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Seed suitability and oviposition behaviour of wild and selected populations of *Zabrotes subfasciatus* (Boheman) (Coleoptera: Bruchidae) on different hosts

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Abstract

The major host for *Zabrotes subfasciatus* (Boheman) (Coleoptera: Bruchidae) is the common bean (*Phaseolus vulgaris* L.). The seeds of this host, which have been developed into many commercial varieties, vary greatly in size and colours. These are sympatric to other host species of Leguminosae which apparently are not typically used as hosts, but with which *Z. subfasciatus* also has contact. The response of a wild population of beetles in terms of acceptability and host suitability was observed in five different varieties of the usual host (varieties Bolinha amarela, Branco, Carioquinha, Jalo, and Preto) and in three atypical host species (chickpea, soy, and lentil). The data were compared with those from selected populations, which spent seven generations in each host. The adaptation ability of the wild population to different hosts was observed and it was verified that both the oviposition behaviour and the host suitability were modified in a few generations in some of the beetle populations. The results also allowed us to discuss the influence of oviposition behaviour and larval performance on host range determination.

Keywords: Adaptation; Leguminosae; Bruchidae; Oviposition; Host range evolution

1. Introduction

In holometabolous insects, where the immatures have restricted movements, the oviposition behaviour of adults and larval development in the host are decisive factors in terms of host range (Wasserman and Futuyma, 1981; Janz and Nylin, 1997; Carrière, 1998). There are many factors that may influence the oviposition of insects on a specific host, such as morphology (Johnson and

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Kistler, 1987), nutritional quality, host abundance (Janz and Nylin, 1997; Barros and Zucoloto, 1999), places free of predators (Bernays and Graham, 1988) and competition (Siemens et al., 1991). Bruchid beetles are excellent subjects for empirical studies on the evolutionary and biological theories related to oviposition and to host use because they are easy to manipulate and the laboratory can simulate the grain storage environment (Fox and Tatar, 1994).

Wasserman and Futuyma (1981) established two basic components related to the use of a host by a species of Bruchidae (*Callosobruchus maculatus* (F.)). The first was the decision taken by the female whether or not to lay eggs on a particular seed. This is defined by the term acceptability, which describes the likelihood of a plant being accepted if it is encountered by an insect. This term was used in the present study rather than preference, because no host-choice experiments were performed (Singer, 1986). The second component is the ability of the larvae to develop inside this particular host. Host suitability is defined as survival, growth, and reproduction of an insect after feeding on a host (Singer, 1986). The bean (*Phaseolus vulgaris* L.) is the usual host of *Zabrotes subfasciatus* (Boheman). The adult female determines the quality and quantity of food for its immatures (Dendy and Credland, 1991), because larvae are restricted to the place where the female had laid the egg. When eggs hatch the larvae enter the seed where all development occurs (Southgate, 1979). The adult does not usually feed (Carvalho and Rosseto, 1968; Abate and Ampofo, 1996), which makes the choice of oviposition sites even more important to the biological success of the descendants. A female may have a variety of oviposition sites, i.e., in addition to different varieties of beans (which vary greatly in size and colour), she may choose other Leguminosae species that are also stored in buildings where *Z. subfasciatus* mainly occurs (Carvalho and Rosseto, 1968).

The objectives of the present study were to determine whether there are differences in host suitability for this bruchid and the acceptability of different varieties of their main host and of other species of potential hosts, and to observe the specificity of a wild population and the adaptive modifications that occurred in the population after several generations in other hosts. The experiments were conducted with a wild population of *Z. subfasciatus* and five commercial varieties of beans and three species of Leguminosae common to the region where the wild population was collected.

2. Materials and methods

The wild *Z. subfasciatus* used for the experiments were acquired from infested seed collected in houses and stores from the Ribeirão Preto region, SP, Brazil (21°05′–21°15′S and 47°50′–47°55′W). Five commercial varieties of the usual host, *P. vulgaris*, (Bolinha amarela, Branco, Carioquinha, Jalo, and Preto) and three species of atypical hosts including chickpea (*Cicer arietinum* L.), soy (*Glycine max* L.), and lentil (*Lens culinaris* Medik) were used. Several characteristics of these varieties and species that were determined were: (1) *weight of grain*—50 seeds of each host were randomly collected and were weighed individually to the nearest 0.1 mg; (2) *size of seeds*—50 randomly collected seeds of each host were measured for the width, length, and height of each seed and multiplied by each other (for the data from characteristics 1 and 2 the Student–Newman–Keuls multiple comparison method was applied ($P<0.05$)); (3) *seed water contents* were calculated by normal weight-dry weight/normal weight × 100; the dry weight of seeds was determined after 7 days at 80°C; (4) *protein content* was determined according to the method of Lowry et al. (1951) with bovine seralbumin as a standard; (5) *colours and textures* were determined by visual examination. The bean varieties were chosen because they are common in the region where the wild insect population was collected; there are no studies of *Z. subfasciatus* behaviour in any of them, and all of the varieties differ in colour and size. The atypical hosts were chosen because they belong to the usual host's family (Leguminosae), are frequently stored in areas where the wild insect populations occur, *Z. subfasciatus* populations had infrequently been observed in chickpea, and some *Z. subfasciatus* eggs had occasionally been observed in soy and lentil (*personal observation*).

The seed were examined individually and those with any flaw in the seed coat were discarded (Credland and Dendy, 1992a). The seeds were stored at −10°C for at least 48 h to eliminate infestation by other insects and 48 h before use they were placed inside an incubator to allow equilibration to the experimental temperature (Carvalho and Rosseto, 1968). Recently emerged (0–24 h) wild bruchid pairs (a male and a female) were put separately in cylindrical glass tubes (7 cm length × 3 cm diameter) in which 6 g of one host were offered as substrate for oviposition (15 replicates for each host).

Acceptability was measured on the basis of the average number of eggs laid by females on each host (Singer, 1986). Eggs were counted 16 days after the beginning of the experiment when the oviposition period was completed. During the oviposition period the tubes were not disturbed to avoid disrupting the females. *Zabrotes subfasciatus* adults did not feed.

Host suitability was measured in terms of (1) percentage emergence in relation to the number of laid eggs (the number of emerging adults divided by the total number of eggs times 100); (2) distribution of adult emergence in time (the emergence period was defined as the interval of time between the first and the last adult emergence) (tubes were observed daily and after 21 days, day 1 of the emergence period, the emerging adult numbers were noted daily); (3) number of eggs laid by descendants; (4) percentage of descendant eggs emerging as adults; and (5) the average number of emerged adults per descendant female. In the population from chickpea the number of eggs/female (a host suitability parameter) was observed on chickpea and on bean, because the number of eggs/female can be altered by the rejection of a host for oviposition as well as by the inability to lay more eggs.

Samples of the wild population of *Z. subfasciatus* were reared on the alternative hosts for seven generations, in which time selection could occur. The same parameters determined for the first generation were measured after seven generations of selection had occurred. All the experiments were maintained in an incubator at 29 ± 2°C and 70 ± 10% r.h. Differences among hosts exposed to the same insect population were compared using the Kruskal–Wallis test (significance level of <0.05) and the Mann–Whitney test (significance level of <0.05) was used to compare the differences between the wild and the selected generation in the same host. The program used was SigmaStat for Windows (1994-Jandel Corporation, San Rafael, CA).

3. Results

The characteristics of the hosts were different in many respects (Table 1). The acceptability was high for all varieties of the usual host (Table 2). The atypical hosts had lower levels of

Table 1
Characteristics of the seeds used as hosts by *Z. subfasciatus* ($n = 50$, mean ± SE). The seeds followed by the letter U are varieties of *P. vulgaris*, those followed by AT are atypical hosts. The Student–Newman–Keuls test ($P < 0.05$) was used to compare the parameters weight and size (width × length × height): all of the host seeds were statistically different in weight and size

Hosts	Size (±SE) (mm)	Weight (±SE) (mg)	Protein content (%)	Water content (%)	Texture	Colour
Branco (U)	615.3±134.0	584.8±55.0	27.3	12.6	Smooth	White
Bol. amarela (U)	255.6±296.7	327.9±37.0	20.7	12.9	Smooth	Yellow
Preto (U)	225.2±54.3	246.7±36.1	30.0	12.9	Smooth	Black
Jalo (U)	406.6±75.1	439.1±103.7	23.8	12.2	Smooth	Light brown
Carioquinha (U)	260.9±47.3	296.7±3.0	22.1	12.3	Smooth	Brown
Chickpea (AT)	681.1±172.4	659.6±133.9	20.5	8.7	Irregular	Beige
Soy (AT)	183.7±73.9	172.1±3.0	36.1	9.0	Smooth	Yellow
Lentil (AT)	88.8±11.3	70.6±9.5	24.0	12.2	Smooth	Green

Table 2
Number of eggs laid per female by *Zabrotes subfasciatus* on different hosts. The hosts followed by U are varieties of the usual host, *P. vulgaris*. Those followed by the letters AT are atypical hosts. The acceptability of the population reared on chickpea was also tested for the host Carioquinha. Fifteen replicates were used (mean ± SE)

Hosts	Wild population	Population from chickpea		After 7 generations in each host
		First generation	Seventh generation	
Branco (U)	24.1±15.4a	—	—	45.7±11.7a*
Bol. amarela (U)	36.1±15.1a	—	—	36.4±8.6a
Carioquinha (U)	31.3±12.9a	48.2±15.3a	45.3±13.8a	33.6±14.2a
Jalo (U)	30.2±15.5a	—	—	46.1±12.7a*
Preto (U)	32.8±8.6a	—	—	35.3±10.3a
Chickpea (AT)	0.4±0.8c	—	—	17.7±13.b*
Soy (AT)	11.1±11.8b	—	—	—
Lentil (AT)	10.0±7.6b	—	—	—

Host acceptability of the two populations was compared by the Kruskal–Wallis test ($P < 0.05$); data followed by different letters indicate statistical differences among hosts in the same population. (*) indicates statistical differences between the two generations on the same host (Mann–Whitney test-$P < 0.05$).

acceptability by the insects than the usual hosts. Chickpea was the atypical host on which the females of *Z. subfasciatus* showed highest oviposition rejection. When the insect population from chickpea was placed on bean the number of eggs was very high. This shows the influence of rejection of a host on the quantity of eggs laid (many authors call it fecundity and it is associated with fitness). After seven generations in the respective hosts, an increase of acceptability was noted on those hosts and it was statistically significant in the wild insect population for the bean varieties Branco and Jalo. Chickpea was also significantly more acceptable but still had the lowest egg production (Table 2).

Although the acceptability of lentil and soy was higher than the acceptability of chickpea, no adult insects emerged from these two hosts. The population from chickpea had a high emergence percentage, similar to that from the usual host varieties (Table 3).

Table 3
Host suitability for wild populations of *Z. subfasciatus* of each host (including descendant performance). The data represented below indicate the results of the parameters used to measure performance

Hosts	% of emergence egg-adult	Average number of descendants	Number of eggs (*)	% adult emergence of descendants (*)	Average number of descendants (*)
Bol. amarella (U)	83.8±8.6a	34.7±13.7a	31.2±15.3a	80.12±14.0a	25.01±10.8a
Branco (U)	77.0±12.2ab	20.7±11.6b	28.1±15.0a	79.00±13.9a	23.19±12.3a
Carioquinha (U)	95.7±11.3a	30.9±9.6a	35.5±16.9a	93.31±8.5a	32.12±9.1a
Jalo (U)	67.00±10.3b	24.9±8.5b	31.9±5.6a	73.98±10.2a	23.52±7.5a
Preto (U)	87.12±13.4a	30.9±9.3a	30.1±9.5a	84.38±10.1a	25.39±9.7a
Chickpea (AT)	83.33±28.8a	0.3±0.7c	6.6±8.6a	75.75±14.9a	4.99±1.0b
Soy (AT)	0	—	—	—	—
Lentil (AT)	0	—	—	—	—

The Kruskal–Wallis test ($P<0.05$) was used and the significant differences are indicated by different letters. The hosts followed by U are varieties of the usual host (*P. vulgaris*) and those followed by AT are atypical hosts. There were 15 replicates for each variable and host (mean±SE). (*) In each column indicates the data for the wild population's descendants.

Table 4
Host suitability for the selected populations of *Z. subfasciatus* (after seven generations in each host variety). The data represented indicate the results for the parameters used to measure performance

Hosts	% emergence egg-adult	Number of descendants	Number of eggs (*)	% adult emergence (*)	Average number of descendants (*)
Bol. amarela (U)	89.6±12.2a	32.4±4.3a	41.7±13.4a	89.3±10.5a	37.2±11.1a
Branco (U)	88.6±8.8a	41.8±11.7ab	43.0±7.6a	93.5±9.8a	40.2±8.5ab
Carioquinha (U)	80.1±26.3a	35.7±7.7ab	36.4±9.8a	96.1±8.8a	35.0±10.1a
Jalo (U)	96.3±13.3a	39.4±1.1ab	41.0±16.2a	83.3±11.5a	34.2±13.9a
Preto (U)	80.5±7.8a	29.4±8.3ac	35.4±12.4a	81.6±13.4a	28.9±10.1ac
Chickpea (AT)	58.6±23.5b	10.4±18.6d	13.8±15.6b	73.2±14.3a	10.1±4.8d

The Kruskal–Wallis test ($P<0.05$) was used and the significant differences in each column are indicated by different letters. U indicates that this seed is from one of the varieties of the usual host (*P. vulgaris*) and AT is from an atypical species. (*) indicates the data of the wild population's descendants. There were 15 replicates for each variable and host (mean±SE).

During subsequent generations insects originating from Jalo and Branco beans found these varieties to be significantly more suitable than did the wild population of insects. The average number of descendants per female originating from Branco was higher than those from Preto. The percentages of emergence of *Z. subfasciatus* in Jalo were significantly higher than for the wild population. However, the percentage of emergence in chickpea decreased (Table 4).

The descendants from the wild population of *Z. subfasciatus* emerged uniformly (without peaks) and slowly; the adult emergences were distributed from day 3 to 10 of the emergence period. The descendants from the selected population generally emerged more rapidly, having an emergence peak on day 3 (Fig. 1). The adult insects of the wild, unselected, population took

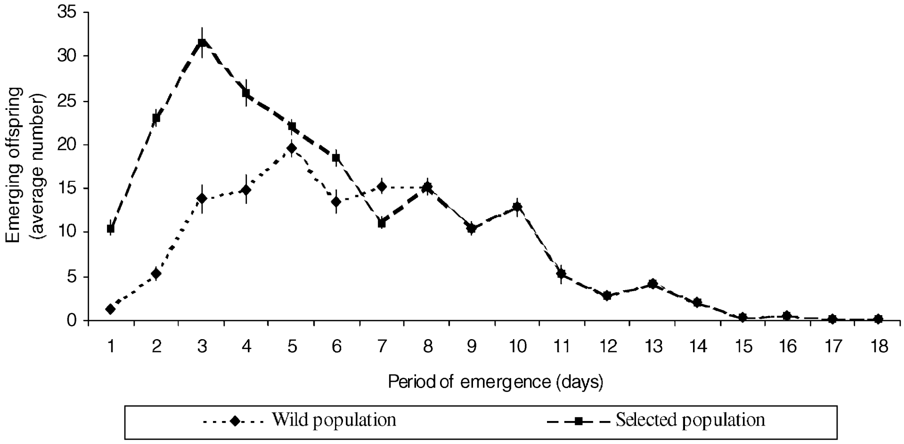

Fig. 1. Period of adult emergence of wild and selected populations of *Z. subfasciatus* (seven generations). The data represent the average of adult emergence from all varieties per day; 75 replicates were used.

Table 5
Percentage of emerging adults of *Z. subfasciatus* from day 1–5 of the emergence period (total duration 16.0 ± 1.5 days) in relation to total number of adults that emerged (15 replicates) in each host variety; comparison between wild and selected insect populations (mean ± SE)

Host	Wild population (%)	Selected population (%)
Bol. Amarela	50.4 ± 10.2a*	90.4 ± 15.1a*
Branco	32.0 ± 8.4b*	69.0 ± 12.1b*
Carioquinha	43.3 ± 11.0a	56.8 ± 9.1b
Jalo	27.7 ± 10.7b*	51.6 ± 10.1b*
Preto	45.5 ± 13.4a	56.8 ± 16.3b
Chickpea	50.2 ± 12.3a	70.6 ± 15.4a*

The percentage of emergence during the first 5 days was compared among hosts using the Kruskal–Wallis test ($P < 0.05$); data followed by different letters indicate statistical differences among hosts in the same population. (*) indicates statistical differences between the two populations on the same host (Mann–Whitney test-$P < 0.05$).

longer to emerge from Branco and Jalo beans than the other hosts. The selected individuals from Bolinha amarela beans emerged significantly faster than selected individuals from other varieties. The emergence of the selected populations was significantly faster than that of the wild population in most cases (Table 5).

4. Discussion

The present study confirmed that oviposition behaviour and host suitability can independently influence the use of a host. This could possibly lead to an increase in the acceptability of a host and to an improvement of the suitability of a particular host after several generations of insect development if a range of natural variation in the insect population is present.

The high number of eggs laid on all varieties of *P. vulgaris*, despite their variations in size and colour, shows that there might be other factors which act as stimuli for oviposition. Although the colours are important for host selection to many insects such as the pollinators, colours are probably not important to *Z. subfasciatus* (Ofuya and Credland, 1996). Yet, the size of the seed has been considered an important factor for the choice of hosts by the Bruchidae (Janzen, 1969; Simmonds et al., 1989). However, the different sizes of the bean varieties may not have influenced the females' oviposition (it is possible that none of the beans had an inappropriate size for larval development). The lower acceptability of atypical hosts could be caused by many factors. The lowest acceptability was for chickpea and it may be associated with the irregular texture of the seeds. Mark (1982) verified that *C. maculatus* also laid few eggs on this host, and attributed this to the texture. Seed colonisation by bruchids is affected strongly by morphological parameters (Johnson and Kistler, 1987).

The suitability of Branco and Jalo for the wild population of insects was lower than that of other varieties but the selected populations found them more suitable. The lower suitability could be because these two varieties are not as abundant as the others in the region where the wild population of *Z. subfasciatus* was collected. Therefore the individuals from this population possibly were not completely adapted to develop in these seeds, being more likely to use them after selection. *Ascia monuste* (Godart), for example, oviposits on the hosts *Brassica oleraceae* L. and *B. juncea* L., but this butterfly would rather lay eggs on *B. oleraceae*, which is more frequent in the region (consequently the population had more contact with it) and where the immatures develop more successfully (Barros and Zucoloto, 1999). When a population of *A. monuste* was reared for 10 generations in *B. juncea*, there was an increase in acceptability and an improvement in host suitability (Barros and Zucoloto, unpublished data). The abundance of hosts is a factor that might also influence the oviposition of Bruchidae (Johnson and Kistler, 1987), and the abundance of the bean and its world-wide distribution might have contributed to this high specificity of *Z. subfasciatus* to this host and the insect's high adaptation ability to the many varieties of bean. This fast adaptation may reflect the phenotypic plasticity of this insect species, revealed by the environmental effect (host) on fitness (Tucic et al., 1997). The phenotypic plasticity can be considered a primary requirement for the colonisation of a new host or for the use of additional hosts. For instance, *Rhagoletis alternata* (Walsh) was able to diversify the range of its diet and to adapt to new hosts, such as *Rosa rugosa* (Haedang) in Europe (Leclair and Brandl, 1994).

The increased suitability of the varieties of *P. vulgaris* can also be seen in the reduction of the emergence time of adult descendants in the selected populations. The emergence peak on the third day of the emergence period of *Z. subfasciatus* coincided with the oviposition peak found by Meik and Dobie (1986) on the third day of adult life. This result may indicate that the larval development was faster and more uniform than in the wild population. The long contact with the same host throughout the generations may also have favoured the development of a faster "decision" to lay eggs by adults. The time spent to make this "decision" involves a high ecological risk that can be reduced by a fast choice, which would favour the specialisation for a resource (Bernays, 1998).

Lentil and soy had a higher acceptability than chickpea, but no adults emerged; here the larval inability (physiological adaptation) to use these seeds defined these two plants as non-hosts. Larvae entered the seed coat, dying inside the cotyledon. This probably eliminated the physical barriers and indicates a high toxicity and/or a low nutritional value as the cause of death.

Quantitative factors (Simmonds et al., 1989), such as the small size of the lentil seeds may also have contributed to the lack of development of the larvae. The high concentration of protein in the soy (more protein quantity and less water content) may have contributed to the mortality of the larvae, since a high protein concentration is toxic to many insects (Haydak, 1953; Ferro and Zucoloto, 1990).

Another factor that may have influenced the oviposition behaviour is the increased oviposition on a suitable host after several generations of feeding on atypical hosts. When female insects from chickpea were placed on bean, the number of eggs was very high, so the number of eggs laid on the chickpea only indicates its acceptability, not the females' fecundity. Although the selected population showed a large increase in acceptability, there was no improvement in chickpea suitability, which worsened as the generations progressed (reflected by the low percentage of emergence). This might be associated with the low water content of chickpea. Tucic et al. (1997) observed 60 generations of *Acanthoscelides obtectus* (Say) in chickpea and inferred that it can be expected that genetically isolated populations using different host species would tend to utilise their own hosts efficiently not because of a physiological adaptation, but because of a higher preference (that is, a higher number of eggs laid on one particular host). The behaviour of the female seemed to be the main factor for low chickpea use. *Acanthoscelides obtectus* larvae, could develop under artificial conditions in unsuitable hosts, but with a large range of suitable host species it was nevertheless viewed as, *sensu stricto*, a monophagous species (Thiery et al., 1995).

However, it is difficult to understand what determines the host use in Bruchidae, since some species share alternative hosts and yet can have different normal hosts that are often unsuitable to other species. *Zabrotes subfasciatus*, has *P. vulgaris* and *P. lunatus* L. as usual hosts (Credland and Dendy, 1992b), but it is also found in *Vigna* seed (Pacheco and Paula, 1995) and chickpea, although it did not develop in lentil and soy. *Callosobruchus maculatus* mainly develops on the *Vigna* species but it can be found on chickpea, lentil, and soy, although it does not develop in *P. vulgaris*. The border that separates and defines which hosts are used by which species seems to be very thin and unstable. This corroborates Bernays' (1998) argument that host use is not constant because the range of insects' diet has both increased and decreased during evolution, indicating that the patterns of host use must be seen as a dynamic process (Bernays and Graham, 1988). This process has been demonstrated by many experiments both in nature and in the laboratory (Canato and Zucoloto, 1993; Bush, 1994; Radtkey and Singer, 1995; Szentesi and Jermy, 1995; Fox et al., 1996), including the present study.

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