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Selection of Oviposition Sites by Wild *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) Based on the Nutritional Composition

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Seleção de Sítios de Oviposição por *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) Selvagem Baseada na Composição Nutricional

RESUMO - São raros os trabalhos que detalham os nutrientes associados aos hospedeiros que são atrativos para as fêmeas de *Anastrepha obliqua* (Macquart) e determinam a escolha dos sítios de oviposição. A relação do macho na fisiologia e no comportamento das fêmeas também é pouco estudada e parece ter relações ecológicas importantes para o conhecimento da biologia da espécie. O objetivo deste trabalho foi avaliar o comportamento de escolha de *A. obliqua* entre sítios de oviposição contendo diferentes nutrientes. A presença do macho e o "status" nutricional das fêmeas foram, também, abordados. Foram desenvolvidos dois experimentos; no primeiro foi verificada a escolha por fêmeas de *A. obliqua* entre alguns substratos artificiais de oviposição; no segundo experimento as fêmeas foram colocadas para escolher entre dois tipos de substratos de oviposição, quando mantidas na ausência e presença dos machos e alimentadas com dieta pobre ou adequada de sacarose. No primeiro experimento, *A. obliqua* evidenciou maior preferência por substrato contendo levedo de cerveja e sacarose. Substrato contendo apenas levedo foi o segundo mais escolhido. O desenvolvimento da prole e a alimentação do adulto podem ter sido os fatores que determinaram a escolha do substrato contendo levedo e sacarose. A presença da proteína no levedo pode sinalizar para as fêmeas a qualidade nutricional do hospedeiro, de forma mais precisa, que a sacarose. Também no segundo experimento, o levedo foi preferido pelas fêmeas. A ausência do macho foi um fator importante na decisão da escolha do hospedeiro e produção de ovos por *A. obliqua*.

PALAVRAS-CHAVE: Comportamento de oviposição, seleção de hospedeiros, mosca-das-frutas, ausência dos machos

ABSTRACT - Few works have studied in detail the types of nutrients associated to hosts which are attractive to females of *Anastrepha obliqua* (Macquart) and influence the choice of the oviposition site. The relationship of the males in the physiology and in the behavior of those females has also been scarcely studied and some ecological relationships seem to be quite important for the knowledge of this species' biology. Our objective in this study was to evaluate the discriminatory behavior of *A. obliqua* between oviposition sites containing different nutrients. The presence of the male and the nutritional status of the female were also considered in this work. Two experiments were developed: in the first, the preference of *A. obliqua* females between artificial oviposition substrates was evaluated; in the second, females were submitted to two types of artificial oviposition substrates in the presence and in the absence of males and were fed either on a poor diet or on an adequate diet concerning sucrose concentration. In the first experiment, *A. obliqua* showed higher preference for substrates containing brewer's yeast and sucrose. Substrate containing only yeast was the second most accepted. Offspring development and adult feeding may have determined the choice for the substrate containing brewer's yeast and sucrose. In addition, the presence of protein in the brewer's yeast may indicate nutritional quality to the females in a more accurate way than the sucrose. In the second experiment, the brewer's yeast was the most accepted by the females. The male absence was also an important factor in the selection of hosts and in the egg production of *A. obliqua*.

KEY WORDS: Oviposition behavior, selection of hosts, fruit fly, male absence

Most of the studies using holometabolous insects are directed to the immature stages and they involve the performance of larvae on different hosts and less frequently provide information regarding oviposition behavior (Krainacker *et al.* 1987). Research concerning this subject faces many difficulties in the experimental design, especially those performed under natural conditions, mainly due to the presence of predators, competition between females, host availability and weather variations (Thompson & Pellmyr 1991).

The majority of female insects find and approach their host plants in response to several stimuli, such as, feeding attractants, search for mates and resting sites, as well as the response to the oviposition stimuli (Díaz-Fleischer *et al.* 1999). Oviposition preference is a way of maternal investing; the females spend time and energy in such activity, which may result or not in providing the offspring development (Krainacker *et al.* 1987). The major hypothesis of the evolution of oviposition behavior is that the females would choose species of plants that could maximize larval survival and growth (Thompson & Pellmyr 1991). However, other factors besides the offspring development are involved in the choice of the oviposition site (Mayhew 2001). Studies on *Ascia monuste* (Godart) (Lepidoptera: Pieridae) showed that even though the apical region of the kale leaf was the most adequate for the offspring development, the choice of this region as an oviposition site is determined by the presence or the absence of predators (Catta-Preta & Zucoloto 2003).

Among the generalist tephritids, oviposition on hosts unsuitable for the development of the immatures is a common behavior (Krainacker *et al.* 1987). Few studies are available regarding the oviposition behavior of the tephritids; it is well known that specialists respond more positively to chemical compounds of host plants than generalists (Díaz-Fleischer *et al.* 1999). The types of nutrients associated to hosts which are attractive to females and which determine the choice of the oviposition site are not often studied in detail (Diaz-Fleischer *et al.* 1999). Similarly, studies on female choice for oviposition sites and offspring development are also rare (Thompson 1988).

Aluja *et al.* (2001) observed that egg production in *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) might be stimulated by the male presence, with no need of copulation. In *Ceratitis capitata* (Wied.) (Diptera: Tephritidae), the male presence changes the female behavior from foraging to the search for oviposition sites (Jang 1995). The influence of the male on the behavior and physiology of the female is not completely understood for *A. obliqua* and seems to have very important ecological relationships and implications for the knowledge of this species' biology.

Some species of fruit flies become more attracted to sugar and protein when fed on items poor in these nutrients (Cresoni-Pereira & Zucoloto 2001, Cohen & Voet 2002, Fontellas & Zucoloto 2003). However, whether this condition is also applicable to the selection of oviposition sites is not very clear. Our objective was to evaluate some variables in the selection behavior of *A. obliqua* in relation to oviposition sites containing different nutrients. The male presence and the nutritional status of the females are some of the factors that were also analyzed in this work.

Material and Methods

Biological Material. Pupae were obtained from *Spondias lutea* L. and *Spondias dulcis* L. fruits, Ribeirão Preto Campus, USP, and Estação Experimental do Instituto Agronômico de Campinas (S 21°17' and 75", W 47°81' and 2"), Ribeirão Preto, SP, Brazil. After emergence, the adults were separated at random in the experimental groups.

Selection Between Different Pairings of Oviposition Substrates by Females of *A. obliqua* Kept Without Males. The diet supplied to the females consisted of 6.5 g brewer's yeast (Boneg, Juiz de Fora, Brazil), 11 g sucrose (Synth, Diadema, Brazil), 100 ml distilled water, 2.5 g agar-agar (Merck, Darmstadt, Brazil), and 1.5 ml Nipagin (methylparaben, Merck) in 20% alcohol, prepared as described by Fontellas e Zucoloto (1999). The females had free access to water and to the diet.

Newly emerged females were kept in plastic boxes (20 x 13.5 x 13.5 cm) from emergence to the end of the experiment. Holes on the plastic boxes were covered with a 15-cm long nylon mesh, allowing for internal handling and preventing the females from escaping.

The oviposition substrates were prepared as follows: a) agar substrate = 100 ml distilled water and 3 g agar-agar; b) sucrose substrate = 100 ml distilled water, 3 g agar-agar and 11 g sucrose; c) protein substrate = 100 ml distilled water, 3 g agar-agar and 6.5g brewer's yeast; and d) protein + sucrose substrate = 100 ml distilled water, 3 g agar-agar, 11 g sucrose and 6.5 g brewer's yeast.

Each mixture was placed into 3-cm diameter x 1.5-cm wide plastic plates. The procedure used to prepare the substrates was the same used for the diets, except for the absence of Nipagin.

Each substrate was covered with Parafilm® in the attempt to provide a slight resistance to the females' ovipositor, as it happens on the surface of the host fruits. The artificial substrates were placed in plastic boxes, from the 17th day on, when oviposition begun. The substrates were daily replaced by new ones and the old ones were stored in the freezer for further egg counting.

The following pairings of artificial substrates were offered to the females: PS (protein + sucrose) x A (agar); PS (protein + sucrose) x P (protein); PS (protein + sucrose) x S (sucrose); P (protein) x S (sucrose); and S (sucrose) x A (agar). Ten replicates were performed for each substrate pairing with 10 females in each plastic box. The experiment was carried out for 20 days from the beginning of the egg laying, so that all the females were still young at the moment of choice.

The t-test (Sigma Stat for Windows, 1994- Jandel Corporation, California) with P = 0.05 was used for the statistical analysis of all the results.

Selection Between the Two Substrates by Females Kept in Different Conditions. Standard diet: The diet was prepared similarly to the preceding one, except for the fact that the brewer's yeast and the sucrose were offered concurrently, in separate pieces. Sucrose diet: 11 g sucrose, 100 ml distilled water, 2.5g agar-agar and 1.5 ml Nipagin. Protein diet: 6.5 g brewer's yeast, 100 ml distilled water, 2.5g agar-agar and 1.5 ml

Nipagin. Low sucrose diet: the difference between this diet and the sucrose diet is the sucrose content, which was reduced to 3.5g.

The influence of the male absence on the choice of the oviposition substrate by the females was tested in this experiment. The females were placed to select only between substrates containing brewer's yeast and substrates containing sucrose. Eight females were placed in each box, and the experiment was carried out until all females were dead. Diets were offered in separate pieces of yeast diet and sucrose diet.

Females fed on a standard diet and kept in the presence of males were also studied. The procedure was the same adopted in the preceding experiment, except that the males were confined with the females. The same number of males and females were placed in each box, with the diets protein and sucrose, in separate pieces. The experiment was carried out until all the females were dead.

The behavior of females fed on low sucrose diet and kept in the male presence was also studied, in order to verify whether low dietary energy supply might influence the choice of the oviposition substrate. Such diet was offered in separate pieces of yeast and sucrose, because the females would not survive in a homogeneous mixture with yeast, in such sucrose concentration (see discussion in Fontellas & Zucoloto 2003). When the diet is supplied in separate pieces, the females are able to regulate yeast and sucrose ingestion, assuring survival and egg production (Cresoni-Pereira & Zucoloto 2001).

The males were placed in the same recipient as the females, although in a smaller box (5 x 4 x 4 cm) provided with lateral holes through which diet and water were offered. The top of the box, made of transparent acrylic, was covered with a thin nylon mesh, preventing the females to get in touch with the male's diet.

Females fed on a diet of low sucrose content and kept in the absence of males were also studied. In this experiment the females were submitted to two adverse conditions: reduction of energy supply and male absence. The objective was to analyze whether or not the females would change the oviposition site selection in these adverse conditions.

The t-test (Sigma Stat for Windows, 1994- Jandel Corporation, California) with P = 0.05 was used for the statistical analysis of all the results.

Results

Selection Between Different Pairings of Oviposition Substrates by Females of *A. obliqua* Kept Without Males. *A. obliqua* showed higher preference to oviposit on substrates containing brewer's yeast and sucrose together, rather than on substrates containing only yeast. The substrate containing no nutrients (agar) was the least accepted. When both brewer's yeast and sucrose substrates were offered, the females selected the yeast substrate. Between yeast plus sucrose and sucrose alone, the females selected the substrate containing both sugar and yeast; the same choice was made for the pairing yeast plus sucrose and yeast alone. The sucrose substrate was selected only when it was paired with the agar substrate. This substrate, although showing some egg laying, was never selected (Table 1).

Table 1. Number of eggs deposited by females of *A. obliqua* on different oviposition substrates. The females were placed to select between two substrates, totaling five pairings, in laboratory. (L14:D10 photocycle, 28 ± 2°C and 75 % RH)

Pairings	Average (± SD) of eggs in each oviposition site
P	45.5 ± 13.26 a
S	10.8 ± 2.54 b
S	12.9 ± 5.27 a
PS	54.6 ± 16.04 b
A	11.2 ± 4.59 a
PS	34.8 ± 6.72 b
S	15.1 ± 6.37 a
A	10.2 ± 2.05 b
P	28.2 ± 6.87 a
PS	31.9 ± 5.19 b

S = sucrose, P = protein, PS = protein + sucrose and **A** = agar-agar Comparisons are valid for each pair P x S, S x PS, A x PS, S x A and P x PS. Different letters between pairs show significant difference (t-test, P = 0.05).

The total number of eggs laid in each pairing was higher in the substrates containing both yeast and sucrose. The pairing sucrose and agar resulted in the lower number of eggs laid in all pairings (Table 1). When the sucrose substrate was paired with protein and protein plus sucrose, the amount of eggs found in the sucrose substrate was very similar to the agar substrate. An increase on the amount of eggs deposited in sucrose substrate was only observed when this substrate was paired with agar.

Selection Between the Two Substrates by Females Kept in Different Conditions. In this experiment it was also evident that between yeast and sucrose, the yeast is preferred as oviposition site. The physiological status of females and the absence of males did not change this choice (Table 2). Females fed on the standard diet in the male presence laid more eggs on the yeast than the females fed on the same diet, but without males. Females fed on low sucrose diet and kept in the male presence laid less eggs on the sucrose substrate than the females fed on the same diet and kept without males. The number of eggs laid by females kept without males and fed on a standard diet was very similar to the one presented by females kept with males and fed on a diet poor in sucrose (Table 2).

Discussion

The total number of eggs found in the substrates containing yeast was significantly higher, twice as many on average, compared to the number of eggs laid in the substrates without this item. Such situation may be related to at least

Table 2. Number of eggs deposited by *A. obliqua* on artificial oviposition substrates containing protein or sucrose under the following conditions: females fed with diet with low content of sucrose kept with or without males and females fed with regular diet also kept with or without males. (L14:D10 photocycle, 28 ± 2°C, 75 % RH)

Oviposition substrate	Diet with low content of sucrose		Standard diet	
	Females	Males and females	Females	Males and females
Protein	15.1 ± 11.95 a	16.4 ± 6.89 a	15.4 ± 3.74 a	31.7 ± 10.96 a
Sucrose	9.6 ± 10.24 b	3.3 ± 2.49 b	4.8 ± 2.10 b	7.5 ± 1.92 b

Different letters between pairs in the same column show significant difference (t-test, P = 0.05).

two factors: 1 – the presence of protein in the yeast stimulates oviposition, considering that nutrient is essential in adult feeding for egg production (Braga & Zucoloto 1981), 2 - protein is essential for larval development, and the absence of this nutrient may result in eggs retained inside the female. Although an artificial diet, effective to maintain several generations of *A. obliqua* in the laboratory, was not yet developed, preceding tests showed that newly emerged larvae kept on artificial diet containing only sucrose could not survive longer than two days, while diets containing only yeast assured larvae survival until adult emergence (T. M.L. Fontellas-Brandalha & F.S. Zucoloto unpublish. data).

The fact that egg laying increased when the protein was present in at least one substrate may show a positive correlation between the choice of protein and oviposition. Similar results were obtained with *Pieris rapae* L., which laid more eggs on kale, the most acceptable host for the immatures, than on wallflower, the least acceptable host (Hopkins & van Loon 2001). Even though the tests with lepidopteran were acceptability tests rather than choice tests, both behavior responses may be understood through the same process.

The selection of oviposition substrate containing yeast plus sucrose, when paired with the substrate containing only yeast, may also be related to the offspring development. In the initial stage of the larvae development, protein is the most required nutrient, but both nutrients (sucrose and protein) are required to complete the larval stage (Zucoloto 1987). In some species of insects, for example some lepidopteran, sugar is not essential for the development of the larval stage; however when sugar is added to the diet, the number of individuals to complete the larval cycle increases (Savopoulou-Soultani *et al.* 1994).

The higher amount of laid eggs in the substrate containing yeast plus sucrose may also be understood through the relationship with the adult's diet and not necessarily with the offspring success. The substrate yeast plus sucrose presents nutritional value similar to the food source used by the adult during the whole experiment and such similarity may have influenced the females' choice.

Studies on *C. capitata* reared in laboratory showed that the mechanisms involved in the discrimination among hosts are not very refined, many times resulting in laying that do not assure the survival of the immatures. Such non-discriminatory characteristic expands the hosts range; occasionally, some larva may present physiologic and genetic characteristics, which allow for the adaptation to new hosts (Krainacker *et al.* 1987). This fact would explain the eggs found on agar substrate.

Wild *A. obliqua* may also present a non-adaptive oviposition behavior, as well as *C. capitata* kept under laboratory conditions, which would lay eggs in substrates without any nutritional stimulus (Schwartz *et al.* 1981). Furthermore, although there were eggs in the agar, the total number of eggs in the pairings in which the agar was present was smaller than in other pairings. Hosts of low nutritional quality for larvae seem to reduce egg production in several species of insects (Fletcher *et al.* 1978).

Aluja *et al.* (2001) observed that the presence of hosts and their volatile substances are important for ovarian maturation of *A. obliqua*. In addition, the presence of ripe fruits also influences the females' oviposition decision, probably due to the sugar content (Fernandes-da-Silva & Zucoloto 1997, Díaz-Fleischer & Aluja 2003). So, according to our results, the protein is the nutrient that most stimulates oviposition. Why, if carbohydrate is also stimulating and the most abundant in the fruits?

The answer to this question is probably related to minimizing the energy costs in the search for hosts. Sucrose is an important carbohydrate which is present in most food sources and, therefore, widely distributed in nature (Dadd 1985). Thus it becomes a quite inaccurate chemical clue for host acceptance (Zucoloto 2000).

We believe that the discussion presented by Díaz-Fleischer and Aluja (2003) regarding the oviposition behavior of *Anastrepha ludens* (Loew) is also applicable to what was observed for *A. obliqua*. Ripe fruits, with higher sugar content, are more attractive and susceptible to predation by vertebrates, occasionally leading to larva's death. So, the lower attraction for sucrose may be an adaptive characteristic and probably an attempt to assure offspring survival. Therefore, when insects lay eggs on lower sugar content fruits (unripe fruits), despite the higher toxicity, it is possible that more larvae survive in this toxic environment than when vulnerable to predators. These aspects must be subjects of further research in order to analyze whether or not there is an adaptive relation between the amount of laid eggs both on unripe and ripe fruits and the offspring success (Díaz-Fleischer & Aluja 2003).

Regarding the second experiment, the hypothesis that the condition of the females fed on a diet of low sucrose content and the male absence could influence the choice of the oviposition substrate was not confirmed. It was expected that females with less energy would lay a lower number of eggs and would not show preference for any kind of substrate. However, the females preferred the substrate containing yeast and the male absence did not influence the amount of eggs laid.

Females fed on the standard diet and kept without males laid less eggs in comparison with the females fed on the same diet and kept with males. The females kept with males laid, approximately, twice as many eggs when compared to the females kept without males. Male absence may have caused an egg re-absorption process. This process probably provides some energy saving, which might be spent on other activities, such as the search for sites where males can be found.

Yuval *et al.* (1998) found out that the females of *C. capitata* use nutrients, especially protein of the sperm which is transferred from the males after copulation. However, the amount of protein provided by the diet in this experiment is enough for egg production, as demonstrated in other papers (Cresoni-Pereira & Zucoloto 2001, Kaspi *et al.* 2002). Therefore, it is more likely that the females kept without males have the eggs re-absorbed or retained than that females kept with males have had an additional gain of proteins transferred by the males.

When females were fed on low sucrose diet, such behavior was not evident. Probably, both groups of females (with or without males) have their eggs re-absorbed or retained, due to the low energy provided by the diet. Even though the amount of eggs have not distinguished females fed on of low sucrose diet, the females kept with males laid less eggs in the substrate containing sucrose when compared to the females kept without males. At least in the initial phase of the larval development, the sucrose does not support the survival of the immature ones, as it was previously discussed. This behavior seems to indicate that when males are present, the females select more adequate hosts for the offspring survival.

Our results show that the preference for substrates containing protein is outstanding. The importance of protein in the adult's diet for the egg production was already quite emphasized in many species of tephritidae (Tsiropoulos 1992, Mangan 2003). The importance of the protein as a host marker or as an important nutrient for the larval development should be better analyzed, especially for *A. obliqua*, whose records in relation to these aspects are yet quite a few.

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