ECOLOGY, BEHAVIOR AND BIONOMICS

Effect of Sucrose Ingestion on the Performance of Wild *Anastrepha obliqua* (Macquart) Females (Diptera: Tephritidae)

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Efeito da Ingestão de Sacarose no Desempenho de Fêmeas Selvagens de *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae)

RESUMO - Os carboidratos representam a maior fonte de energia para os insetos, e sua carência na alimentação pode causar sérios danos à biologia desses artrópodos. No sentido de obter uma melhor compreensão a cerca da influência da sacarose no desempenho e seleção de alimentos em adultos de *Anastrepha obliqua* (Macquart)*, foram elaborados os seguintes experimentos: 1- influência de diferentes quantidades de sacarose sobre o consumo da dieta, longevidade e produção de óvulos; 2- seleção de dietas com diferentes quantidades de sacarose; 3- limiar de discriminação para sacarose de adultos alimentados e não alimentados de carboidrato. A dieta controle proporcionou o maior consumo da dieta, longevidade e produção de óvulos para essa espécie, provavelmente, devido ao fato de essa dieta apresentar um equilíbrio nutricional ótimo entre sacarose e levedo. A dieta controle também foi a escolhida pelas fêmeas, no teste de seleção de dietas, indicando uma correlação positiva entre o valor nutritivo do tratamento e a percepção química de *A. obliqua*. As fêmeas que não foram alimentadas de sacarose foram capazes de perceber o carboidrato em quantidade menor do que as fêmeas que foram alimentadas. Essa percepção pode representar uma vantagem biológica, uma vez que pode diminuir o tempo de procura por alimento desses insetos.

PALAVRAS-CHAVE: Insecta, nutrição, limiar de discriminação, mosca-das-frutas, seleção de dietas

ABSTRACT - Carbohydrates are the main source of energy for insects and the lack of these nutrients in the diet can cause serious damage to the biology of these arthropods. In order to better understand the effect of sucrose on the performance and dietary selection of adult *Anastrepha obliqua* (Macquart), the following experiments were carried out: 1) effect of different amount of sucrose on diet ingestion, longevity and egg production; 2) dietary selection that contains different amounts of sucrose, and 3) discrimination threshold for sucrose in adult individuals deprived or not of carbohydrates. The control diet showed the best results in relation to ingestion, longevity and egg production for these species, probably due to the fact that it presents an optimal nutritional balance between sucrose and yeast. The control diet was also the preferred diet of females, indicating a positive correlation between the nutritional value of a diet and chemical perception by *A. obliqua*. Sucrose-deprived females were able to perceive lower carbohydrate quantity than non-deprived females. This characteristic might represent a biological advantage since it reduces the food foraging time for these insects.

KEY WORDS: Insect, nutrition, discrimination threshold, fruit fly, dietary selection

Carbohydrates are the main nutrient in the insect diet and play an important role in life maintenance in most species (Dadd 1985). These nutrients are a large source of energy for insects, participate in the structural composition of chitin, are phagostimulant, regulate the amount of diet ingested and stimulate oviposition (Nayer & Sauerman 1974, Cangussu & Zucoloto 1995, Joachim-Bravo & Zucoloto 1997).

Depending on the species and on the development stage, carbohydrate shortage in the insect diet might result in a decrease in phagostimulation and metabolic protein deviation (Hsiao 1985, Slansky & Rodrigues 1987, Simpson *et al.* 1995). The feeding behavior can be altered by carbohydrate deficiency, because the functioning and structure of neuroreceptors responsible for the perception and adequate selection of diets are modified (Hendricks *et al.* 1990, Robacker 1991). Adult *Ceratitis capitata* (Wied.) individuals

deprived of carbohydrates during the larval phase showed a ten times higher sucrose discrimination threshold than the control group, indicating that carbohydrate ingestion during the immature phase is important for the development of neuroreceptors, or even for the development of specific chemoreceptors (Canato & Zucoloto 1998).

Food ingestion can also be altered because of carbohydrate shortage in the insect diet. Several studies have shown that insects compensate for diets with low carbohydrate concentrations by ingesting larger amounts of the diet or by foraging for other diets with a higher concentration of these nutrients (Simpson *et al*. 1995), as demonstrated for *C. capitata* (Nestel *et al*. 1985) and *Anastrepha obliqua* (Macquart) (Fontellas & Zucoloto 1999). When the diet has a higher carbohydrate concentration than that required by the insect, excess carbohydrate is eliminated through respiration as demonstrated for the grasshopper *Locusta migratoria* L. (Zanotto *et al*. 1993).

Although most tephritid species depend on protein ingestion for egg production during the adult phase, studies have shown that carbohydrate ingestion is also related to egg production (Robacker 1991, Landolt & Davis-Hernandez 1993). *Anastrepha suspensa* (Loew) and *C. capitata* males deprived of sugar show a marked decrease in sexual pheromones, although the cause of this finding is unknown (Landolt & Sivinski 1992, Landolt *et al*. 1992). Adult *A. obliqua* females do not produce eggs if the diet lacks a protein source (Braga & Zucoloto 1981) and do not survive more than three days without a sugar source (Fontellas & Zucoloto 1999), indicating a strong dependence on these two nutrients for both survival and egg production. The specific effects of carbohydrate deficiency on fruit flies are not completely understood, but, in general, the absence of this nutrient reduces their activities such as dispersal and foraging food behavior probably due to a lack of energy (Landolt & Davis-Hernandez 1993).

In order to better understand the effect of sucrose on the performance and dietary selection of *A. obliqua* adults, the following experiments were carried out: 1) effect of different amount of sucrose on diet ingestion, adult longevity and egg production; 2) dietary selection that contain different amounts of sucrose, and 3) discrimination threshold for sucrose in adult individuals deprived or not of carbohydrates.

Material and Methods

Isolation of Adult *A. obliqua* Females. Wild adult *A. obliqua* individuals were collected from *Spondias lutea* L. and *Spondias dulcis* G. Forst fruits, on the Ribeirão Preto Campus, USP, and experimental station of the Instituto Agronômico de Campinas (S 21°17' and 75", W 47°81' and 2"), Ribeirão Preto, SP, Brazil. When adults emerged, females were randomly separated and placed in acrylic boxes (11 x 11 x 3 cm) containing four lateral holes (one on each side) measuring ±1 cm in diameter, through which water and diet were offered. No males were included in any of the experiments in order to have a precise control of the relationship between egg production and diet ingestion, since the presence of males is not required for egg production or oviposition in this species.

The Artifical Control Diet. The control diet used throughout the study consisted of 6.5 g brewer's yeast (Boneg, Juiz de Fora, Brazil), 11 g sucrose (Synth, Diadema, Brazil), 100 ml distilled water, 3 g agar-agar (Merck, Darmstadt, Brazil), and 1.5 ml nipagin (methylparaben, Merck) in 20% alcohol.

Sucrose was chosen as the carbohydrate to be tested mainly because it represents a universal phagostimulating sugar for insects (Hsiao 1985), and is of nutritional value for most insect species studied (Dadd 1985), including *A. obliqua* (Fontellas & Zucoloto 1999).

Food Ingestion Determination. Food ingestion and the number of females placed in each box were the same for all experiments. Food pieces were offered to the flies using entomologic pins fixed to cork measuring about 1 cm in diameter (Cangussu & Zucoloto 1992) and fitted into two of the four lateral holes of the box. Water was offered in small test tubes (5 cm long and 1 cm diameter) sealed with cotton and placed in the other two holes of the box. Recently emerged females (10 females/box) had free access to the diets (initial weight 400 mg) which were changed every 24h; after 24h, the diets were dried in an electric incubator for an additional 24h and weighed. Control boxes without flies were used to obtain total dry weight of the diet (Cangussu & Zucoloto 1995). Diet ingestion was determined according to the following formula: I = TDM-RDM/N, where I = ingestion, TDM = total dry matter, RDM = remaining dry matter, and N = number of live flies in the box. All rates are reported as mg.

All experiments were carried out in a laboratory under conditions of L14:D10 photocycle using a 400-lux fluorescent lamp at 28°C to 30°C and about 75% relative humidity. The Sigma Stat for Windows software (Jandel Corporation 1994) was used for all statistical analyses.

Influence of Different Amounts of Sucrose on Diet Ingestion, Longevity and Egg Production in *A. obliqua* at the Sucrose Quantity Tested. Diets containing variable amounts of sucrose: 2, 5, 8, 14, 17g/100 ml diet and diet without sucrose (WS) were tested. Each of these diets was compared to the control diet containing 11 g sucrose, which corresponds to the mean quantity of carbohydrates found in the host fruits (Franco 1982).

Diet ingestion, longevity and egg production were determined for each amount of sucrose. Based on these results, the efficiency of the diet in terms of egg production was calculated. Protein ingestion was obtained based on total diet ingestion according to the formula by Ferro & Zucoloto (1990): mean egg production/protein ingestion/ female. The efficiency of the diet in terms of longevity was also determined: longevity/sucrose ingestion/female. Sucrose ingestion was obtained by the same procedure. Egg production and longevity were shown to be important parameters for the comparison of carbohydrate and protein use by *A. obliqua*.

The boxes were examined daily and dead females were removed to control longevity. Diet ingestion was measured three times per week on alternate days until the death of all females in each box.

Since females started laying eggs in the boxes by the 18th

day, the box was replaced with a new one whenever a female died and live females were transferred to clean boxes. The number of eggs in the boxes was recorded and was reported as laid eggs/female. Dead females were frozen and dissected. The number of eggs observed in their ovaries was reported as eggs in the ovaries/female. Five replicates were carried out for each diet. The t test was used for comparison, with P = 0.05.

Dietary Selection by *A. obliqua* Females. This experiment was divided into part A and part B. In part A, the females were allowed to choose between the control diet and diets containing the different amounts of sucrose established in previou experiment. Each quantity was paired with the control diet and selection was determined by measuring diet ingestion for three days. These experiments permitted the correlation between the nutritional value of the different diets and the preference of the females for these diets. Ten replicates were carried out for each experiment and the Wilcoxon test was used for statistical analysis, with P = 0.05.

Part B differed from part A in only two aspects, i.e., the absence of yeast in the diets and duration of the experiment, which was three and 18 days (thus including the reproductive period). Brewer's yeast is rich in protein and, since protein is important for the insect's biological success (Brewer *et al*. 1985), the presence of protein in the diet might have an influence on food selection.

Only quantities that did not show any significant difference compared to the control diet in part A were paired, thus the following diets were included: control diet without yeast (CD-Y), and diets without yeast containing 8 g (8g-Y), 14 g (14g-Y) and 17 g sucrose (17g-Y). The statistical test and the number of replicates were the same as described for part A.

Discrimination Threshold for Sucrose-Deprived and Non-Deprived Flies. Sucrose deprivation was studied as a variable

that influences the sucrose discrimination threshold of *A. obliqua* females. Food ingestion was measured as previously described. Recently emerged females of the experimental group were maintained without food for three days, while the control group received 11 g sucrose (without yeast) since emergence. Both groups had free access to water throughout the experiment. The discrimination threshold was determined on the third day for both deprived and non-deprived females.

Fontellas & Zucoloto (1999) observed a discrimination threshold of 0.1 g sucrose/100 ml diet for recently emerged females that were not deprived of food. Therefore, in the present experiment the initial sucrose quantity was 0.09 g/100 ml diet, which was reduced to 0.07 g and then to 0.05 g. Mean ingestion was determined per female per day for a period of three days. The mean food ingestion on the first day and the mean food ingestion over three days were compared. Ten replicates were carried out for each experiment and the Wilcoxon test was used for statistical analysis, with P = 0.05.

Results

Influence of Different Amounts of Sucrose on Diet Ingestion, Longevity and Egg Production in *A. obliqua* at the Sucrose Quantity Tested. The diet containing 5 g sucrose provided the highest total food ingestion and the largest number of eggs in the ovaries compared to the control diet, while no significant difference with respect to oviposition in the box was observed (Table 1). The shortest time of longevity was observed for the diets without sucrose (WS) and 2 g sucrose, followed by the diet containing 5 g sucrose.

Values similar to those obtained for the control diet were observed for the diet containing 8 g sucrose, except for longevity that was significantly lower.

A smaller number of eggs and a longer survival time were observed for the 17-g diet when compared with the

Table 1. Performance of *A. obliqua* females fed different amounts of sucrose compared with the control diet (CD). All tests were carried out in laboratory under conditions of L14:D10 photocycle at 28 ± 2°C and 75% R.H. The results are reported as mean ± standard deviation for the groups tested.

Diets	Number of eggs in the ovary/ female	Number of laid/ female	Longevity (days)	Sucrose ingestion mg/female/day	Yeast ingestion mg/female/day	Total ingestion mg/female/day	ESL	EPO
WS	0.0 a	0.0 a	5.4 ± 1.67 a	0.0 a	0.5 ± 0.13 a	0.7 ± 0.18 a	0.0 a	0.0 a
CD	18.0 ± 4.56 b	3.3 ± 3.30 b	63.2 ± 25.72 b	1.0 ± 0.20 b	0.6 ± 0.12 a	1.9 ± 0.38 b	61.4 ± 19.9 b	0.8 ± 0.53 b
2-g	0.0 a	0.0 a	7.8 ± 3.63 a	0.2 ± 0.13 a	0.6 ± 0.44 a	1.1 ± 0.78 a	40.7 ± 15.75 a	0.0 a
CD	21.9 ± 7.39 b	1.1 ± 0.98 b	64.6 ± 15.56 b	1.0 ± 0.08 b	0.6 ± 0.05 a	1.8 ± 0.15 a	67.8 ± 19.22 b	0.7 ± 0.37 b
5-g	50.3 ± 31.86 a	3.0 ± 3.20 a	25.2 ± 15.91 a	0.7 ± 0.05 a	0.9 ± 0.07 a	2.1 ± 0.15 a	34.3 ± 19.12 a	1.9 ± 1.92 a
CD	29.2 ± 18.85 b	2.8 ± 0.82 a	91.6 ± 16.35 b	0.9 ± 0.08 b	0.5 ± 0.05 b	1.7 ± 0.16 b	103.0 ± 16.86 b	1.0 ± 0.66 b
8-g	15.9 ± 11.62 a	1.5 ± 1.06 a	60.0 ± 17.19 a	0.7 ± 0.08 a	0.6 ± 0.06 a	1.6 ± 0.16 a	80.4 ± 17.65 a	0.5 ± 0.31 a
CD	14.9 ± 5.96 a	1.4 ± 0.69 a	111.0 ± 24.17 b	1.0 ± 0.23 a	0.6 ± 0.14 a	1.8 ± 0.43 a	117.3 ± 16.78 b	0.4 ± 0.08 a
14-g	7.5 ± 1.85 a	0.8 ± 0.55 a	90.8 ± 16.18 a	0.8 ± 0.14 a	0.4 ± 0.07 a	1.4 ± 0.24 a	77.1 ± 24.59 a	0.2 ± 0.12 a
CD	16.9 ± 6.66 b	2.4 ± 1.52 a	84.0 ± 25.23 a	1.1 ± 0.04 b	0.6 ± 0.03 b	2.0 ± 0.09 b	113.9 ± 17.17 b	0.5 ± 0.20 b
17-g	5.6 ± 3.89 a	0.3 ± 0.24 a	119.4 ± 9.80 a	0.9 ± 0.05 a	0.3 ± 0.02 a	1.4 ± 0.09 a	134.1 ± 15.72 a	0.1 ± 0.10 a
CD	19.3 ± 10.63 b	1.7 ± 1.03 b	85.8 ± 20.66 b	0.9 ± 0.26 a	0.6 ± 0.15 a	1.8 ± 0.49 b	91.9 ± 7.56 b	0.8 ± 0.88 b

The means of pairs followed by different letters are significantly different (t test, P = 0.05).
ESL = Efficiency of sucrose ingestion in terms of longevity.
EPO = Efficiency of protein ingestion in terms of egg production

control diet and with the other amounts of sucrose. The diet containing 14 g sucrose showed results similar to those observed for the 17-g diet, although no significant difference was found between the 14-g diet and the control diet with respect to longevity.

Dietary Selection by *A. obliqua* Females. Part A. Comparing the control diet and the diets WS, 2 and 5 g sucrose, a preference was observed for the diet with the higher sucrose content, i.e., the control diet. No significant preference was observed for the other pairs (Fig. 1).

Part B. There was no significant difference in dietary selection between the 14g-Y and CD-Y diets at either time (3 and 18 days), similar to the results obtained in part A (Fig. 2). Comparison of the CD-Y and 8g-Y diets showed a

preference for the CD-Y diet during the first three days but not at 18 days. With respect to the 17g-Y and CD-Y diets, females preferred the diet with the higher carbohydrate content (17g-Y) at both time points.

Discrimination Threshold for Sucrose-Deprived and Non-Deprived Flies. The sucrose-deprived flies perceived a lower amount of sucrose after emergence than non-deprived flies (Table 2). On the first day of the experiment, deprived flies showed a threshold of 0.07 g sucrose/100 ml diet, while this value was higher than 0.09 g sucrose/100 ml diet for non-deprived flies. When analyzing the mean food ingestion of three days, no significant difference in the discrimination threshold was observed between deprived and non-deprived flies (0.09 g sucrose/100 ml diet for both groups).
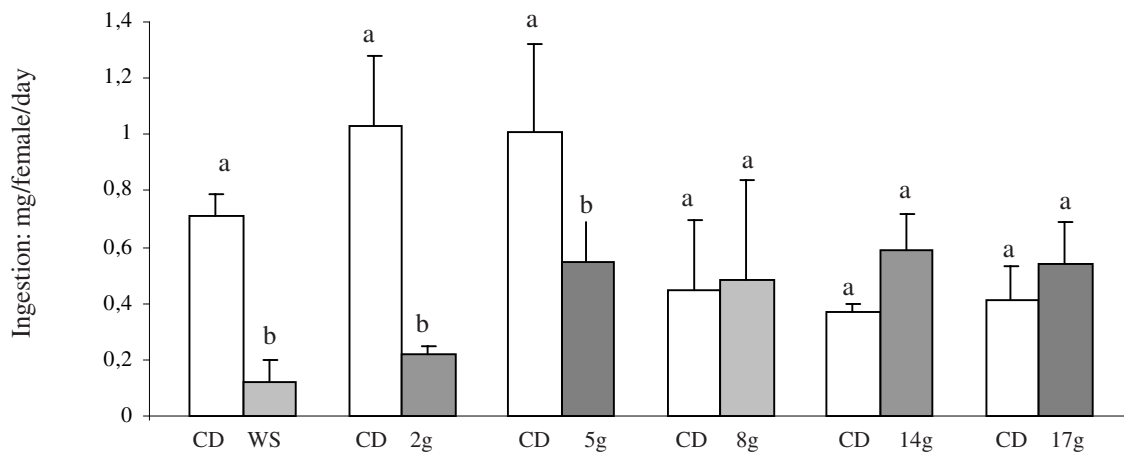

Figure 1. Selection by *A. obliqua* females between the control diet (CD) and diets containing different concentrations of sucrose per 100 ml diet (all containing brewer's yeast) evaluated over a period of three days. All tests were carried out in laboratory under conditions L14:D10 photocycle at 28 ± 2°C and 75% R.H. The results are reported as mean ± standard deviation for the groups tested. Different letters between pairs indicate significant differences (Wilcoxon, P = 0.05).
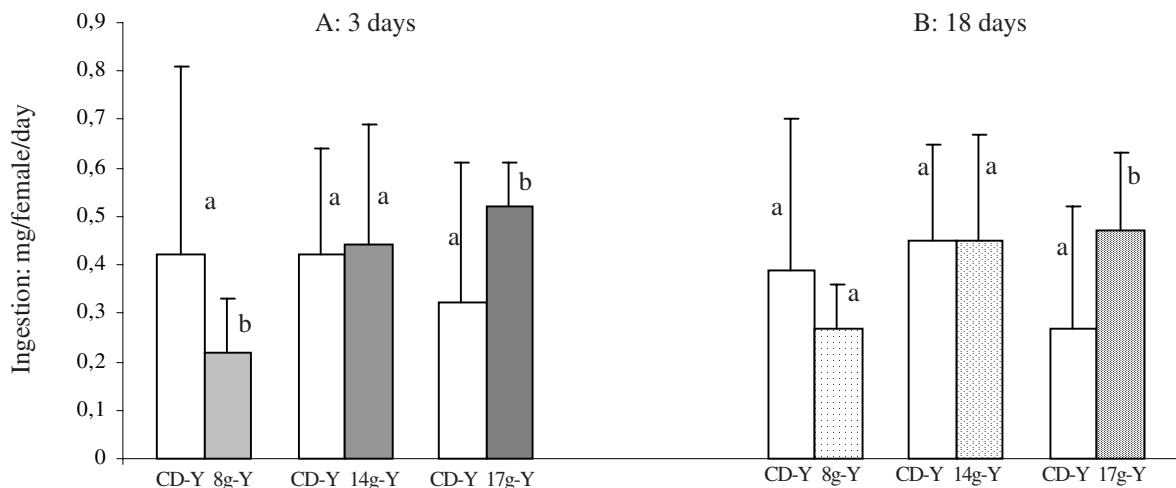

Figure 2. Selection by *A. obliqua* females between the control diet without yeast (CD-Y) and diets without yeast containing 8, 14 and 17 g sucrose/100 ml diet. All tests were carried out in the laboratory under conditions of L14:D10 photocycle at 28 ± 2°C and 75% R.H. The results are reported as mean ± standard deviation for the groups tested for three days (A) and the groups tested for 18 days (B). Different letters between pairs indicate significant differences (Wilcoxon, P = 0.05).

Table 2. Discrimination threshold between the diet without sucrose (agar) and the test diets obtained for *A. obliqua* females deprived or not of food after emergence. All tests were carried out in laboratory under conditions of L14:D10 photocycle at 28 ± 2°C and 75% R.H. The results are reported as mean ± standard deviation for the groups tested.

Groups	Amounts of sucrose (g/100 ml of diet)	Mean ingestion on the first day		Mean ingestion for the three days	
		Sucrose diet ingestion (mg/female/day)	Agar diet ingestion (mg/female/day)	Sucrose diet ingestion (mg/female/day)	Agar diet ingestion (mg/female/day)
Deprived flies	0.09	0.052 ± 0.030 b	0.003 ± 0.005 a	0.091 ± 0.054 b	0.003 ± 0.003 a
	0.07	0.201 ±0.111 b	0.007 ± 0.022 a	0.101 ± 0.10 a	0.222 ± 0.187 a
	0.05	0.004 ± 0.013 b	0.048 ± 0.06 a	0.196 ± 0.326 a	0.058 ± 0.016 a
Non-deprived flies	0.09	0 b	0.003 ± 0.010 a	0.019 ± 0.017 b	0.002 ± 0.001 a
	0.07	0.012 ± 0.021 a	0.006 ± 0.013 a	0.041 ± 0.040 a	0.029 ± 0.038 a
	0.05	0 b	0.036 ± 0.046 a	0.059 ± 0.097 a	0.018 ± 0.016 a

Different letters between pairs indicate significant differences (Wilcoxon, P = 0.05).

Discussion

The diets containing 2 g sucrose and WS (without sucrose) were found to have the lowest nutritional value for *A. obliqua* females. Although these diets were deficient in sucrose, the protein content was the same as that of the other diets and, therefore, survival longer than seven days was observed for flies ingesting these two diets. *A. obliqua*, like *C. capitata*, does not use protein or uses it poorly as an alternative energy source during the adult phase (Cangussu & Zucoloto 1992). Romeis & Wäckers (2002) observed that amino acid consumption by *Pieris brassicae* L. also had no influence on the longevity of these insects. It is possible that in these species protein is mainly or exclusively intended for the reproductive system and growth during the immature phase.

Yeast ingestion for the 2-g diet was similar to that observed for the 5-g diet. However, despite this similarity in yeast ingestion, the energy provided by the 2-g sucrose diet was insufficient to keep the flies alive until the reproductive phase, thus impairing egg production. *A. obliqua* needs to ingest sucrose amounts higher than 2 g/100 ml diet to guarantee its survival until the reproductive phase. This characteristic dependence on carbohydrate during the adult phase for a rapid energy supply is even more evident in some lepidopterans, which basically feed on carbohydrates (nectar) during the adult phase and use protein stored during the larval phase for egg production (Wheeler *et al*. 2000). In addition, since carbohydrates are not a rare nutrient compared to others such as protein, it is possible that *A. obliqua* did not suffer selective pressure in terms of the use of lower amounts of carbohydrates, or amounts close to 5 g.

The total amount of diet consumed was higher for the 5-g diet than for the 8-g diet; however, sucrose ingestion was similar for the two diets. The higher ingestion of the 5-g diet probably demonstrates a compensatory behavior with respect to the low amount of sucrose. Since *A. obliqua* is a generalist species (during the adult phase), it is probably able to regulate food ingestion according to the composition of the diet in such a way as to favor nutritional gain. Although this compensatory behavior provided sucrose

ingestion similar to that of the diet containing 8 g sucrose, longevity was low. Furthermore, as a consequence of compensation, the females also consumed more protein and, therefore, produced more eggs. These females probably spent more energy producing eggs and thus lived less. The mechanisms involved in the regulation of the amount of diet ingested in the present experiments are still not completely understood.

Although a larger number of eggs in the ovaries per female was observed upon dissection for the diet containing 5 g sucrose, the number of eggs laid in the boxes did not differ significantly from that observed for the control diet. The amount of energy provided by the 5-g diet was not sufficient to provide large egg production plus the energy spent with oviposition.

The opposite was observed for the diet containing a high amount of sucrose (17 g); females lived longer and produced fewer eggs compared to controls. The increased longevity provided by this diet was possibly due to the absence of energy deviation for egg production. In addition, it is possible that yeast ingestion within this proportion was insufficient to satisfy the energy demand necessary for egg production.

The diet containing 14 g sucrose showed intermediate results between those obtained with the 17-g and control diets. Females fed on the 14-g diet consumed less food (total ingestion) and, consequently, less sucrose compared to controls. Concentrated sucrose solutions take a longer period of time for crop emptying than less concentrated solutions (Simpson *et al*. 1989), although in the present study the diets were not offered in solution. In addition, Savopoulou-Soultani *et al*. (1994), in a study on *Lobesia botrana* (Denis & Schiffermüller) (Lepidoptera: Tortricidae), showed that very high carbohydrate concentrations reduce the phagostimulating potential of this nutrient. Although ingestion of the 14-g and 17-g diets was lower than that of the control diet, the longevity of the females fed on these diets was higher, probably due to the absence of energy expenditure for egg production as discussed earlier for the 17-g diet. Romeis & Wäckers (2002) also mentioned this aspect: females that produce fewer eggs have more energy to satisfy their basic metabolic needs and, thus, show increased survival.

The control diet showed the best results and its sucrose

and yeast proportion (1:1 or 2:1) was close to that reported to guarantee an "optimal nutritional" balance (Savopoulou-Soultani *et al*. 1994, Cresoni-Pereira & Zucoloto 2001). In addition, this diet was the preferred diet of females in experiment 2 (part A) when compared to the diets containing 5-g sucrose and WS, indicating a positive correlation between the nutritional value of a diet and chemical perception by *A. obliqua* (Fig. 1).

In experiment dietary selection (part A), the absence of preference of females for the 8-g and 17-g diets can be attributed to the interference of yeast. Brewer's yeast is rich in protein and free amino acids and since protein is an important nutrient for the success of insects (Brewer *et al*. 1985), its presence in the diet may influence dietary preferences. This hypothesis was confirmed with the 8g-Y (3 days) and 17g-Y diets that showed significant differences compared to the CD-Y diet after protein removal (Fig. 2). Another possibility is the attempt of females to consume diets combining the proportions of sucrose and yeast, masking the selection of any of the diets above 8 g sucrose. This behavior of ingesting a diet that provides the best nutritional gain in view of the variation in food quality has also been observed for the cockroach *Blattella germanica* L., another generalist species (Jones & Raubenheimer 2001).

Sucrose is a highly phagostimulating carbohydrate (Hsiao 1985, Cangussu & Zucoloto 1992, Fontellas & Zucoloto 1999), and this characteristic was confirmed in the present study by the preference of females for the diet with the higher carbohydrate content. It is also possible that these insects were able to perceive and choose diets that provide increased longevity, the main function of carbohydrates (Simpson *et al*. 1989, Wäckers 1999). The lack of a significant difference in the preference for the CD-Y diet and the 8g-Y and 14g-Y diets was probably due to the similar carbohydrate content of these diets.

Obtaining energy that will guarantee longer survival has various advantages: the insect can search for oviposition sites for a longer period of time as shown in studies on other *Anastrepha* species that demonstrated that oviposition and feeding sites do not always coincide (Sugayama *et al*. 1998); the female can search for mating partners for longer periods of time, and greater dispersal is possible, thus reducing the susceptibility to variations in the fructification period of the natural host. Blay & Yuval (1999) observed that *C. capitata* females that lived longer produced more eggs. In addition, *A. obliqua* females were shown to be able to produce eggs after being deprived of protein for 60-90 days during their adult life as soon as a yeast-containing diet was offered (Cresoni-Pereira, personal communication). Although the viability of the eggs was not verified, this fact, together with the preference of females for diets containing more carbohydrate, confers an important adaptive value.

In addition to its capacity to select between diets, *A. obliqua* was also found to perceive lower amounts of sucrose when deprived of this nutrient after emergence. Simpson & Simpson (1990) and Cangussu & Zucoloto (1995) have suggested that deprivation of a certain nutrient may change the discrimination threshold, generally increasing discrimination for this nutrient. In the present study, this behavior was demonstrated in the discrimination threshold for sucrose-deprived and non-deprived flies, when only the first day of the experiment was analyzed. Females deprived of food after emergence discriminated the diet containing 0.07 g sucrose/100 ml diet, while non-deprived flies were unable to discriminate between diets at any of the concentrations tested. This characteristic might represent a biological advantage since it reduces the food foraging time for these insects.

When analyzing the mean food ingestion over three days of the experiment, the discriminatory behavior observed on the first day was altered. Deprived flies started to forage for new food sources (generalist behavior), ingesting more of the agar diet, masking the perception of sucrose at a concentration of 0.07 g/100 ml diet. Simpson & Raubenheimer (1993) postulated that the nutritional status of the insect reflects on its capacity to respond to a given nutrient. After three days, non-deprived flies showed a nutritional deficiency similar to that of deprived flies, thus eliminating the claimed physiological difference between the two groups. Based on these considerations, only the first day was considered for the analysis of behavioral differences regarding the variation in the physiological status (sucrose deprived and non-deprived) of the groups tested.

The behavior of *A. obliqua* in relation to sucrose was the opposite of that observed for the same species in relation to protein (Cresoni-Pereira & Zucoloto 2001). Females deprived of yeast after emergence showed a discrimination threshold similar to that observed for recently emerged females. In the present study, females not deprived of sucrose after emergence showed a discrimination threshold similar to that observed for recently emerged females by Fontellas & Zucoloto (1999), i.e., 0.1 g sucrose/100 ml diet. Cresoni-Pereira & Zucoloto (2001) suggested that recently emerged females use all their protein reserves during transformation from the immature to the adult insect, resulting in a physiological condition similar to that observed for flies deprived of protein after emergence. In this case, it is possible that the carbohydrate reservoir is not exhausted during the transformation process, leading to a similar nutritional condition between recently emerged females and females that were not deprived of sucrose after emergence. After emergence, the insect requires energy for dispersal and exploration of the environment in the search for good food sources, and therefore the acquisition of distinct mechanisms of carbohydrate and protein use is an essential condition for the success of these insects.

Acknowledgments

Literature Cited

Blay, S. & B. Yuval. 1999. Oviposition and fertility in the Mediterranean fruit fly (Diptera: Tephritidae): effects of male and female body size and the availability of sperm. Ann. Entomol. Soc. Am. 92: 278-2849.

Braga, **M.A.S**. **& F.S. Zucoloto. 1981.** Estudos sobre a melhor concentração de aminoácidos para moscas adultas de *Anastrepha obliqua.* Rev. Brasil. Biol. 41: 75-79.

Brewer, **W.J., J.L. Capinera, R.E. Deshon Jr. & M.L. Walmsley. 1985.** Influence of foliar nitrogen levels on survival, development, and reproduction of Western Spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae). Can. Entomol. 117**:** 23-32.

Canato, C.M. & F.S. Zucoloto. 1998. Feeding behavior of *Ceratitis capitata* (Diptera, Tephritidae): influence of carbohydrate ingestion. J. Insect Physiol. 44: 149-155.

Cangussu, J.A. & F.S. Zucoloto. 1992. Nutritional value and selection of different diets by adult *Ceratitis capitata* fruit flies. J. Insect Physiol. 38: 485-491.

Cangussu, J.A. & F.S. Zucoloto. 1995. Self-selection and perception threshold in adult females of *Ceratitis capitata.* J. Insect Physiol. 41: 223-227.

Cresoni-Pereira, C. & F.S. Zucoloto. 2001. Dietary self-selection and discrimination threshold in wild *Anastrepha obliqua* (Diptera, Tephritidae). J. Insect Physiol. 47: 1127-1132.

Dadd, R.H. 1985. Nutrition: Organisms, p. 313-389. In G.A. Kerkut & L.I. Gilbert (eds.)**,** Comprehensive insect physiology, biochemistry and pharmacology. Pergamon Press, Oxford, IV, 1176p.

Ferro, M.I.T. & F.S. Zucoloto. 1990. Influence of amino acid deletion on egg production and egg laying by *Ceratitis capitata.* Rev. Brás. Biol. 51: 407-412.

Franco, G. 1982. Nutrição. Livraria Ateneu, Rio de Janeiro, 227p.

Fontellas, T.M.L. & F.S. Zucoloto. 1999. Nutritive value of diets with different carbohydrates for adult *Anastrepha obliqua* (Macquart) (Diptera, Tephritidae). Rev. Bras. Zool. 16: 1135-1147.

Hendrichs, J.M., J. Hendrichs, J. Prokopy & R.J. Prokopy. 1990. How do apple maggot flies detect the presence of distant food? Massach. Fruit Notes 55: 3-5.

Hsiao, T.H. 1985. Feeding behavior, p. 471-512. In G.A. Kerkut & L.I. Gilbert (eds.), Comprehensive insect physiology, biochemistry and pharmacology. Pergamon Press, Oxford, IV, 1176p.

Joachim-Bravo, I.S. & F.S. Zucoloto. 1997. Oviposition preference in *Ceratitis capitata* (Diptera, Tephritidae): influence of rearing diet. Iheringia Sér. Zool. 82: 133-140.

Jones, S.A. & D. Raubenheimer. 2001. Nutritional regulation in nymphs of the German cockroach, *Blattella germanica*. J. Insect Physiol. 47: 1169-1180.

Landolt, P.J. & J. Sivinski. 1992. Effects of time of day, adult food, and host fruit on incidence of calling by male Caribbean fruit flies (Diptera: Tephritidae). Environ. Entomol. 21: 382-387.

Landolt, P.J. & K.M. Davis-Hernandez. 1993. Temporal patterns of feeding by caribbean fruit flies (Diptera: Tephritidae) on sucrose and hydrolyzed yeast. Ann. Entomol. Soc. Am. 86: 749-755.

Landolt, P.J., R.R. Heath & D.L. Chambers. 1992. Oriented flight responses of female Mediterranean fruit flies to calling males, odor of calling males, and synthetic pheromone blend. Entomol. Exp. Appl. 65: 259-266.

Nayer, J.K & D.M. Sauerman. 1974. Long-term regulation of sucrose intake by the female mosquito *Aedes taeniorhynchus*. J. Insect Physiol. 20: 1203-1208.

Nestel, D., R. Galun & S. Friedman. 1985. Long-term regulation of sucrose intake by tha adult Mediterranean fruit fly *Ceratitis capitata*. J. Insect Physiol. 31: 533-536.

Robacker, D.C. 1991. Specific hunger in *Anastrepha ludens*: effects on attractiveness of proteinaceous and fruit-derived lures. Environ. Entomol. 20: 1680-1686.

Romeis J. & F.L. Wäckers. 2002. Nutritional suitability of individual carbohydrates and amino acids for adult *Pieris brassicae*. Physiol. Entomol. 27: 148-156.

Savopoulou-Soultani, M., D.G. Stavridis, A. Vassiliou, J.E. Stafilidis & I. Iraklidis. 1994. Response of *Lobesia botrana* (Lepidoptera: Tortricidae) to levels of sugar and protein in artificial diets. J. Econ. Entomol. 87: 84-90.

Simpson, S.J. & C.L. Simpson. 1990. The mechanisms of nutritional compensation by phytophagous insects p. 111-160. In E.A. Bernays (ed.), Insect-plant interactions. CRC Press, Boca Raton, 560p.

Simpson, S.J.& D. Raubenheimer. 1993. The central role of the haemolymph in the regulation of nutrient intake in insects. Physiol. Entomol. 18: 395-403.

Simpson, S.J., D. Raubenheimer & P.G. Chambers. 1995. The mechanisms of nutritional homeostasis, p.251-278. In R.F. Chapman & G. de Boer (eds), Regulatory mechanisms in insect feeding. Chapman & Hall, New

York, 876p.

Simpson, S.J., L.B. Barton & A.C.M. van Gerwen. 1989. The patterning of compensatory sugar feeding in the Australian sheep blowfly. Physiol. Entomol. 14: 91-105.

Slansky, F. & J.G. Rodrigues. 1987. Nutritional ecology of insects, mites, spides, and related invertebrates: an overview. In G.A. Kerkut & L.I. Gilbert (eds.), Comprehensive insect physiology and pharmacology. Wiley, New York, 1016p.

Sugayama, R.L., A. Kovaleski, P. Liedo & A. Malavasi. 1998. Colonization of a new fruit crop by *Anastrepha fraterculus* (Diptera; Tephritidae) in Brazil: a demographic analysis. Environ. Entomol. 27: 642-648.

Wäckers, F.L. 1999. Gustatory response by the hymenopteran parasitoid *Cotesia glomerata* to a range of nectar and honeydew sugars. J. Chem. Ecol. 25: 2863-2877.

Wheeler, D.E., I. Tuchinskaya, N.A. Buck & B.E. Tabashnik. 2000. Hexameric storage proteins during metamorphosis and egg production in the diamondback moth, *Plutella xylostella* (Lepidoptera). J. Insect Physiol. 46: 951-958.

Zanotto, F.P., S.J. Simpson & D. Raubenheimer. 1993. The regulation of growth by locusts through post-ingestive compensation for variation in the levels of dietary protein and carbohydrate. Physiol. Entomol. 18: 425-434.