ECOLOGY, BEHAVIOR AND BIONOMICS

Oviposition Behavior of *Ceratitis capitata* Wiedemann (Diptera: Tephritidae): Association Between Oviposition Preference and Larval Performance in Individual Females

Iara S. Joachim-Bravo[1], Odair A. Fernandes[2], Sérgio A. de Bortoli[2] and Fernando S. Zucoloto[3]

[1]*Depto. Biologia Geral, Instituto de Biologia, Univ. Federal da Bahia*
Rua Barão do Geremoabo s/n, 40170-290, Campus Universitário de Ondina, Salvador, BA, ibravo@ufba.br
[2]*Depto. Entomologia e Nematologia, Faculdade de Ciências Agrárias e Veterinárias, Univ. Estadual Paulista*
Rod. Carlos Tonanni km 5, 14870-000, Jaboticabal, SP
[3]*Depto. Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Univ. de São Paulo*
Av. Bandeirantes, 3900, 14040-901, Ribeirão Preto, SP, zucoloto@ffclrp.usp.br

Neotropical Entomology 30(4): 559-564 (2001)

Comportamento de Oviposição de *Ceratitis capitata* Wiedemann (Diptera: Tephritidae): Correlação Entre Preferência de Oviposição e Performance Larval em Fêmeas Individuais

RESUMO – Estudou-se a preferência para oviposição e a performance larval de fêmeas de *Ceratitis capitata* (Wiedemann). Fêmeas selvagens ou criadas em laboratório foram testadas, individualmente, quanto à preferência de oviposição em relação a uma espécie de fruto (mamão) em diferentes estágios de maturação e em relação a dois frutos de espécies diferentes: mamão e maçã. Tanto as fêmeas criadas em laboratório como as selvagens ovipositaram preferencialmente nos frutos de mamão maduro em relação aos verdes e que o mamão maduro foi o melhor para a performance larval. Com relação aos testes de preferência de oviposição e performance larval com frutos diferentes, mamão e maçã, evidenciou-se que as larvas, tanto selvagens quanto de laboratório, desenvolveram-se melhor no mamão. No entanto, apenas as fêmeas selvagens preferiram ovipositar no mamão em relação a maçã. As fêmeas criadas em laboratório não mostraram preferência de oviposição pelo fruto que permitiu melhor performance larval.

PALAVRAS-CHAVE: Comportamento de oviposição, mosca-das-frutas, maçã, mamão.

ABSTRACT – The oviposition preference and larval performance of females of *Ceratitis capitata* (Wiedemann) were examined. Wild or laboratory-reared females were tested for oviposition preference in relation to papaya fruit in different stages of ripeness, as well as to two different fruits: papaya and apple. The results demonstrated that both laboratory-reared and wild females preferred ripe papaya fruit compared to unripe fruit for oviposition, and that ripe papaya was the best for larval performance. When oviposition preference was tested with different fruits (papaya and apple), both wild and laboratory-reared larvae developed better in papaya. However, only wild females showed a preference for oviposition on papaya as opposed to apple. Laboratory-reared females showed no oviposition preference on fruits that resulted in better larval performance.

KEY WORDS: Oviposition behavior, fruitfly, apple, papaya.

In holometabolous insects, oviposition behavior is critical for larvae survival, since they have relatively little mobility and depend on the nutritive resources of the host plant selected by adult females (Singer 1986, Renwick 1989). The existence of a possible positive correlation between the choice of a host for oviposition and offspring performance has been extensively studied over the last few years and has been demonstrated in some species (Barros & Zucoloto 1999, Gu & Walter 1999, Huk & Kuhne 1999), but not in others (Underwood 1994, Berdegue *et al*. 1998, Cronin & Abrahamson 1999, Craig *et al*. 2000).

Several studies have demonstrated the existence of inter- or intrapopulational variability of host recognition and selection, as well as an inter- or intrapopulational variability of correlation between oviposition preference and larval performance (Ng 1988, Courtney *et al*. 1989, Sadeghi & Gilbert 1999). This behavioral variability may be due to genetic variation among individuals in terms of the possibility of finding or choosing different hosts (Wasserman & Futuyma 1981, Jaenike 1990), or it may also be the result of experiencing different environments as adults and/or as immatures. These experiences may include different types of learning as well as the effects of the physical environment (Rausher 1985).

Most of the studies on host plant selection for oviposition involve experiments with groups of females, providing a general idea of what occurs within the insect/host-plant relationship. Studies focusing on individual females are important for the interpretation of group studies as they may vary among themselves in the degree of discrimination between, or preference for, different hosts. Additionally, competition among females for oviposition sites may lead to a more uniform egg distribution among the different hosts (Thompson & Pellmyr 1991).

A previous study (Joachim-Bravo & Zucoloto 1997) with *Ceratitis capitata* Wiedemann females demonstrated the absence of a positive correlation between oviposition preferences and larval performance in laboratory experiments with different fruits. Fernandes-da-Silva & Zucoloto (1993) also demonstrated that groups of *C. capitata* females do not show oviposition preference for parts of the fruit that are more nutritionally adequate.

The aim of the present work was to determine if there is a correspondence between larval performance and the oviposition preference of individual females in relation to different stages of ripeness of a given fruit, or to two different species of fruits, as well as to determine if there exist differences in the behavior of wild flies as compared to laboratory-reared flies in terms of these preferences.

Materials and Methods

The flies employed in the present study were derived from a colony reared since 1980 in the laboratory of the Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto-USP. Wild flies were collected in orchards in Ribeirão Preto county region.

In experiment 1, choice and no-choice tests were carried out using ripe and unripe fruits of the same species (*Carica papaya* L.). Papaya was chosen because of its acceptance for oviposition in previous experiments (Zucoloto 1993). Larval performance was evaluated.

In experiment 2, oviposition preference was tested with two different fruits, papaya (*C. papaya*) and apple (*Pyrus malus* L.). Choice tests between papaya and apple and no-choice tests were carried out with individual flies. Larval performance on each fruit was evaluated.

The general methodology used in the two experiments is described below.

Oviposition Preference. A pair of newly emerged flies was placed in a cage (20 x 20 x 20 cm) and fed a diet composed of 6.5 g brewer's yeast (Boneg), 11.0 g sucrose (União), 1.0 g citric acid (Merck), 1.0 ml nipagin (Merck), 2.0 g agar-agar (Difco), and 100 ml distilled water. During the period of oviposition, the fruits offered were cut into small pieces (±5,0 g) and wrapped in aluminum foil, leaving only the peel exposed. In choice tests, two pieces of each type of fruit (unripe papaya x ripe papaya) or (papaya x apple) were placed in each cage. In no- choice tests, four pieces of a same fruit were presented to each pair of flies. After 24h all fruits were renewed, and the eggs in each piece were counted. For each experimental regime 20 couples were used, and oviposition was followed for six days. Cages were maintained at 29 ± 1^{o}C, and 70-80% RH. The data obtained in the choice tests were analyzed statistically using the Wilcoxon test for two dependent samples, and the data from no-choice tests were analyzed by the Mann-Whitney test for comparison of two independent samples. The significance level was set at 5% in both cases (Siegel 1956).

Larval Performance. The performance of larvae was tested as follows: 20 wild or laboratory-reared newly hatched larvae were placed in Petri dishes lined with slightly moistened filter paper containing a piece (5 g) of the tested fruit. New pieces of the fruit were added daily until pupation. The dishes were incubated in the dark at 29 ± 1^{o}C and 70-80% RH. The following parameters were evaluated: percent emergence, life cycle duration, and adult size (estimated by measuring a wing nervure, R_{4+5} to cu-m). Six replications were carried out for each performance test and the data were analyzed statistically by Mann-Whitney test at the 5% level of significance (Siegel 1956).

Results

In experiment 1, oviposition preference of *C. capitata* and larval performance were examined in papaya fruit in different stages of ripeness (unripe vs. ripe).

In the choice tests (Fig. 1) both wild and laboratory-reared females of *C. capitata* deposited higher number of eggs in ripe fruits. Similar results were observed in no-choice tests (Fig. 2).

The results of larval performance on unripe or ripe papaya fruits (Table 1) showed differences and the best larval performance was obtained with the ripe fruits, for both, wild and laboratory-reared flies.

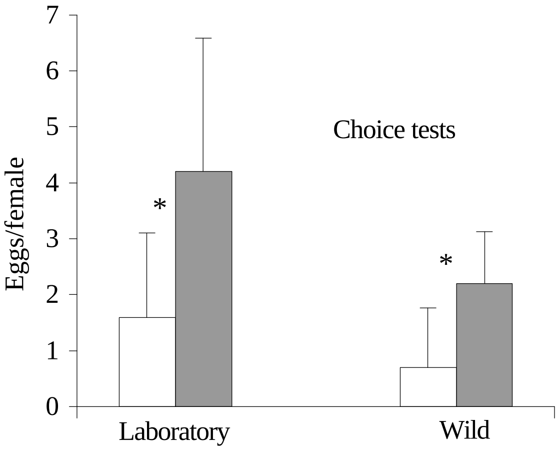

Figure 1. Mean number of eggs deposited by wild and laboratory-reared *C. capitata* females (n=20) in unripe papaya (blank columns) and in ripe papaya (filled columns), in choice tests. (*) = significant difference (Wilcoxon test, P<0.05).

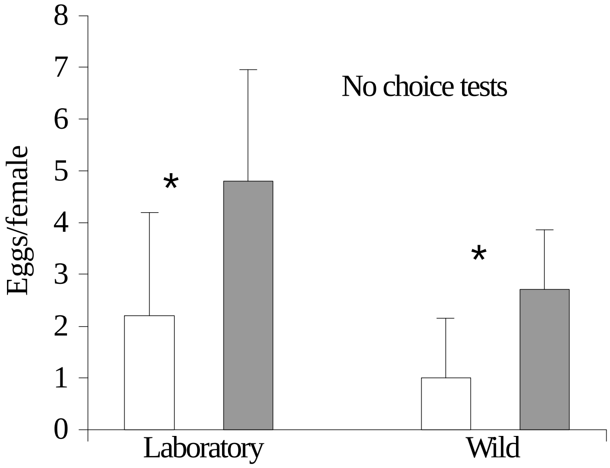

Figure 2. Mean number of eggs deposited by wild and laboratory-reared *C. capitata* females (n=20) in unripe papaya (blank columns) and in ripe papaya (filled columns), in no-choice tests. (*) = significant difference (Mann-Whitney test, P<0.05).

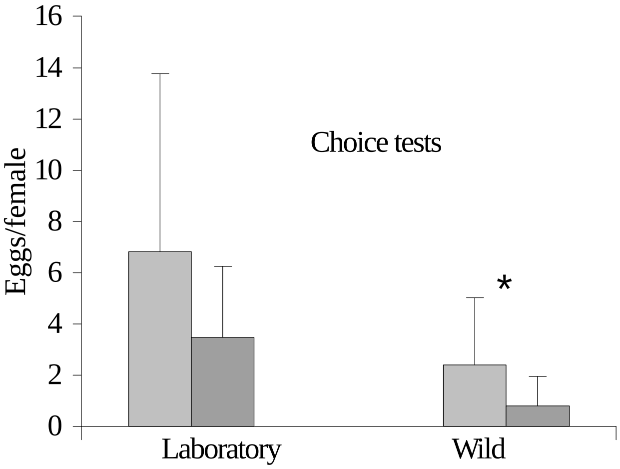

Figure 3. Mean number of eggs deposited by wild and laboratory-reared *C. capitata* females (n=20) in papaya (stippled columns) and in apple (hatched columns), in choice tests. (*) = significant difference (Wilcoxon test, P<0.05).

Experiment 2 was carried out to test larval performance and oviposition preference of *C. capitata* in two different species of fruits, papaya and apple. Laboratory-reared flies did not show oviposition preference between the two fruits tested (Fig. 3), the wild flies instead showed preference for oviposition on papaya as opposed to apple. In no-choice tests (Fig. 4) the results were similar: the number of eggs deposited by laboratory-reared flies on papaya and apple was similar, but with wild flies, a larger acceptance was verified for papaya.

Larval performance tests (Table 2) showed that percent emergence was larger for wild or laboratory-reared larvae fed on papaya. The time to emergence of laboratory-reared larvae was similar when they fed on papaya or on apple. For wild flies the time to emergence was shorter when they fed on papaya. In relation to the adult size, the laboratory-reared flies showed similar results among larvae fed on papaya or apple. For wild population, the adults from larvae fed on papaya were bigger. Considering all analyzed parameters, the best larval performance was obtained with papaya, especially for wild flies.

Discussion

The main findings of the present study are: 1) both laboratory-reared and wild flies preferentially oviposited on ripe papaya fruit compared to unripe fruit and this preference was related with better larval development; 2) laboratory-reared females did not show oviposition preference for fruits that permitted better larval performance, whereas wild females preferred papaya over apple, being papaya a better substrate for larval development.

In the situation of choice between fruits of the same species in different stages of ripeness there was a choice for the ripe fruit that permitted a better larval performance for both fly groups tested. The preference for ripe fruits over unripe ones in *C. capitata* confirms data obtained by Oi & Mau 1989. When the oviposition preference and larval performance tests were assessed by comparing fruits of different species – papaya and apple – the results were less homogeneous. Wild females preferred to lay on papaya, the better fruit for larval performance; laboratory females did not show this preference. The development of laboratory-

Table 1. Biological parameters of wild and laboratory-reared *C. capitata* larvae fed on unripe and ripe papaya. The results show the means (±SD) of six replications. The larvae were maintained in the dark at 29±1°C and 70-80% RH.

Papaya	Emergence (%) (n= 20)		Time to emergence (days) (n= 20)		Wing measurement (mm) (n= 15)	
	Laboratory	Wild	Laboratory	Wild	Laboratory	Wild
Unripe	28,0 a	13,3 a	19,7 ± 0,58 a	18,3 ± 1,52 a	2,8 ± 0,09 a	2,7 ± 0,07 a
Ripe	75,0 b	81,7 b	15,7 ± 0,31 b	15,2 ± 0,29 b	2,8 ± 0,08 a	2,8 ± 0,06 a

Means, within columns, followed by different letters differ from one another (Mann-Whitney test at 5%).

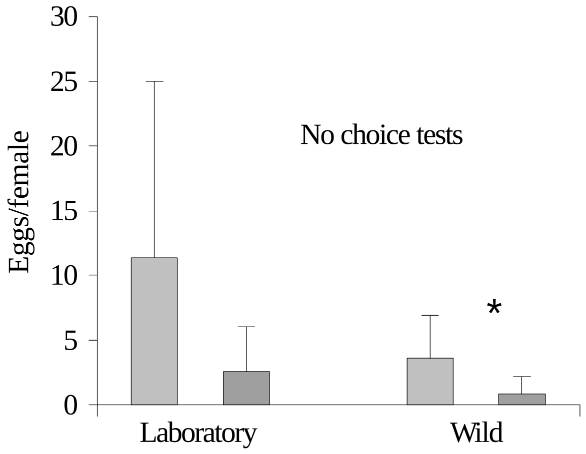

Figure 4. Mean number of eggs deposited by wild and laboratory-reared *C. capitata* females (n=20) in papaya (stippled columns) and in apple (hatched columns), in no-choice tests. (*) = significant difference (Mann-Whitney test, P<0.05).

reared larvae on apple was slightly better than the development of wild larvae on the same fruit, since a significant difference was observed only for percent emergence.

In a previous study by our group (Joachim-Bravo & Zucoloto 1997) in which the oviposition preference and larval development was tested in fly groups, the results did not show an oviposition preference for fruits that were better for larval performance in either wild or laboratory-reared flies. By testing flies individually, as done in the present study, we may have eliminated factors such as competition for oviposition sites and effect of oviposition-deterring pheromones that might have influenced the results obtained previously. Studies on other species have also shown that different results may be obtained when the experiments are conducted with individual insects or with insects in groups (Thompson & Pellmyr 1991).

Laboratory-reared females deposited larger amount of eggs than wild females, independent of the fruit type. It may be due to the rich protein diet on which they have been maintained by several years.

Comparing the laboratory-reared and wild females behaviors, in the two populations studied, it may be suggested that wild flies can better discriminate between host fruits. Probably, being reared on an artificial diet, with no contact with fruits, that are their natural hosts, may affect the discriminatory behavior in laboratory-reared flies. These data agree with some reports in the literature demonstrating that insects reared in the laboratory for a long period of time discriminate less than wild insects in addition to presenting other behavioral and physiological alterations (Szentesi *et al*. 1979, Suzuki & Koyama 1980, Economopolous 1992).

In nature, a positive correlation between oviposition preference and larval performance on different plants suggests that holometabolous phytophagous insects have the ability to choose the host plant on which their offspring develop more fully and quickly (Via 1986). This also implies that the characteristics of the plants, including secondary substances and their nutritional value, are the most important factors for adequate larval performance. Even though it seems obvious that adult females should select individual host plants or parts of these plants that are better for their offspring, there is no constant evidence of this. In monophagous and oligophagous species (Kouki 1993, Barker & Maczka 1996, Barros & Zucoloto 1999), this positive correlation has been observed more frequently than in polyphagous species (Courtney 1986, Thompson 1988, Roininen & Tahvanainen 1989).

The oviposition of *C. capitata* and other Tephritidae in hosts inadequate for larval development are not an uncommon behavior. Krainacker *et al*. (1987), in a study on biological parameters of *C. capitata* kept in laboratory and reared on various hosts, observed that the flies sometimes deposited eggs on hosts in which the larvae would not survive. Carey (1984) reported similar results with wild *C. capitata* from Greece. Females of *Bractocera tryoni* (Froggatt) and *Rhagoletis pomonella* (Walsh) also eventually laid eggs on hosts that were inadequate for larval development (Neilson 1967, Fletcher 1987). It is known that, in general, phytophagous insects infest other plants when no adequate host is available (Fitt 1986). The data obtained here showed that wild flies can lay eggs in an inadequate host, but the number of eggs laid is reduced.

Table 2. Biological parameters of wild and laboratory-reared *C. capitata* larvae fed on papaya and apple. The results show the means (±SD) of six replications. The larvae were maintained in the dark at 29±1°C and 70-80% RH.

Fruits	Emergence (%) (n= 20)		Time to emergence (days) (n= 20)		Wing measurement (mm) (n= 15)	
	Laboratory	Wild	Laboratory	Wild	Laboratory	Wild
Papaya	76,7 a	86,0 a	16,2 ± 1,04 a	15,3 ± 0,27 a	2,8 ± 0,09 a	3,0 ± 0,11 a
Apple	13,3 b	16,7 b	17,0 ± 0,00 a	19,8 ± 0,76 b	2,7 ± 0,09 a	2,7 ± 0,06 b

Means, within columns, followed by different letters differ from one another (Mann-Whitney test at 5%).

This discussion is interesting in relation to *C. capitata* because it is a species of a highly polyphagous nature. Polyphagy is primarily associated with the unpredictability of environmental resources, while monophagy and oligophagy are linked to predictable availability of these resources (Krainacker *et al*. 1987). Fruits, the resource utilized by *C. capitata*, are ephemeral and, even though their availability may be seasonally predictable, their abundance is not predictable from one season to another (Fitt 1990). In addition, a multivoltine species with no diapause such as *C. capitata* may encounter a variety of environments during the year, so that the occurrence of selection for specialization on some fruit is impaired (Krainacker *et al*. 1987). Several characteristics are associated with polyphagy, and in polyphagous species of Tephritidae adult mobility and fecundity are usually elevated with a long reproductive phase, in contrast to what occurs with specialist species. According to some investigators, the lack of discrimination in polyphagous species may be advantageous since their environments are unpredictable and may facilitate change and adaptation to new hosts (Krainacker *et al*. 1987, Fletcher & Prokopy 1991).

However, the potential preference for the best host shown by *C. capitata* females, especially wild ones, in the present study, demonstrates that, despite the polyphagous nature of these insects, this discrimination must be adaptively important, permitting good reproductive success in favorable situations, such as the presence of qualitatively better hosts than others in the same environment.

Acknowledgments

To CNPq for fellowship.

Literature Cited

Barker, A.M. & J.M. Maczka. 1996. The relationships between host selection and subsequent larval performance in three free-living graminivorous sawflies. Ecol. Entomol. 21: 317-327.

Barros, H.C.H. & F.S. Zucoloto. 1999. Performance and host preference of *Ascia monuste* (Lepidoptera, Pieridae). J. Insect Physiol. 40: 7-14.

Berdegue, M., S.R. Reitz & J.T. Trumble. 1998. Host plant selection and development in *Spodoptera exigua*: do mother and offspring know best? Entomol. Exp. Appl. 89: 57-64.

Carey, J.R. 1984. Host-specific demographic studies of the mediterranean fruit fly *Ceratitis capitata*. Ecol. Entomol. 9: 261-270.

Courtney, S.P. 1986. The ecology of pierid butterflies: dynamics and interactions. Adv. Ecol. Res. 15: 51-131.

Courtney, S.P., G.K. Chen & A. Gardner. 1989. A general model for individual host selection. Oikos 55: 55-65.

Craig, T.P., J.K. Itami, C. Shantz, W.G. Abrahamson, J.D. Horner & J.V. Craig. 2000. The influence of host plant variation and intraespecific competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis*. Ecol. Entomol. 25: 7-18.

Cronin, J.T. & W.G. Abrahamson. 1999. Host-plant genotype and her herbivores influence goldenrod stem galler preference and performance. Oecologia 121: 392-404.

Ecomonopoulos, A.P. 1992. Adaptation of the mediterranean fruit fly (Diptera: Tephritidae) to artificial rearing. J. Econ. Entomol. 85: 753-758.

Fitt, G.P. 1986. The influence of a shortage of hosts on the specificity of oviposition behaviour in species of *Dacus* (Diptera: Tephritidae). Physiol. Entomol. 11:133-143.

Fitt, G.P. 1990. Variation in ovariole number and egg size of species of *Dacus* (Diptera: Tephritidae) and their relation to host specialization. Ecol. Entomol. 15: 255-264.

Fletcher, B.S. 1987. The biology of dacine fruit flies. Ann. Rev. Entomol. 32: 115-144.

Fletcher, B.S. & R.J. Prokopy. 1991. Host location and oviposition in tephritid fruit flies, p. 139-171. In W.J. Bailey & J. Ridsdill-Smith (eds.), Reproductive behaviour and mechanisms. Academic Press, New York, 423p.

Gu, H. & G.H. Walter. 1999. Is the common sowthistle (*Sonchus oleraceus*) a primary host plant of the cotton bollworm, *Helicorvepa armigera* (Lep., Noctuidae)? Oviposition and larval performance. J. Appl. Entomol. 123: 99-105.

Huk, T. & B. Kuhne. 1999. Substract selection by *Carabus elatratus* (Coleoptera, Carabidae) and its consequence for offspring development. Oecologia 121: 348-354.

Jaenike, J. 1990. Host specialization in phytophagous insects. Annu. Rev. Ecol. Syst. 21: 243-273.

Joachim-Bravo, I.S. & F.S. Zucoloto. 1997. Oviposition preference and larval performance in *Ceratitis capitata* (Diptera Tephritidae). Rev. Bras. Zool. 14: 795-802.

Kouki, J. 1993. Female's preference for oviposition site and larval performance in the water-lily beetle, *Galerucella nymphaeae* (Coleoptera: Chrysomelidae). Oecologia 93: 42-47.

Krainacker, D.A, J.R. Carey & R.I. Vargas. 1987. Effect of larval host on life history traits of the mediterranean fruit fly, *Ceratitis capitata*. Oecologia 73: 583-590.

Neilson, W.T.A. 1967. Development an mortality of the apple maggot, *Rhagoletis pomonella*, in crab apples. Can. Entomol. 99: 217-219.

Ng, D. 1988. A novel level of interactions in plant-insect systems. Nature 334: 611-613.

Oi, D.H. & R.F.L. Mau. 1989. Relationship of fruit ripeness to infestation in "Sharwil" avocados by the mediterranean fruit fly and oriental fruit fly (Diptera: Tephritidae). J. Econ. Entomol. 82: 556-560.

Rausher, M.D. 1985. Variability for host preference in insect populations: mechanistic and evolutionary models. J. Insect Physiol. 31: 873-889.

Renwick, J.A.A. 1989. Chemical ecology of oviposition in phytophagous insects. Experientia 45: 223-228.

Roininen, H. & J. Tahvanainen. 1989. Host selection and larval performance of two willow-feeding sawflies. Ecology 70: 129-136.

Sadeghi, H. & F. Gilbert. 1999. Individual variation in oviposition preference, and its interaction with larval performance in a insect predator. Oecologia 118: 405-411.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. MacGraw-Hill, New York, 340 p.

Singer, M.C. 1986. The definition and measurement of oviposition preference in plant-feeding insects pp. 65-94. In J.R. Miller and T.A. Miller (eds.), Insect-plant interactions. Springer-Verlag, New York, 462p.

Suzuki, Y. & J. Koyama. 1980. Temporal aspects of mating behavior of the melon fly, *Dacus cucurbitae* Coquillett (Diptera:Tephritidae): A comparison between laboratory and wild strains. Appl. Entomol. Zool. 15: 215-224.

Szentesi, A., P.D. Greany & D.L. Chambers. 1979. Oviposition behavior of laboratory-reared and wild caribbean fruit flies (*Anastrepha suspensa*; Diptera: Tephritidae): I. Selected chemical influences. Entomol. Exp. Appl. 26: 227-238.

Thompson, J.N. 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol. Exp. Appl. 47: 3-14.

Thompson, J.N. & O. Pellmyr. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. Annu. Rev. Entomol. 36: 65-89.

Underwood, D.L.A. 1994. Intraspecific variability in host plant quality and ovipositional preferences in *Eucheria socialis* (Lepidoptera:Pieridae). Ecol. Entomol. 19: 245-256.

Via, S. 1986. Genetic covariance between oviposition preference and larval performance in an insect herbivore. Evolution 40: 778-785.

Wasserman, S.S. & D.J. Futuyma. 1981. Evolution of host plant utilization in laboratory populations of southern cowpea weevil, *Callosobruchus maculatus* Fabricius. Evolution 35: 605-617.

Zucoloto, F.S. 1993. Acceptability of different Brazilian fruits to *Ceratitis capitata* (Diptera, Tephritidae) and fly performance on each species. Brazilian J. Med. Biol. Res. 26: 291-298.

Received 22/09/00. Accepted 15/11/01.