013	0.014
	p(ED)	0.001*	0.000*	0.488	0.517
Without allometric effect	Dec	0.030	0.036	0.009	0.014
	p(Dec)	0.000*	0.000*	0.072	0.010*

*Statistically significant differences values ($p < 0.05$). d.f.: degrees of freedom. ED: Euclidian Distance.

Fig. 3. Right-forewing shape variation of *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae) by sexes and hosts (*Cedrela odorata* and *Swietenia macrophylla*) using principal component analysis (PCA).
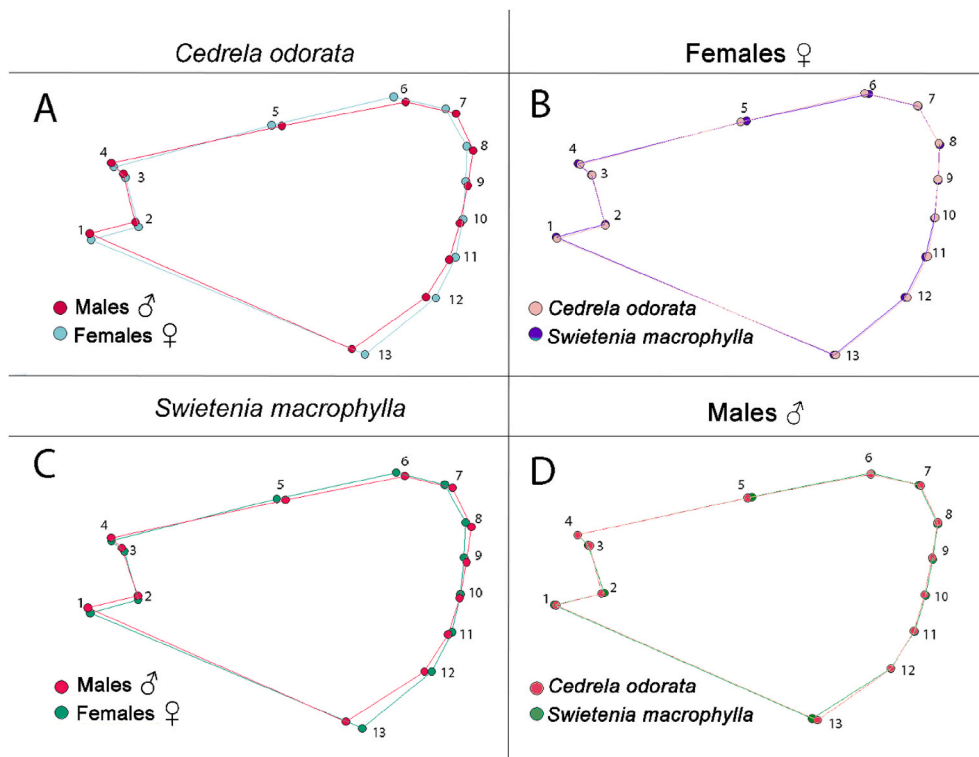
Fig. 4. Right-forewing shape variation of *Hypsipyla grandella* Zeller (Lepidoptera: Pyralidae) after allometric correction. A) Females over males in *Cedrela odorata*. B) Females over males in *Swietenia macrophylla*. C) Females from *C. odorata* over females from *S. macrophylla* D) Males from *C. odorata* over males from *S. macrophylla*.

with the multivariate analysis (females $p < 0.001$; males $p = 0.024$). Given this, we found common model slopes ($p = 0.307$ and $p = 0.791$), we removed the allometric effect (Table 3) and found shape differences in the males' right-forewing between hosts. These findings show that hosts influence the shape of the males' right-forewing.

4. Discussion

We tested the hypothesis that *C. odorata* and *S. macrophylla* induce forewing variation in terms of size and shape in *H. grandella* using geometric morphometry and measured the phenotypic changes in a single generation, avoiding potential bias by selection. Also, we estimated the role of sex on the phenotypic variations, as this may influence the results.

Although sexual-size dimorphism in the right-forewing was non-significant, the right-forewing showed a clear sexual-shape dimorphism in both hosts. Heavier *H. grandella* females also show sexual-size dimorphism (Taveras et al., 2004). Other Pyralidae also display sexual dimorphism. For instance, *Amyelois transitella* (Walker) females have larger forewings (Sappington and Burks, 2014) and *Sarata tephrella* Ragonot females have smaller forewings (Ferris and Noidin, 2004). Also, sexual-size dimorphism is present in the form of heaviest females in *Cactoblastis cactorum* (Berg) (Sarvary et al., 2008).

Sexual-shape dimorphism is common in Lepidoptera (Allen et al., 2010), being this study the first report on *H. grandella*. It could be due to diverse selection pressures, given that males and females use wings and flight in different ways (Camargo et al., 2015), similar to what happens in Pyralidae: *Achroia grisella* (Fabricius) males call females striking its tegula with the forewing (Spangler et al., 1984) and *H. grandella* flaps their wings without flying, a beautiful phenomenon explained as the spreading of sexual pheromones (Grijpma, 1971). Also, *C. cactorum* and *H. grandella* females fly more distance and initiate more flights than males, but this phenomenon does not happen in *A. transitella, Cnapha-locrocis medinalis* (Guenée) and *Loxostege sticticalis* (Linnaeus, 1761) (Table 3).

Raised individuals in *C. odorata* showed larger forewings in both sexes and non-allometric differences in males' forewing shape. These size variations may result from nutritional differences in which *C. odorata* provided more qualified resources for getting larger wings than *S. macrophylla*, with *C. odorata* preferred over *S. macrophylla* (Grijpma, 1970). The variation in wing size in response to host is also observed in other Pyralidaesuch as *Ectomyelois ceratoniae* (Mozaffarian et al., 2007) and other Lepidoptera as *S. frugiperda* (Cañas-Hoyos et al., 2016). A larger right-forewing influenced by *C. odorata* could also affect the general size of *H. grandella*, probably making it heavier and affecting its flight abilities, as reported for other insects (Betts and Wootton, 1988).

At this point, we wonder if those changes induced by hosts in the right-forewing also influence the *H. grandella* flying system. Regarding this, literature shows that forewing size and shape variation are of foremost importance for flying in Lepidoptera, and trade-offs between the two are specific for diverse types of flights. As indicated in the introduction, long forewing with a narrow tip is crucial for long-distance flights (DeVries et al., 2010), whereas small and broad forewing allow controlled flights (Betts and Wootton, 1988; DeVries et al., 2010). In our case, *H. grandella* has a long right-forewing with a narrow tip (Fig. 1) leading to the thinking that its wings are suited for long-distance flights. Given this and considering the hots effects on *H. grandella*, we build the hypothesis that *C. odorata* and *S. macrophylla* also influence *H. grandella* flying system.

Our study is of future reference in evolutionary and behavioural studies of *H. grandella*, as changing host (*C. odorata* & *S. macrophylla*) produces changes in right-forewing size and shape. These changes could be of interest when planting one of the two studied hosts, avoiding the host that produces larger wings and probably long-distance fliers—*C. odorata*. Future works should study the influence of the right-forewing size on flight abilities. We expect that individuals with the larger right-forewing be more frequent in *C. odorata* plated areas, with an increased capacity of long-distance flights, which is undesired in integrated pest management.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

Acknowledgements

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