J Pest Sci (2018) 91:459–468
https://doi.org/10.1007/s10340-017-0860-1

ORIGINAL PAPER

Changes in the insecticide susceptibility and physiological trade-offs associated with a host change in the bean weevil *Acanthoscelides obtectus*

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Received: 19 August 2016 / Revised: 24 March 2017 / Accepted: 3 April 2017 / Published online: 12 April 2017

Abstract For most of the seed weevils (Coleoptera: Chrysomelidae: Bruchinae), the ability to survive environmental stresses like insecticide exposure and reproduction is variable and depends on the host. Here, we evaluated the physiological costs and benefits of a host shift from kidney beans of the landrace “Vermelho” to cranberry beans of the landrace “Manteigão” in the bean weevil *Acanthoscelides obtectus*. We assessed the susceptibility of *A. obtectus* to the commercial pyrethroid deltamethrin and clove and cinnamon essential oils as potential alternative insecticides and measured its reproductive performance (e.g., oviposition and emergence rates) on both hosts. The females of *A. obtectus* reared on kidney beans were less susceptible to both deltamethrin and clove essential oil and showed more sources of energy in the trophocytes although the attraction of adult females to both hosts was similar. However, the females reared on cranberry beans had higher reproductive performances and respiration rates, indicating that more energy was expended on reproduction than on the mitigation of the insecticide actions. Thus, with a change in hosts, a trade-off between reproductive fitness and the susceptibility to insecticides was demonstrated for *A. obtectus*. These results should not only affect the management of *A. obtectus* in storage units but also the understanding of these insects’ host adaptativeness.

Keywords Bruchids · Host range · Adaptation costs · Trophocyte area · Botanical insecticides · Respiratory rates

Key messages

- *Acanthoscelides obtectus* reared on cranberry beans exhibited higher susceptibility to synthetic and botanical insecticides and smaller trophocytes areas.
- Host change seems to affect the energy investment between the contrasting processes of reproduction and protection against insecticides in *A. obtectus*.
- Host type affected the oviposition and emergence rates as well as the respiratory activity of the bean weevil *Acanthoscelides obtectus*.

Introduction

Herbivorous insects generally specialize on one or a few closely related hosts, and, for most of these insects, the use of a specific host and the detoxification of secondary metabolites may be negatively correlated with fitness in new environments (Gompert et al. 2015; Jaenike 1990; Messina 2004; Scheirs et al. 2005). The seed weevils in the coleopteran subfamily Bruchinae easily adjust to new nutritional or toxic environments (Sales et al. 2000), which

Communicated by J.J. Duan.

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is likely a primary reason for their adaptability to a wide range of hosts. However, the mechanisms for adaptation require alterations in physiological and behavioral processes that typically affect reproductive performance traits such as oviposition, emergence and population growth (Bifano et al. 2010; Milanović et al. 1991; Šešlija and Tucić 2003; Silva et al. 2001).

Among the seed weevils, the bean weevil *Acanthoscelides obtectus* (Say) (Coleoptera: Chrysomelidae: Bruchinae) is a widespread pest that uses the seeds of the common bean, *Phaseolus vulgaris* (L.), as the primary host; however, these weevils reproduce in a wide range of ecological conditions, causing severe losses in several stored products (Alvarez et al. 2005; Thakur 2012; Vilca Mallqui et al. 2013). Females of *A. obtectus* scatter eggs among bean grains, but the host is selected by the early stage larvae and not the female adults (Parsons and Credland 2003). The growth of larvae is restricted to the inside of mature seeds, which is typically the only source of nutrient reserves and resources used to reach maturity and to survive during the adult stage (Hamraoui and Regnault-Roger 1995; Savković et al. 2012; Šešlija and Tucić 2003).

Adults of *A. obtectus* are facultatively aphagous and are capable of initiating their colonization in the fields or in storage facilities, where these insects cause major losses (Baier and Webster 1992). Because the availability of a specific host is highly discontinuous and beans are treated with insecticides both in the field and in storage, the selection pressures on weevils are high, and the adaptations reflect the differential investment of energy between the contrasting processes of reproduction and defence against toxicants such as pesticides (Hamraoui and Regnault-Roger 1995; Milanović and Gliksman 2004; Savković et al. 2012; Stojković et al. 2012, 2014).

For instance, an adaptive allocation of energy between reproductive fitness and susceptibility to toxicants has been investigated for several insect species (Guedes et al. 2006; Huang et al. 2005; Messina and Fry 2003; Oliveira et al. 2007; Santos et al. 2015; Šešlija and Tucić 2003), where it has often been described that lower susceptibility to insecticides may derive from higher energy investments favoring the detoxification of the toxic molecules at the expense of reproduction (Guedes et al. 2016). The respiration rate, an indicator of physiological stress, can be used to detect both reversible and irreversible toxicosis in insects (Karise et al. 2015; Kestler 1991; Mänd et al. 2005). Furthermore, the fat body in insects is composed mainly of cells called trophocytes which are characterized morphologically by the presence of lipid droplets, glycogen rosettes and protein components (de Oliveira and Cruz-Landim 2003). As these trophocytes constantly exchange compounds with the hemolymph through absorption or exocytosis, the intensity of these exchanges can be morphologically estimated, which has allowed the use of the trophocytes morphology as an indicator of the availability and mobilization of energy reserves for organism maintenance, survival and reproduction during exposure to toxic compounds (Alves et al. 2010; Guedes et al. 2006; Hsieh and Hsu 2011; Nath 2002).

Insect populations need to continuously adapt to alterations in their environments (Gbaye and Holloway 2011; Gbaye et al. 2011). It is likely that the nature of available feeding substrates, through energy allocations, will play a crucial role on the reproduction capabilities especially in the presence of toxic compounds such as insecticides. Our hypothesis is that a change in the host food source will impact the allocation of energy reserves and consequently the ability to mitigate the stress of xenobiotics like insecticides. Thus, this study was conducted to evaluate the physiological costs and benefits of a host shift (i.e., from kidney beans of landrace “Vermelho” to cranberry beans of the landrace “Manteigão”) in *A. obtectus*. We measured the susceptibility to insecticides (i.e., the pyrethroid deltamethrin and the essential oils of clove, *Syzygium aromaticum* L., and cinnamon, *Cinnamomum zeylanicum* L.,) and the reproductive (e.g., oviposition and emergence rates) performance of *A. obtectus* on both bean types.

Materials and methods

Weevils and beans

The original population of *A. obtectus* was field-collected from bean-producing small farms in the Viçosa Region (Minas Gerais State, Brazil). These insects were collected in *P. vulgaris* beans of the landrace “Ouro Vermelho” (common name: “Feijão vermelho” and here referred to as “kidney beans”). Insect populations were started with a minimum of 500 individuals and developed and reared in laboratory conditions (27 ± 2 °C, 75 ± 5% relative humidity, and 12 h of scotophase). Prior to the experiment beginning, we used the kidney beans obtained from a local market as substrates to rear the beetles for several generations. However, for the host-change experiments, we also used the *P. vulgaris* beans of the landrace “Manteigão” (common name: “Feijão manteigão” and here referred to as “cranberry beans”) obtained in the local market. The bean types were selected because of the size difference, with the kidney beans (25 ± 0.77 g/100 grains) being approximately half the size of the cranberry beans (40 ± 1.13 g/100 grains) (Oliveira et al. 2015). These beans also differ in terms of their nutritional contents. According to the beans’ provider (Cerealista Pereira, Cajuri, MG, Brazil), while in a portion of 60 g of beans, both bean types have similar amounts of proteins (cranberry: 8.0 g, kidney: 11.0 g), the amount of lipids (cranberry: 0.8 g, kidney: 6.4 g) and carbohydrates (cranberry: 39.0 g, kidney: 29 g) are different. To avoid possible infestations from the field and to reduce the potential effects of residual insecticides, the bean grains were stored at −10 °C for 14 days before the addition of *A. obtectus*. The water content of the kidney and cranberry bean grains was 11.8%, which were offered ad libitum to the weevils.

Insecticide and plant essential oils

In order to assess the susceptibility to insecticides, we used synthetic pyrethroid deltamethrin and plant essential oils as insecticide probes. Deltamethrin is the most common compound used to control insect pests in fields and in storage units (Ceruti and Lazzari 2005; Sehgal and Subramanyam 2014). A commercial formulation of deltamethrin (Decis® 25 CE; 25 g a.i./L, emulsifiable concentrate; Bayer CropScience, São Paulo, Brazil) was used. For the plant products, we used essential oils extracted from cinnamon bark and dried flower buds of clove, following a previously described procedure (Viteri Jumbo et al. 2014). Based on chromatographic analyses, eugenol (>90%) and sesquiterpene β-caryophyllene (>7%) are the primary constituents of clove and cinnamon essential oils, respectively. These two essential oils have been suggested as potential replacement of synthetic insecticides for controlling insects that infest stored beans (Viteri Jumbo et al. 2014).

Insecticide bioassays

To evaluate the effect of rearing host beans on the susceptibility of *A. obtectus* to insecticides, we assessed the mortality of newly emerged adults (<3 days old) when exposed to deltamethrin (5 µg of a.i./kg of beans; equivalent to the rate recommended for controlling weevil infestations in Brazilian storage units) and to the essential oils of clove (µL of essential oil/kg of beans: $LD_{10} = 13.5$; $LD_{50} = 45.6$; $LD_{90} = 141.0$) and cinnamon (µL of essential oil/kg of beans: $LD_{10} = 17.9$; $LD_{50} = 46.8$; $LD_{90} = 122.4$), based on their efficacies against *A. obtectus* (Viteri Jumbo et al. 2014). All the experiments were done under controlled conditions (27 ± 2 °C, 75 ± 5% relative humidity).

For the bioassay with deltamethrin, the insecticide emulsion (0.5 mL, with distilled and deionized water as the solvent) was sprayed on 200 g of beans using an artist's air brush (Sagyma SW440A; Yamar Brasil, São Paulo, SP, Brazil) coupled to an air pump (Prismatec 131A Tipo 2VC; Itu, SP, Brazil). The insecticide was sprayed at a pressure of 0.7 kgf/cm^2. The grains remained in the container after spraying for 1 h to dry. Each replicate was 200 g of deltamethrin-treated bean grains (in 0.8-L jars) with 25 unsexed adult *A. obtectus*. In the bioassays with essential oil-treated beans, pure doses of each essential oil (i.e., without dilution in a solvent) were applied with a 25-µL Hamilton syringe (Hamilton, Reno, NV, USA) to 200 g of beans in 0.8-L glass jars. After the application, the jars were manually shaken for 60 s to ensure the complete distribution of the essential oil.

For all bioassays, 25 unsexed 1- to 3-day-old *A. obtectus* adults were placed in each jar. Four replicates were used for each dose, and the mortality was assessed after 24 h of exposure. The insects were recorded as dead when they did not respond to a touch with a fine probe. The control treatment consisted of untreated beans.

Cell morphometry of *A. obtectus* reared on both bean types

To evaluate the effect of rearing host beans on the energy reserves of *A. obtectus,* the trophocyte size was measured in five males and five females recently emerged (<3 days old) from each bean type using a Periodic Acid-Schiff (PAS) staining technique. This technique is commonly used to highlight structures with high percentage content of carbohydrates where the reaction of these sugars with periodic acids results in aldehydes. The aldehydes give a purple-magenta color in the presence of Schiff reagent and the distinct staining densities demonstrate the tissue components to which the carbohydrates are attached (Guedes et al. 2006). Briefly, the insects were dissected in a saline solution (0.1 M NaCl, 20 mM KH2PO4, 20 mM Na2HP4), fixed in Zamboni's fixative solution (paraformaldehyde + picric acid), dehydrated in an ascending ethanol dilution series (70–95%) and embedded overnight in Leica historesin (Leica Biosystems, São Paulo, SP, Brazil). The samples were then embedded in historesin with hardener for microtomy. Sections of 4 µm were stained with hematoxylin and eosin and mounted in Eukitt mounting medium (Sigma-Aldrich Brasil, São Paulo, SP, Brazil). Using the Image Pro-Plus 4.5 software (Media Cybernetics, Rockville, MD, USA), the morphometrics of 10 fatty cells was measured for each individual, and the area of each cell was calculated (in µm^2).

Reproduction outputs and bean type preference assays

In order to investigate the effect of rearing host beans on the reproductive performances of *A. obtectus*, we measured the bean type preference, and the oviposition and emergence rates.

Bean type preference

In this experiment, the aim was to determine the bean type which was most attractive to *A. obtectus* (i.e., cranberry beans or kidney beans). Five circular, plastic containers (12 cm diameter and 8 cm height) were used as the apparatus in this experiment, with a central container (E) connected to four other containers (A, B, C and D) by plastic cylinders (12 cm long and 1 cm diameter) (Mazzonettto and Vendramim 2003; Viteri Jumbo et al. 2014). The four side containers were filled alternately with either bean type, and five replicates of 50 newly emerged adults (<12 h old) adult *A. obtectus* were released in the central container; the total number of insects per side container was recorded after 24 h. The attractiveness index was calculated using the following equation: $AI = (2 \times T)/(T + C) \times 100$, where $AI =$ the attractiveness index, $C =$ the number of insects in the containers filled with kidney beans, and $T =$ the number of insects in the containers filled with cranberry beans. The AI values indicate the level of attraction and range between 0 and 2: $AI = 1$ neutral activity; $AI > 1$ repellence; and $AI < 1$ attraction. As a margin of safety for this classification, the standard deviation (SD) of each treatment was added/subtracted from a value of 1 (indicative of neutrality). The kidney beans were used as the T factor in the equation because the insects used in these experiments were all reared on kidney bean masses.

Oviposition and emergence rates assays

The oviposition rate of early-stage adult *A. obtectus* reared on each bean type was measured. Twenty newly emerged adults (<12 h old) were provided with 20 g of the bean type in which they were raised as immatures for oviposition (for 3 days). After this period, the identical groups of insects were transferred to another 20-g bean mass of the identical type for 3 more days. The eggs laid in the bean masses were counted for each 3-day period and for the total number of days (i.e., 6 days). Five repetitions were used for each type of bean (i.e., cranberry or kidney beans).

The bioassays for population density were conducted using groups of 50 recently emerged adults (<3 days old). These insects were allowed to colonize bean masses (100 g of beans) for 10 days. Thirty days after removal of the insects, the number of newly emerged adults was monitored at 3-day intervals for 4 weeks. Four repetitions were used for each type of bean mass.

Respirometry assay

In order to evaluate whether the host type would affect the respiratory responses of *A. obtectus*, we conducted respirometry bioassays using a CO_2 Analyzer TR2 (Sable Systems International, Las Vegas, NV, USA) following previously described methods (Guedes et al. 2006; Haddi et al. 2015b; Oliveira et al. 2005, 2007). The average rate of respiration (CO_2 production) was measured at 25 °C (±2) for five replicates of 20 unsexed adults (less than 3 days old) that emerged from the kidney bean or cranberry bean masses. The insects were placed in 25-mL chambers that were connected to a completely closed system. The chambers were connected to the system for 90 min before injecting CO_2-free air into the chambers for 2 min at a rate of 600 mL/min. The air current directed the CO_2 that was produced by insect respiration to an infrared reader that was connected to the system for the immediate quantification of the CO_2 produced. After determining the respiration rate, the insects were removed from the chambers and weighed on an analytical balance (BP 210 D; Sartorius, Göttingen, Germany). Respiration values were not normalized by body mass, in accordance with recommendations by Packard and Boardman (1999) and Hayes (2001).

Statistical analyses

All statistical analyses were conducted using either the SAS (SAS Institute 2008) or the Sigma Plot (SPSS, Chicago, IL, USA) software. The data of mortality bioassays of essential oils were analyzed with three-way analysis of variance (ANOVA), followed by pairwise multiple comparisons using the Holm–Sidak method. The bean types (2), oil types (2) and doses (3) were the factors in the analyses. The data obtained in the bioassays for the deltamethrin susceptibility, and oviposition rates were analyzed with one-way ANOVA, followed by pairwise comparisons (based on Duncan's method) to distinguish the treatments. The bean type preference was analyzed using Likelihood Chi Square test. Using the curve fitting procedure of the Sigma Plot 8.0 software, we conducted regression analyses to determine the emergence rate. The data of the respiration rate assay (μL of CO_2/h/insect) were analyzed with ANOVA on Ranks, followed by pairwise comparisons using Dunn's method. The data for cell morphometry were submitted to ANOVA, and the averages were tested with *t*-tests at 0.05 probability. The assumptions of normality and homogeneity of variance were tested, and no data transformations were required (UNIVARIATE procedure).

Results

Insecticide bioassays

The insects that were reared on cranberry bean masses were more susceptible ($F_{1,7} = 32.4$; $P = 0.001$) to deltamethrin than were their co-specifics that were reared on

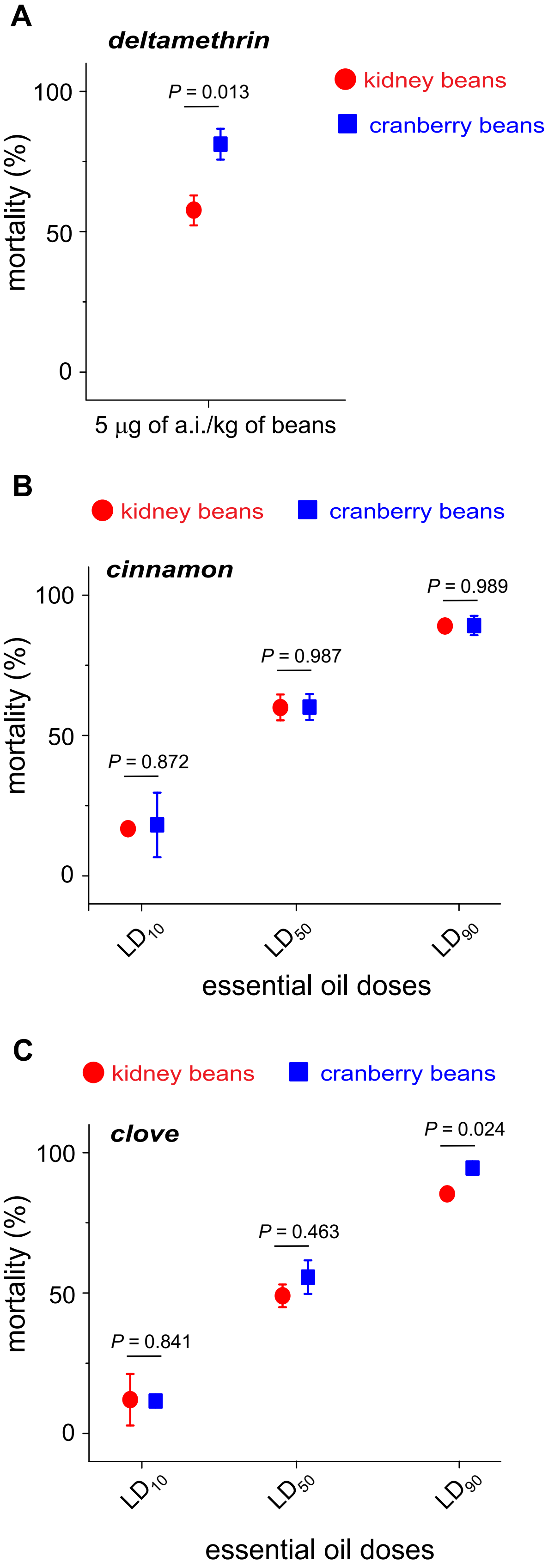

Fig. 1 Susceptibility (mean ± SD; $n = 5$) of *Acanthoscelides obtectus* reared on kidney beans or on cranberry beans to the pyrethroid insecticide *deltamethrin* (**a**) and to essential oils of *cinnamon* (**b**) and *clove* (**c**). For deltamethrin, we used the recommended field rate (i.e., 5 µg of a.i./kg of beans). For the essential oils, we used the LD_{10}, LD_{50} and LD_{90} values [cinnamon (in µL of essential oil/kg of beans): $LD_{10} = 17.9$; $LD_{50} = 46.8$; $LD_{90} = 122.4$; clove (in µL of essential oil/kg of beans): $LD_{10} = 13.5$; $LD_{50} = 45.6$; $LD_{90} = 141.0$]

kidney bean masses (Fig. 1a). In the bioassays with essential oils, the mortality increased with each increase in dose for both essential oils. However, although the bean type did not affect the mortality caused by cinnamon essential oil at any dose (Fig. 1b), the application of clove LD_{90} caused higher mortality ($F_{1,63} = 9.0$; $P = 0.024$) in the insects reared on cranberry bean masses than in those from kidney bean masses (Fig. 1c).

Cell morphometry of *A. obtectus* reared on two bean varieties

Morphologically, the fat body of males and females of *A. obtectus* reared on both beans types (i.e., cranberry beans or kidney beans) was uniformly opaque white. The cytoplasm had heavy vacuolization, and the nucleus was variable in size and location (Fig. 2). Although the bean type did not affect the trophocyte area of males ($F_{1,19} = 1.3$; $P = 0.27$), the trophocyte size in females reared on kidney beans was significantly larger ($F_{1,19} = 8.4$; $P = 0.005$) than that in those reared on cranberry beans (Fig. 2). Furthermore, no significant differences were found in the size of the trophocytes between males and females reared on cranberry beans ($F_{1,19} = 3.5$; $P = 0.063$) or on kidney beans ($F_{1,19} = 0.1$; $P = 0.71$) (Fig. 2). However, in the histochemical tests with cells of the fat body, the intensity of the reaction to carbohydrates was the highest in females reared on kidney beans, followed by that of females reared on cranberry beans. The intensity of the reaction to carbohydrates in male fat body cells was low for both bean types (Table 1).

Reproduction outputs and bean preference assays

Bean type preference assay

In the preference assays, 46.6% (±2.84) of *A. obtectus* adults chose the containers filed with cranberry beans, while 53.1% (±2.62) of the insects preferred containers filled with kidney beans, demonstrating that the attraction of the two bean types to *A. obtectus* adults was not significantly different ($df = 4$; $\chi^2 = 18.6$; $P = 0.17$). Furthermore, the average values for the kidney bean

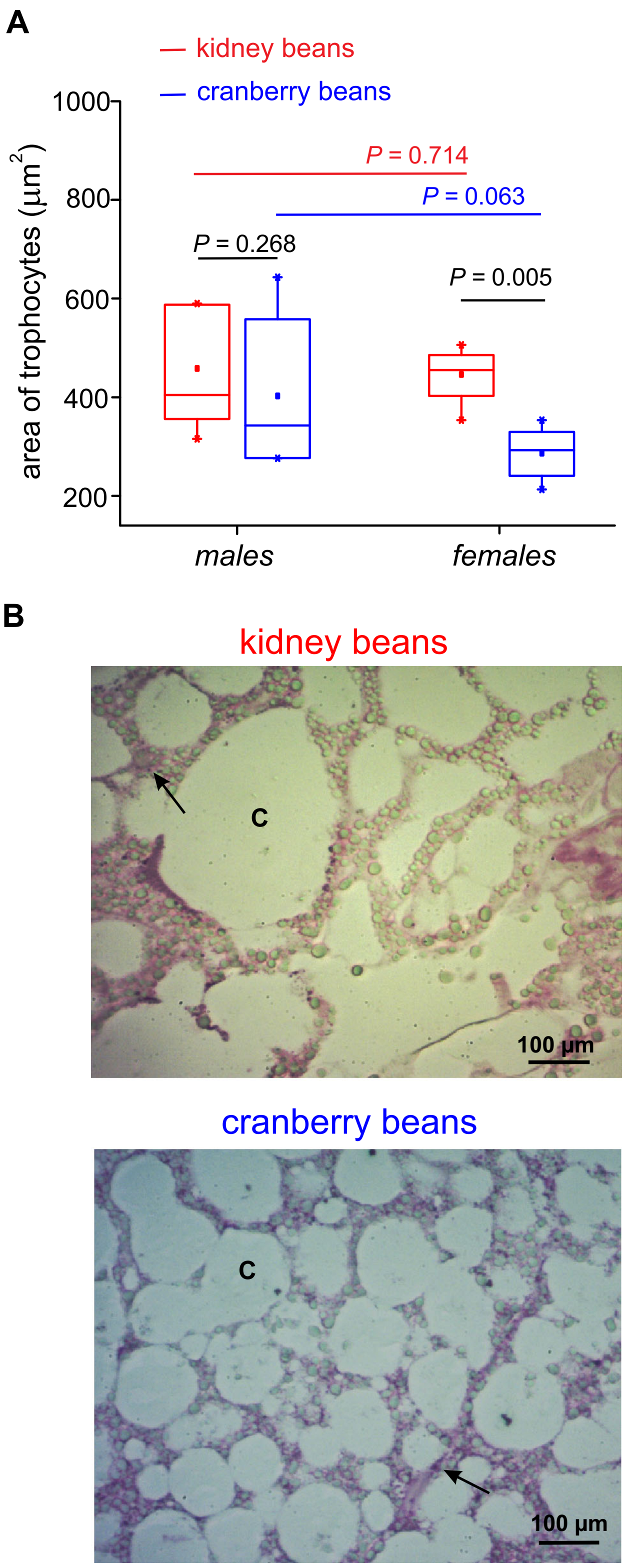

Fig. 2 Trophocyte (fat body) area of adult males and females of *A. obtectus* reared on kidney beans (in *red*) or from cranberry beans (in *blue*). **a** The *box plots* indicate the median and the dispersion (lower and upper quartiles) of the mean trophocyte area. The *filled rectangles* inside the *box plots* indicate the mean values. The *horizontal lines* indicate the plots that were compared with *t* tests at 0.05 probability. **b** Fat body of adult females of *A. obtectus* reared on kidney beans (*upper panel*) or from cranberry beans (*bottom panel*); the cytoplasm (*c*) and nucleus *arrows* are indicated. (Color figure online)

attractiveness (estimated by the AI) over the attractiveness of cranberry beans was of 0.91 (±0.17), which was not statistically different from 1.

Oviposition and emergence rates assays

In the oviposition assays, the number of eggs laid was significantly different on each bean type after the first 3 days ($F_{1,9} = 15.8$; $P = 0.004$), for the second 3-day period ($F_{1,9} = 11.5$; $P = 0.01$) and for the total period of colonization ($F_{1,9} = 15.2$; $P = 0.004$; Fig. 3). The number of the eggs laid on cranberry beans was always higher than the number of eggs laid on the kidney beans.

The total number of *A. obtectus* that emerged after one generation (42 days) from cranberry beans was significantly higher ($F_{1,9} = 50.9$; $P = 0.002$) than that from kidney beans (Fig. 4a). The rate of emergence (i.e., the daily emergence) confirmed this finding, and a significantly higher peak of emergence from the cranberry beans than that from kidney beans was observed on approximately day 40 (Fig. 4b).

Respirometry bioassays

The body mass of adults that emerged from each bean type was not significantly different ($P > 0.05$). However, the respiration rates were significantly higher ($H = 7.67$; $df = 1$; $P = 0.01$) for the insects that were reared on cranberry beans (0.022 ± 0.002 µL CO_2/h/insect) than for those reared on kidney beans (0.016 ± 0.001 µL CO_2/h/insect).

Discussion

Here, we evaluated whether the investment of energy between the contrasting processes of reproduction and protection against insecticides on *A. obtectus* would be affected after a host change (i.e., from kidney beans to cranberry beans). Compared with those reared on kidney beans, the insects reared on cranberry beans had higher susceptibility to insecticides (i.e., deltamethrin and clove essential oil at LD_{90}), a smaller amount of energy in the fat

Table 1 Intensity of PAS reaction conducted on the histological sections of the trophocytes of *Acanthoscelides obtectus* reared on kidney beans or cranberry beans

Gender	Bean type	
	Cranberry	Kidney
Male	+ −	+ −
Female	+	+ +

+ −, weak reaction intensity

+, intermediate reaction intensity

+ +, strong reaction intensity

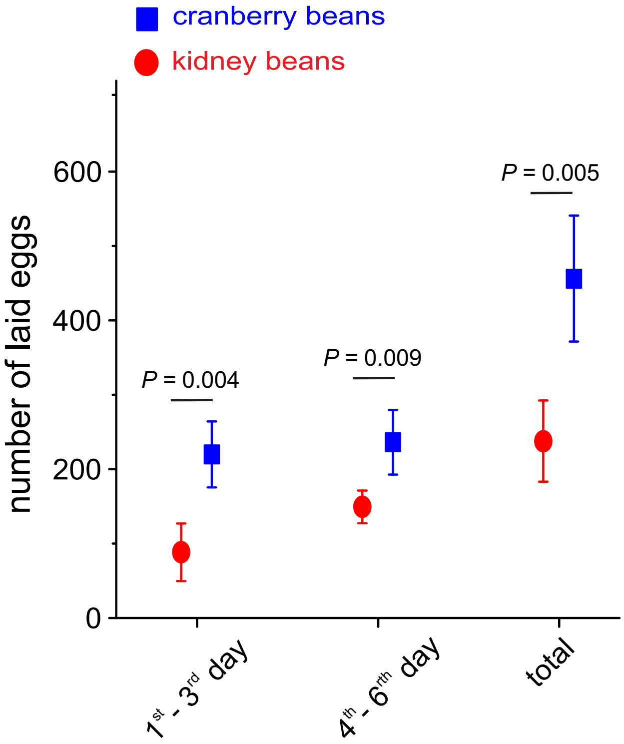

Fig. 3 Number of eggs (mean ± SD; $n = 5$) laid by females of *A. obtectus* reared on kidney bean or from cranberry bean masses during the first 6 days of adulthood

body cells, higher oviposition and emergence rates, and higher respiratory activity.

As observed for many other herbivorous insects, the interactions between bruchids and their seed hosts are complex and are shaped by a co-evolutionary arms race between insect and host (Awmack and Leather 2002; Gbaye et al. 2012; Huang et al. 2005; Lewis et al. 2012; Oyeniyi et al. 2015; Sales et al. 2000). For *A. obtectus*, the development of larvae within different types of legume seed affects adult performance by altering various physiological, morphological, behavioral and life-history traits (Hamraoui and Regnault-Roger 1995; Janković-Tomanić et al. 2015; Khelfane-Goucem et al. 2014; Stojković et al. 2012, 2014).

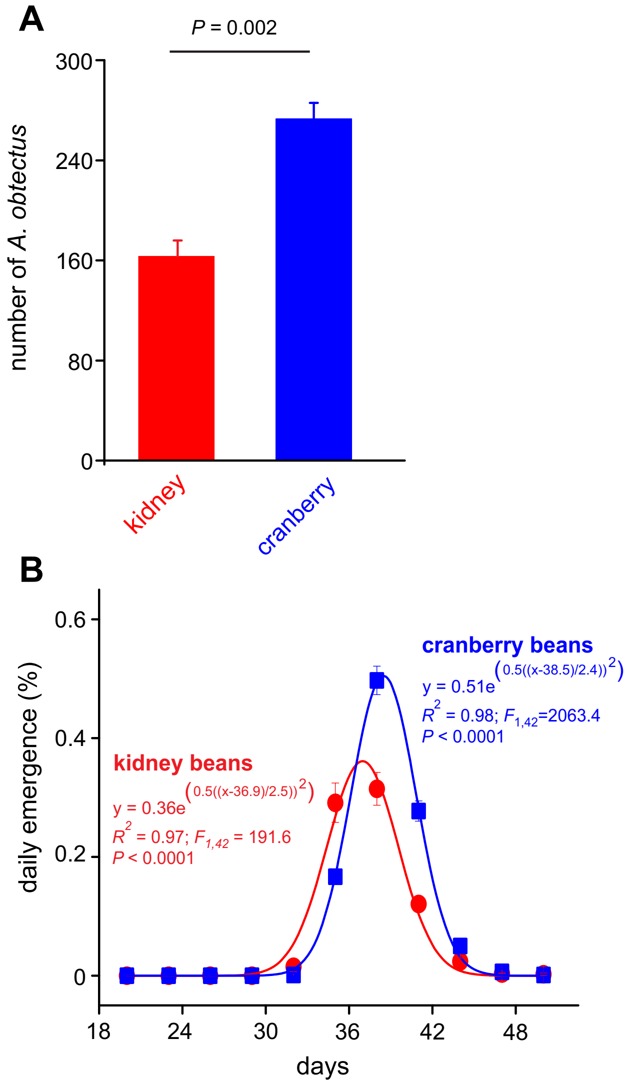

Fig. 4 Effect of bean type on the emergence of *A. obtectus*. **a** Total number (mean ± SD; $n = 4$) of adults emerged after one generation (42 days). **b** Daily emergence of *A. obtectus* reared on kidney bean or from cranberry bean masses

The physical and primarily chemical characteristics of each bean type are also likely important because legume grains have a diverse array of toxins that can influence insect development (Gbaye and Holloway 2011; Lattanzio et al. 2005; Madodé et al. 2012; Vamosi 2005). For example, the arcelins proteins that are differentially found in beans and have insecticidal properties toward bruchid pests as well as inhibitory effects on larval development (Osborn et al. 1988; Cardona et al. 1990). However, arcelins appear to have no effect on the bean bruchid, *A. obtectus*, (Cardona et al. 1990; Paes et al. 2000).

Here, although size did not affect the preference of *A. obtectus* females, the large size of cranberry beans as well as their smaller amount of carbohydrates likely favored larval performance, as indicated by the higher rate of emergence from cranberry beans than from kidney beans. The development of *A. obtectus* is strongly affected by the carbohydrate fraction (especially the arabinose and fucose contents), while the protein fraction has little or no effect (Gatehouse et al. 1987).

To survive the challenges imposed by a change in host or environmental stressors (e.g., insecticides), insects must adapt their arsenal of behavioral, metabolic and physiological defenses (Gonzales Correa et al. 2015; Guedes et al. 2006; Haddi et al. 2015a, b; Liu et al. 2013; Oliveira et al. 2015; Park et al. 2013). However, because energy is a limited resource, the energy allocated to conflicting processes (e.g., reproductive fitness or protection against toxicants) is an essential factor in determining the adaptation and survival of a species. In this study, we observed a hos-type-mediated trade-off in the relationship between reproductive fitness and susceptibility to insecticides for *A. obtectus*, which might be an indication of the effect of the host on the adaptive allocation of energy in this weevil, as reported for several other insect species (Guedes et al. 2006; Messina and Fry 2003; Messina et al. 2009; Oliveira et al. 2005; Santos et al. 2015; Šešlija and Tucić 2003).

The *A. obtectus* females reared on cranberry beans apparently mobilized more of their energy reserves for reproduction than for mitigating the negative effects of insecticides; these females had a less intense reaction to energy molecules, smaller trophocytes and higher rates of oviposition but were more susceptible to insecticides (i.e., deltamethrin and clove essential oil) than were those reared on kidney beans. The respiratory activity was higher for *A. obtectus* females reared on cranberry beans than for those reared on kidney beans, indicating higher metabolism, which might reflect an increase in cost for reproduction or for adaptation to a different environment (Gonzales Correa et al. 2015; Guedes et al. 2006; Haddi et al. 2015b; Unkiewicz-Winiarczyk and Gromysz-Kałkowska 2012).

Although not addressed in detail in this study, the high susceptibility of *A. obtectus* reared on cranberry beans to deltamethrin and clove essential oil might also be the result of an impaired detoxification system. Physiological adaptations to a different host can trigger modifications in detoxification processes (e.g., phosphatase-dependent processes) (Basiouny et al. 2010; Yan et al. 2011) and may reduce protection against xenobiotic compounds. For example, Janković-Tomanić et al. (2015) reported a decline in phosphatase enzymatic activity following the long-term adaptation of *A. obtectus* to a secondary host, which might partially explain the high susceptibility to insecticides observed in this study. Although the relationships between phosphatase activity and energy allocation trade-offs in *A. obtectus* have not been investigated, the close relationship between phosphatase and energy demands and between these enzymes and the development of the embryonic stages of insects has been established (Hashem et al. 2014; Kaur et al. 2013; Oliveira et al. 2013; Zahia et al. 2009).

In the present investigation, morpho-physiological techniques and toxicological and reproductive bioassays were combined to provide valuable information not only for the management of *A. obtectus* in storage units but also to increase the understanding of the adaptability of these insects to their hosts. Understanding the dynamics of pest invasion and establishment in a particular bean type in relation to that bean type's nutritional, physical and chemical contents may help in decision-making for a better insecticide selection and application both in field and in storage units. It may also help with the establishment of a pest monitoring program for the most susceptible bean types. Future experiments that clarify the mechanisms that drive the evolution of such adaptations (e.g., mutation accumulations or antagonistic pleiotropy) or that examine the effect of different hosts on other immune functions (e.g., defense against pathogens, parasitoids or predators) remain essential.

Author contributions

EEO, KH, and LOVJ conceived/designed the research. KH, LOVJ, MC, and MFS conducted the experiments. LRDF, JES and EEO contributed new reagents and/or analytical tools. EEO, LOVJ, KH, JES, LRDF, MC, and MFS analyzed the data. EEO and KH wrote the manuscript. All authors read, corrected and approved the manuscript.

Acknowledgements Grants from the CAPES Foundation, the National Council of Scientific and Technological Development (CNPq), the Minas Gerais State Foundation for Research Aid (FAPEMIG), Secretaria Nacional de Educación Superior Ciencia y Tecnologia of Ecuador (SENESCYT-Ecuador) and the Arthur Bernardes Foundation (FUNARBE) supported this work.

Compliance with ethical standards

Conflict of interest All the authors declare having no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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