

Natural selection in the tropical treehopper *Alchisme grossa* (Hemiptera: Membracidae) on two sympatric host-plants

Daniel Torrico-Bazoberry^{1,2} · Carlos F. Pinto^{1,2,3} · Luis Flores-Prado⁴ · Francisco E. Fontúrbel⁵ · Hermann M. Niemeyer¹

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Abstract The pronotum is the most distinctive and representative structure in treehoppers. Although several functions have been proposed for this structure, its involvement in fitness has not been formally evaluated. Given the high degree of maternal investment exhibited by the subsocial membracid *Alchisme grossa* (Hoplophorionini), the pronotum has been suggested as a shield for offspring protection. We performed selection gradient analyses on *A. grossa* in order to evaluate how natural selection is acting upon two traits associated with this structure considering three different fitness proxies: (1) number of eggs, (2) the ratio between the number of first-stage nymphs and the number of eggs (early survival), and (3) the number of third-stage nymphs (late survival). Since *A. grossa* feeds, oviposits and mates on two alternative host-plants (*Brugmansia suaveolens* and *Solanum ursinum*, both Solanaceae), we also evaluated and compared selection gradients between these host-plants. We found positive

linear selection acting upon pronotum length considering the number of eggs and the late survival fitness proxies and positive linear selection acting on the distance between the suprahumeral horns considering the early survival proxy on females ovipositing on both host-plants. These results highlight the importance of the pronotum in treehoppers females' fitness and suggest that maternal care appears to have a greater importance in the way that natural selection is operating than the host-plant where oviposition occurs.

Keywords Bolivia · Phenotypic selection · Pronotum · Selection gradients · Yungas

Introduction

Parental care in insects, defined as behavioral displays of one or both parents during the post-ovipositional phase that enhance survival, growth and development of the offspring (Tallamy and Wood 1986), is widely distributed among several species, being present in at least 47 families belonging to 13 orders (Choe and Crespi 1997; Lin 2006; Trumbo 2012). Parental care is frequently performed by females (i.e., maternal care) and shows a variable duration in relation to the life cycle stages of the offspring under protection (Godoy et al. 2006). Treehoppers (Hemiptera: Membracidae) are one of the best-known taxonomic groups in which parental care consists mainly in the permanence and vigilance of the mother around its offspring, thus providing active protection against predators (Lin et al. 2004; Godoy et al. 2006; Lin 2006).

In some treehopper species, maternal care shows a short duration and the task is then transferred to hymenopteran insects (mostly ants). These insects defend and take care of the progeny (Bristow 1983; Godoy et al. 2006) and in

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✉ Carlos F. Pinto
cpintonavia@gmail.com

- ¹ Laboratorio de Química Ecológica, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Santiago, Chile
- ² Laboratorio de Ecología Química, Facultad de Ciencias y Tecnología, Universidad Mayor de San Simón, Parque La Torre # 1720, Cochabamba, Bolivia
- ³ Universidad Mayor Real y Pontificia de San Francisco Xavier de Chuquisaca, Estudiantes # 97, Sucre, Bolivia
- ⁴ Instituto de Entomología, Universidad Metropolitana de Ciencias de la Educación, Av. José Pedro Alessandri 774, Santiago, Chile
- ⁵ Laboratorio de Ecología Evolutiva, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Santiago, Chile

return receive a sweet substance (known as honeydew) from nymphs (Del-Claro and Oliveira 1996, 1999), thus establishing a mutualistic interaction (Wood 1984; Godoy et al. 2006). Mutualism with ants and other hymenopterans is totally absent in treehoppers of the tribe Hoplophorionini, and maternal care relies exclusively on females and extends until the progeny reaches the adult stage (McKamey and Deitz 1996; Lin et al. 2004; Torrico-Bazoberry et al. 2014). Species of this tribe show the highest degree of maternal care among treehoppers (McKamey and Deitz 1996), in terms of behavioral (Wood 1974, 1976; Coccoft 2002; Lin 2006), communicational (Nault et al. 1974; Coccoft 1996, 1999a, b; Ramaswamy and Coccoft 2009) and morphological (Creão-Duarte and Sakakibara 1997; Wood 1993; Lin 2006; Camacho et al. 2014) adaptations that allow them to effectively defend their offspring.

Among those morphological adaptations, the pronotum has been associated with roles such as sensorial, crypsis and protection against vertebrate (Poulton 1903; Wood and Morris 1974; Wood 1975, 1976, 1977, 1993) and invertebrate predators and parasitoids (Boulard 1983; Wood 1993; Lin 2006; Camacho et al. 2014). Furthermore, female treehoppers have generally bigger pronotum than males (Creão-Duarte and Sakakibara 1997; Godoy et al. 2006); given the occurrence of maternal care, this suggests that the pronotum is important for offspring protection and/or egg mass covering (Camacho et al. 2014). Although the pronotum of treehoppers seems to represent a morphological adaptation, the way that natural selection operates on this structure in relation with maternal care has not yet been formally evaluated.

Alchisme grossa (Hoplophorionini) is a widely distributed Neotropical treehopper (McKamey and Deitz 1996; Lin et al. 2004), which is characterized by exhibiting maternal care until offspring development is completed (Camacho et al. 2014; Torrico-Bazoberry et al. 2014). According to previous observations performed within a site in the Yungas biogeographical region, the insect develops its life cycle using two species of alternative host-plants: *Brugmansia suaveolens* and *Solanum ursinum* (both Solanaceae) (Torrico-Bazoberry et al. 2014). Additionally, the close dependence of *A. grossa* on its two alternative host-plants (as feeding, mating and oviposition sites) constitute a scenario where the local conditions (biotic and abiotic) of each host-plant may exert differential selective pressures on the insects, as has been suggested and reported for some treehoppers and other insects (Keese and Wood 1991; Wood et al. 1999; Coccoft et al. 2008, 2010; Ruiz-Montoya and Núñez-Farfán 2009; Flores-Prado et al. 2014). Hence, using *A. grossa* as a model organism, we evaluated and compared the type and shape of natural selection acting upon traits associated with the pronotum of reproductive females, which use *B. suaveolens* or *S. ursinum* as host-

plants. Taking into account that the pronotum has been suggested as a shield-like structure (McKamey and Deitz 1996; Camacho et al. 2014), which serves as protection against the attack of the most common predators of this species in this location (Reduviidae and Coccinellidae insects), and that females use it to deter predator attacks against its offspring through body twisting (Torrico-Bazoberry et al. 2014), three traits: pronotum length, distance between the suprahumeral horns, and the distance between the tip of the dorsal process and the right suprahumeral horn were examined under a selection gradient analyses.

Materials and methods

Study area and data collection

Data were collected during two consecutive rainy seasons: December 2012–March 2013 and December 2013–February 2014 at Incachaca (Cochabamba, Bolivia, 17°13'S–65°49'W; 2450 m.a.s.l.), within the Yungas biogeographical region. Plants of *B. suaveolens* and *S. ursinum* that hosted reproductive females associated with egg masses (from now on called families) were identified. A tag was attached to the petiole of the leaf where each family was found; additionally, the pronotum of each female was marked on the right side with a permanent marker. Preliminary observations carried out in *A. grossa* females had shown that there was no significant difference in mortality between marked and unmarked females ($\chi^2 = 0.075$; d.f. = 1; $p = 0.743$), based on a 3-month observation period.

Phenotypic traits

One hundred and eighty-one families were marked during two rainy seasons: 120 during the 2012–2013 season (69 distributed on 30 plants of *B. suaveolens* and 51 on 35 plants of *S. ursinum*) and 61 families during the 2013–2014 season (31 on 9 plants of *B. suaveolens* and 30 on 17 plants of *S. ursinum*). All marked families were monitored every 5 days (between 11:00 and 14:00 h) until nymphs disaggregated from their original families. In order to investigate how natural selection operates on characteristics of the pronotum of each mother, the following traits were measured using a digital caliper (0.01 mm precision): (1) pronotum length (PL), (2) distance between suprahumeral horns (DSH), and (3) distance between the tip of the dorsal process and the right suprahumeral horn (DDPSH) (Godoy et al. 2006) (Fig. 1). Additionally, the length (LEM) and width (WEM) of the egg mass (which has an elongated ellipsoidal shape) were measured. These measurements were taken when the family was first marked. The number

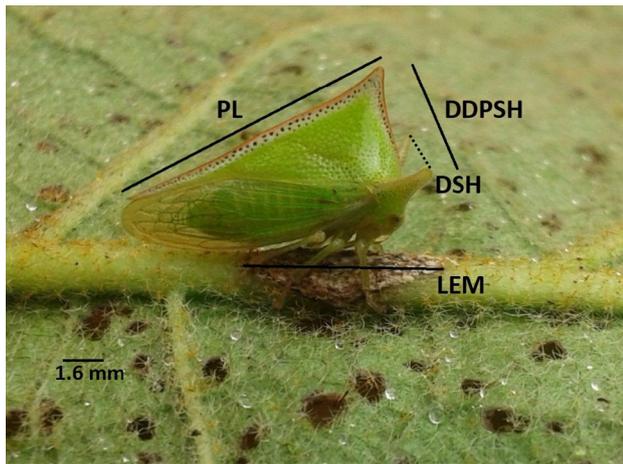


Fig. 1 Traits measured and considered for phenotypic selection analyses in *A. grossa* females: pronotum length (PL), distance between suprahumeral horns (DSH), distance between the tip of the dorsal process and the right suprahumeral horn (DDPSH) and length of the egg mass (LEM)

of eggs conforming each egg mass was estimated based on a regression analysis between egg mass area (using LEM and WEM measurements) (Camacho et al. 2014) as the predictor and the number of counted eggs under a stereo microscope as the dependent variable using 18 abandoned egg masses collected from the same population. The model obtained was number of eggs = $6.209 + (2.883 * \text{area of the egg mass})$ ($n = 18$; $R^2 = 0.551$; $p < 0.001$). The effectiveness of the model was confirmed since no difference was found between the real and the estimated number of eggs present on 15 other abandoned egg masses ($p > 0.05$) based on a t test. Finally, all measured traits were compared using t and Mann–Whitney tests between females that developed on each host-plant.

For the selection gradient analyses, we used PL and DSH as potential traits under selection. DDPSH was excluded from the analyses because it exhibited a strong multicollinearity with DSH (Pearson coefficient = 0.792; $p < 0.001$; $n = 181$), a condition that must be avoided in multiple regression analysis (Hodgins and Barrett 2008; Murúa et al. 2010; Weber and Kolb 2013).

Fitness estimation and phenotypic selection analysis

In order to depict a more comprehensive scenario of *A. grossa* success across the time, three fitness estimates were calculated. The first fitness estimate used was the number of eggs, taken as a fitness measure for each female, since nymphs become mobile around 10 days after hatching (personal observation) and mixed families with nymphs of different instars are common to observe in the field, thus precluding the assessment of fitness of individual mothers based on nymphs. The second fitness estimate was the ratio

between the number of first-stage nymphs and the number of eggs, accounting for the early survival. The third fitness estimate was the number of third-stage nymphs, as a proxy of the late survival. In all cases, relative fitness estimates were calculated as w_i/w_{mean} where w_i is the individual value of each fitness estimate and w_{mean} represents the population average of each fitness estimate. To quantify the expected phenotypic change on each trait, the selection differential (S_i) was calculated as the covariance of each trait and the relative fitness [i.e., $S_i = \text{cov}(z_i, w)$]. Selection differential significances were evaluated using a Pearson correlation analysis (Cuartas-Domínguez and Medel 2010; Murúa et al. 2010).

Linear (β_i) and nonlinear (γ_{ii} , γ_{ij}) selection gradients were estimated using the multivariate models proposed by Lande and Arnold (1983), based on a subsample of 101 families for which reliable data for all the traits and fitness measurements were available (59 families were excluded due to incomplete data, and 21 were lost to external factors such as branch or tree falls). Linear gradients indicate directional selection, and nonlinear gradients indicate quadratic (stabilizing or disruptive) or correlational selection acting on a trait. All traits were standardized to a mean = 0 and a variance = 1, in order to make them comparable (Lande and Arnold 1983; Kudo 2002; Cuartas-Domínguez and Medel 2010; Murúa et al. 2010). Analyses were performed using the pooled data set from the *A. grossa* population (i.e., all families marked on both host-plants); host-plant was included as a covariate in the selection gradient analysis, and its interactions with the measured phenotypic traits were also evaluated. Selection gradient analyses were performed using R 3.10 (R Core Team 2014). Using the library ggplot2 in R, smoothed curves (based on a LOESS estimator) of the trait–fitness relationships for each case were plotted.

As model residuals were not normally distributed in many cases, the significance of the selection gradients were evaluated through 95 % bias-corrected and accelerated (BCa) confidence intervals, calculated using a bootstrap procedure with 5000 permutations (Jordano 1995); gradients were considered significant when 95 % BCa intervals do not cross the zero-value threshold. In order to discard low sample size effects on those traits that showed non-significant linear gradients, a minimum sample required (MSR) analysis to achieve statistical significance at $\alpha = 0.05$ was estimated as: $\text{MSR} = (t\sigma/\beta)^2$, where $t = 1.96$, β is the selection gradient estimate, and σ is the selection standard deviation estimate (Medel 2000). If MSR doubles the sample size considered or exceeds the available size of the population, sample size issues are considered negligible (Medel 2000; Flores-Prado et al. 2014).

Results

A total of 59 families found on *B. suaveolens* and 42 on *S. ursinum* were used in the analysis. DSH and DDPSH were significantly different between females on both host-plants ($t = -3.976$; d.f. = 179; $p < 0.001$ and $t = -4.151$; d.f. = 179; $p < 0.001$, respectively), being both measurements larger on females found on *S. ursinum*. No significant differences were found on the other traits measured or on fitness values.

Selection analysis

Pronotum length showed positive and significant linear selection gradients when the number of eggs and the number of third-stage nymphs (i.e., late survival) were used as fitness proxies. However, the DSH showed a positive and significant linear selection gradient when the ratio between first-stage nymphs and eggs (i.e., early survival) was used as fitness proxy. Nonlinear gradients were not significant, and there was no interaction between the host-plant covariate and the measured traits in any case (Table 1). The relationship between PL and DSH with each of the fitness proxies used is presented in Fig. 2. MSR analysis indicated that we need to sample between 4275 and 20,394 families to obtain significant gradients for those nonsignificant results, far exceeding the existing population at the study site on a 2-year period and discarding potential low sample size artifacts in this study.

Table 1 Phenotypic selection analysis on *A. grossa* females considering three fitness estimates: W1 = number of eggs, W2 = survival from eggs to first-stage nymphs, W3 = number of third-stage nymphs

Fitness	Trait	S'_i	β'_i	γ'_{ii}	γ'_{ij} DSH
W1	PL	0.061*	0.069 ± 0.027*	-0.290 ± 0.716	0.269 ± 0.758
	DSH	0.023	-0.004 ± 0.029	0.033 ± 0.639	-
	Host:PL	-	-0.040 ± 0.046	-	-
W2	Host:DSH	-	-0.290 ± 0.716	-	-
	PL	0.128	0.028 ± 0.111	-0.233 ± 2.945	3.441 ± 3.119
	DSH	0.220*	0.216 ± 0.119*	-1.223 ± 2.631	-
W3	Host:PL	-	-0.026 ± 0.193	-	-
	Host:DSH	-	-0.013 ± 0.209	-	-
	PL	0.324*	0.295 ± 0.146*	2.161 ± 3.845	2.593 ± 4.071
W3	DSH	0.225*	0.047 ± 0.156	-4.457 ± 3.435	-
	Host:PL	-	-0.158 ± 0.252	-	-
	Host:DSH	-	0.173 ± 0.273	-	-

Standardized selection differentials (S'_i), linear (β'_i) and nonlinear [both quadratic (γ'_{ii}) and correlational (γ'_{ij})] selection gradients are presented for the pooled population ($n = 101$), host-plant (*Brugmansia suaveolens* or *Solanum ursinum*) was included as a covariate in the models, the interactions between traits and host-covariate are presented. Estimates ± 1 SE are presented

PL pronotum length, DSH distance between suprahumeral horns

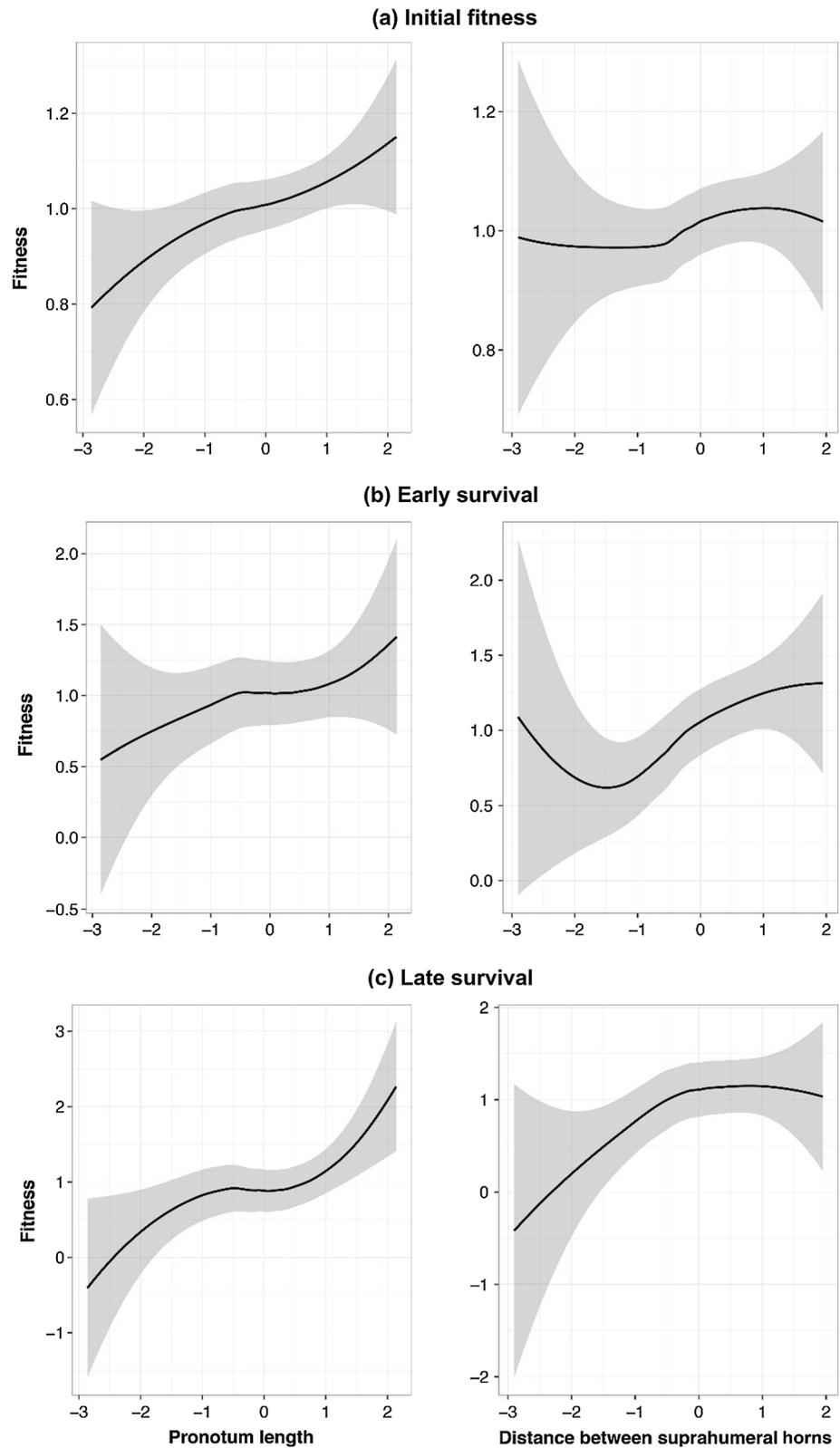
* Significant at $p < 0.001$ according to bootstrap 95 % BCa interval calculations

Discussion

Body size affects almost every aspect of fitness of an organism (Visser 1994; Kingsolver and Huey 2008). In an evolutionary context, the notion of “bigger is better” (Kingsolver and Huey 2008), evaluated across several taxa (vertebrates, invertebrates and plants), proposes that individuals with larger body sizes have greater fitness (in terms of survival, number of matings and fecundity) than smaller individuals in the same population (Kingsolver and Pfennig 2004; Kingsolver and Huey 2008). Results for *A. grossa* females showed that PL experienced positive directional selection considering two different fitness proxies (number of eggs and the number of third-stage nymphs or late survival). Since the size of the pronotum correlates positively with body size in female treehoppers (Stegmann 1998), our result predicts that directional selection will increase body size in the population (Kingsolver and Pfennig 2004; Kingsolver and Huey 2008). In other words, individuals with a longer pronotum (and thus larger body size) have a greater fitness advantage, thus coinciding with the notion that “bigger is better” and highlighting the importance of pronotum size for females of this species (Wood 1993; Kudo 2002; Kingsolver and Huey 2008) and its possible relation to fecundity and offspring survival (Honek 1993; Kingsolver and Pfennig 2004; Kingsolver and Huey 2008).

Distance between suprahumeral horns (DSH) selection gradient was significant when we considered the ratio between first-stage nymphs and eggs (i.e., early survival) as a fitness proxy. Furthermore, this trait was larger on

Fig. 2 Relationship between pronotum length and distance between suprahumeral horns with each of the relative fitness proxies: **a** the number of eggs laid, representing the initial fitness; **b** the ratio between the number of first-stage nymphs and the eggs, representing early survival; and **c** the number of third-stage nymphs, representing late survival. We used standardized trait values in all cases. Smoothed curves were plotted using a LOESS estimator (span = 1) using ggplot2



females found on *S. ursinum*. These results could somehow support the cryptic function of the pronotum, as has been suggested for treehoppers pronotum shapes (Wood 1993;

Godoy et al. 2006), since the suprahumeral horns of *A. grossa* are very similar to the thorns of *S. ursinum* (personal observation). It could be possible that having a larger

DSH (and thus, having longer suprahumeral horns) could benefit the females during egg protection since females could be less detectable for predators if they are similar to the plant thorns, especially taking into account that during the offspring's egg stage females must remain a large period of time almost inactive and that this developmental stage is the longest of the life cycle (Torrico-Bazoberry et al. 2014). This hypothesis is also reinforced since the alternative host-plant, *B. suaveolens*, does not have thorns, and the insects measured on this plant had shorter DSH. However, the defensive role of having a larger DSH cannot be discarded since it could benefit *A. grossa* females as larger and sharp horns have been reported to deter vertebrate predators, such as lizards (Wood 1993), and also since it serves as a physical shield to protect the eggs against invertebrate predators or parasitoids (Lin 2006).

No differences between host-plants were found in the way that natural selection is operating on PL (directional-positive selection), indicating that having a longer pronotum is advantageous to this insect under both environmental conditions. A previous study (Torrico-Bazoberry 2014) showed that treehoppers that develop on *B. suaveolens* have higher predation risk than those developing on *S. ursinum*; on the other hand, those that develop on *S. ursinum* have higher competition by other herbivorous insects. Having a longer pronotum could possibly benefit females ovipositing on *B. suaveolens* by driving away predators (Wood 1993) and could benefit females ovipositing on *S. ursinum* by driving away herbivorous competitors, as previously reported for other Hoplophorionini treehoppers (Lin 2007). On the other hand, same patterns of selection acting on traits directly associated with maternal care in *A. grossa* females ovipositing on each host-plant were obtained, suggesting that the evolutionary history of maternal care, considered an ancient trait in the tribe Hoplophorionini (McKamey and Deitz 1996; Lin et al. 2004), has a greater importance in the way that natural selection is operating than the environment where the insect oviposits. Finally, the results also show for the first time a direct relation between female pronotum size and fitness in treehoppers, suggesting a possible explanation of why female treehoppers have generally bigger pronotum than males (Creão-Duarte and Sakakibara 1997; Godoy et al. 2006).

Although no differences between host-plants were found in the way that natural selection is operating on the chosen traits, possible differences between host-plants under conditions that may be acting as selection agents are likely to occur (Wade and Kalisz 1990; Kudo 2002). Considering that host-plants represent different environments with particular conditions that potentially could act as selective pressures (Caruso et al. 2003), differential natural selection on insects ovipositing on different hosts has been evidenced (Flores-Prado et al. 2014), which is expected on treehoppers on each of its hosts unless different factors

somehow cancel out. To identify the agents or factors promoting selection and the direction such selection takes, it is necessary to perform further studies on the ecology of *A. grossa* under conditions in which environmental parameters that could act as agents of selection can be experimentally assessed and eventually manipulated (Arnold 1983; Wade and Kalisz 1990; Kudo 2002).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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