

Nutritive value of diets with different carbohydrates for adult *Anastrepha obliqua* (Macquart) (Diptera, Tephritidae)

Tânia Mara de Lima Fontellas¹

Fernando Sérgio Zucoloto¹

ABSTRACT. Adult Tephritidae, especially of the genus *Anastrepha* (Schiner, 1868), have been observed to feed on a wide variety of natural diets. The fruit on which they feed, in general, are rich in sugar content, chiefly glucose, fructose and sucrose, which are also the sugars that those insects utilise better. Neither the behavioural mechanisms, nor the physiological ones, that control food selection by insects, are well known. Because some of those aspects are not known for the species *Anastrepha obliqua* (Macquart, 1835) either, and in order to understand their biology better, three experiments were conducted. In the first experiment, it was checked whether there was a difference in metabolic profit by those insects, when fed the carbohydrates more frequently found in nature, as resulting in a bigger egg production and higher survival rate at the end of the experiment. In the second, it was checked whether *A. obliqua* can regulate diet ingestion according to carbohydrate content in dry as well as wet diets. In the third experiment, measurements were made to establish the lowest carbohydrate concentration flies are able to recognise in the diet. Analysis of the data showed that ingestion of carbohydrates which are commonly found in nature, in association with a protein source, is very well utilised by females of *A. obliqua*. It was also shown that those insects are not probably able to compensate for the difference in carbohydrate content in dry diets, whereas they do so for wet diets. In relation to discrimination threshold, it seems that it is related to the higher occurrence of the carbohydrate in their normal diet, that is, they can recognise carbohydrates that are common in their natural diet better than the less frequent ones.

KEY WORDS. Diptera, Tephritidae, *Anastrepha obliqua*, carbohydrates, West Indian fruit fly

Insects, in general, have complex nutritional demands and, although most nutrients are available in their natural diets, some can be obtained from other sources, such as, accumulated reserves from previous developmental stages, synthesis from other nutrients that compose their diet, or from micro-organism activity (CHAPMAN 1971; HAGEN *et al.* 1984).

Tephritidae flies seem to be highly convenient organisms for biological studies, both in natural and in semi-natural conditions, as well as in laboratory (PROKOPY & ROITBERG 1984). Besides that, due to their economical importance, detailed research on their physiology, ecology, genetics and evolution have been carried out (MALACRIDA *et al.* 1996). Based on that knowledge, comparisons with other insect groups can be made.

Adult Tephritidae, especially of the genus *Anastrepha* (Schiner, 1868), have been observed to feed on a wide variety of natural foods, including juices from

1) Departamento de Biologia, Faculdade de Filosofia Ciências e Letras, Universidade de São Paulo. Avenida Bandeirantes 3900, 14040-901 Ribeirão Preto, São Paulo, Brasil.

damaged tissues of rotting fruit, plant saps, flower nectars, bird excretions (BATEMAN 1972), and honeydew (PROKOPY & ROITBERG 1984; ALUJA & BIRKE 1993).

Chemical analysis of the foods which were most frequent in the diets of both larva and adult Tephritidae has shown low nitrogen content and lack of one or more amino acids. Some researchers speculate about the necessity for a symbiotic relation with some micro-organisms that would supply the essential amino acids lacking in the natural diets (HENDRICHS *et al.* 1993b). The fruits on which they generally feed are rich in sugar content, especially glucose, fructose and sucrose, which are also the sugars these insects utilise better (ZUCOLOTO 1992, 1993).

But for a few cases, carbohydrates are the nutrients used by all animals as a primary source of energy (BATEMAN 1972; BARKER & LEHNER 1974; HAGEN *et al.* 1984) and research on some Tephritidae species and other insect groups have shown that carbohydrates, especially sucrose, account for those insects' longevity (HENDRICKS *et al.* 1993b; BINDER 1996; JACOME *et al.* 1995; MCEWEN & LIBER 1995).

Recently, the interest in investigating the relation between the type of food ingested and the relevance of some nutrients present in it has increased (HSIAO 1985; BARTLET *et al.* 1994). Investigations as such are highly important for a better understanding of the mechanisms involved in the control of food ingestion by insects. Researches about diet selection have shown that both larvae and adults of some species can choose the most nourishing diets (ZUCOLOTO 1987, 1991; SIMPSON & SIMPSON 1990; WALDBAUER & FRIEDMAN 1991; FERNANDES-DA-SILVA & ZUCOLOTO 1993; CANGUSSU & ZUCOLOTO 1995). Neither the behavioural nor the physiological mechanisms, that control food choice by insects, are yet very well known (SIMPSON *et al.* 1995). No information is available about the nutritional requirements of the qualitative and quantitative consumption of several of those nutrients for the genus *Anastrepha*, but for what is generally known (MESSAGE & ZUCOLOTO 1980; SHARP & CHAMBERS 1984). Due to the lack of information on those aspects, and in order to know the biology of those insects better, some questions are raised: how fruit flies use metabolically the carbohydrate ingested, that is, is there any difference in metabolic use by those insects of the carbohydrates most available in nature, as shown by a bigger egg production and a higher survival rate? What is the lowest carbohydrate content those flies can recognise in their food? When carbohydrate content decreases, do flies increase food ingestion in order to compensate for the nutrient decrease? This investigation was designed to answer those questions for the species *Anastrepha obliqua* (Macquart, 1835).

MATERIAL AND METHODS

The research was conducted in three phases. In all of them, wild adult females of *A. obliqua*, collected from fruits of *Spondias venulosa* (Linnaeus) (cajimirim), *S. lutea* (Linnaeus) (cajá-manga) and *Mangifera indica* (Linnaeus) (mango), were used. The fruit were collected from trees located in the Ribeirão Preto campus of the Universidade de São Paulo (USP), and at the Instituto Agronômico de Campinas (I.A.C.) km 321, South Ribeirão Preto anel viário, Brazil.

The fruits collected were spread in plastic trays (60x40x10cm) lined with sand of middle size grains and were kept there until they were completely dry. After

that, the dry fruit were removed and the sand sieved through a coarse mesh sieve and the puparia found were transferred to acrylic boxes (11x11x03cm), lined with sterilised sand. Those boxes were kept in a wooden incubator (90x50x30 cm) equipped with a thermostat and electrical resistance to maintain a constant temperature of $29\pm 1^{\circ}\text{C}$. The relative humidity of 70% to 80% was obtained by placing Petri dishes (50x12 mm) full of water in the incubator corners.

After the puparia, the females were sorted out and placed at random in acrylic boxes (11x11x03 cm) with side holes of ± 1 cm in diameter through which the diet and water were offered.

The following carbohydrates were used: monosaccharides: fructose and glucose produced by Merck (Darmstadt – Germany), disaccharide: sucrose (Synth – Diadema, Brazil) and maltose (Merk), and a polysaccharide: soluble starch (Reagen – São Paulo, Brazil). For diet preparation, refer to ZUCOLOTO (1979).

In the first experiment, two control diets were used: control I, prepared with brewer's yeast only (without any carbohydrates), and control II, with sucrose only (without brewer's yeast), both containing distilled water, agar-agar and nipagin (metilparabeno).

The tested diets were composed of: 100 ml distilled water, carbohydrate, 6.5 g brewer's yeast, 3.0 g agar-agar, 1.5 ml nipagin.

RESULTS

Nutritive value of the different carbohydrates

In this phase, the amount of carbohydrate ingested was related to egg production in order to check whether there was any difference in utilisation of the different carbohydrates. To do that, 12 newly emerged females were sorted out and placed in acrylic boxes, as described above. In this experiment, the amount of carbohydrate used was of 11.0 g, as informed by FRANCO (1982), who estimated the carbohydrate content in some *A. obliqua* host fruit.

Three replications were done for each diet. The experiment lasted 18 days, as this is the stretch of time during which it is still possible to count eggs in the ovaries. Flies start laying eggs about 15 to 20 days after they emerge (BRAGA & ZUCOLOTO 1981), thus making it impossible for individual counting of the eggs produced by each female.

To check ingestion, after diets had been prepared they were divided into small bits weighed in precision scales, so that each bit would weigh 0.400 g. Those bits were fed the flies on entomological pins, stuck into corks of about 1cm in diameter, fitted into two of the four side holes in each box. The other two holes were used to supply water which was filled into small test tubes (± 1 cm in diameter and 5 cm long), covered with cotton to prevent its spilling. When the cotton dried out it was replaced and the tube was filled with water again. Boxes identical to the ones described above, but having no flies inside, were used to measure evaporation and the total dry matter in the tested diets. Dead flies were registered and collected daily. After having been used for 24 hours, the diets were replaced by fresh ones and the used diets were dehydrated in incubators heated to $80\pm 1^{\circ}\text{C}$ for another 24 hours.

After that, they were weighed in precision scales in order to measure the dry matter left; the same procedure was used for the diets within the evaporation boxes, that is, the ones without flies. The female flies were fixed in 70° alcohol and glycerine for later egg count.

In order to measure the daily ingestion by females, the following formula was used (CANGUSSU & ZUCOLOTO 1995):

$$I = \frac{TDM - RDM}{N}$$

where: (I) ingestion (mg/female/day), (TDM mg) total dry matter (from box without flies), (RDM) remainder dry matter; and (N) number of live flies.

After working out the ingestion figures for all boxes, the average of all diets tested was calculated.

The efficiency of each diet was calculated by means of the formula (FERRO & ZUCOLOTO 1990):

$$\frac{\text{number of eggs / female / day}}{\text{ingestion / female / day}}$$

In order to obtain the number of eggs, the fixed females were dissected.

The results were analysed statistically by means of the Kruskal Wallis multiple comparison test (HOLLANDER & WOLFE 1973), for a significance level of 5%.

The data (Tab. I) showed that, in relation to ingestion, the starch, glucose, fructose, maltose and sucrose diets and control I, are statistically identical. It was also shown that the starch diet and control I are superior to control II. The glucose, fructose, maltose, sucrose and control II are ingested in statistically identical quantities.

Table I. Ingestion, egg production and efficiency of diet for females of *A. obliqua*, fed with different diets. Results represent the average \pm SD for each diet. The averages of ingestion, egg production and efficiency, followed by a different letter, are statistically different ($P < 0.05$).

Tested diets	Ingestion (mg/female/day)	Egg production (egg/female/day)	Efficiency (egg/production/ingestion)
Control I (without sucrose)	1.60 \pm 1.18 a	0.06 \pm 8.57 b	0.04 \pm 0.06 b
Control II (without brewer's yeast)	1.16 \pm 0.55 b	0.00 \pm 0.00 a	0.00 \pm 0.00 b
Fructose	1.42 \pm 0.52 ab	2.26 \pm 29.96 a	1.58 \pm 0.41 a
Glucose	1.35 \pm 0.31 ab	2.03 \pm 26.73 a	1.51 \pm 0.60 a
Maltose	1.43 \pm 1.14 ab	1.94 \pm 31.53 a	1.36 \pm 0.49 a
Starch	1.65 \pm 1.22 a	2.95 \pm 32.78 a	1.79 \pm 0.57 a
Sucrose	1.44 \pm 0.84 ab	1.53 \pm 23.52 a	1.06 \pm 0.23 a

As to efficiency of diet as related to egg production, results indicate that the starch, glucose, fructose, maltose and sucrose diets are statistically identical. All diets containing carbohydrate and brewer's yeast proved to be superior to the two controls.

The analysis of survival during the experiment time showed that the sugars: glucose, fructose, maltose and sucrose guarantee a survival average of 90% to 100% females at the end of experiment. The starch diet as well as control II guaranteed a survival average of 77% females each. Control I diet resulted in 17% live females at the end of the 18 days of experiment time (Tab. II).

Table II. Survival values for females of *A. obliqua* fed with different diets at the end of the 18 days experiment. The results represent the average \pm SD for each diet. The survival average values followed by the same letters are statistically identical ($P < 0.05$).

Diets used	Survival (number of live flies at the 18° days)
Control I	2.00 \pm 3.46 b
Control II	8.30 \pm 4.04 a
Fructose	11.67 \pm 0.58 a
Glucose	11.33 \pm 0.58 a
Maltose	11.67 \pm 0.58 a
Starch	8.33 \pm 1.53 a
Sucrose	12.00 \pm 0.00 a

Ingestion of diets with two different sucrose content

This experiment tested whether there is a compensatory ingestion of food when sucrose content in one diet is inferior to another. It was also tested whether the behaviour is the same for wet diets.

Dry diets

Two diets with different sucrose content were used, one containing 7.5% and the other, 23.5%. The reason for these figures is that previous studies (not published), have shown that diets containing less than 5% sucrose and more than 25% are ingested in very low quantities, that do not justify testing.

The methodology used was the same as for the previous phase, that is, six boxes with twelve females each were mounted for each sucrose diet (without brewer's yeast), the diet containing 7.5% of sucrose and the other containing 23.5%. The analysis of ingestion was also done according to the same procedure as the one used previously. Replacement of diets happened in two regular intervals during the period of 24 hours (7 hours and 19 hours), in order to prevent any doubts as to whether any variations in the physical characteristics of the diets might cause the flies not to eat them. This procedure was repeated for five days.

Results were analysed by means of t-test for a significance level of 5%.

There is no ingestion compensation for diets with the sucrose contents used (Tab. III). Another fact to be observed from the results of this experiment is that, besides not ingesting bigger amounts of the diet with lower sucrose content, the flies ingested more from the diet with higher content during the night period, when a statistical difference was observed to occur.

Table III. Ingestion of diets with two different sucrose concentrations by females of *A. obliqua*. The results represent the average \pm SD of two diets. The ingestion averages followed by the same letters are statistically identical ($P < 0.05$).

Ingestion (mg/female/day)	Ingestion (mg/female/night)
7.5% = 0.58 \pm 0.21 a	7.5% = 0.80 \pm 0.23 a
23.5% = 0.67 \pm 0.30 a	23.5% = 1.34 \pm 0.66 b

Wet diet

Two types of diet were prepared, one with 5% sucrose and the other with 20% (weight/volume), both without brewer's yeast. For the wet diets, the concentrations used were similar to the sucrose content in the dry diets, with a numerical approximation to round the values in order to turn weighing easier.

Six acrylic boxes containing five female flies each were used for each concentration. A 1x1/100 ml (Pyrex[®]) serological pipette divided into two halves was placed horizontally through one opening in the experimental boxes. The other opening was used for water supply.

The newly emerged females sorted out for this phase were fed a complete diet during 24 hours after which they were left to fast for another 24 hours, so that all of them would achieve the same physiological stage.

The mounting of experiment and ingestion measurements were adapted from SHARP & CHAMBERS (1984); the volume of diet consumed was measured in regular intervals of four hours. During night time only water was supplied (± 16 hours); this routine was repeated for three days. The females that died were removed and disconsidered for the calculation of ingestion. Checking of ingestion was done by direct observation of serological pipette.

To control evaporation, the tested diets were placed within acrylic boxes, without flies, in the same conditions as the test boxes.

The ingestion value was obtained through the following formula:

$$I = \frac{I_v - I_f}{N}$$

where: (I) ingestion of liquid diet ($\mu\text{l}/\text{female}/\text{hour}$); (I_v) initial volume of solution within pipette; (I_f) final volume of solution after being fed the flies for four hours and; (N) number of females that were fed during the four hours.

After working out the ingestion value for four hours, the value of ingestion for one hour was calculated. The results were analysed by the t-test, for a significance level of 5%.

Data analysis showed that consumption of liquid diets varied with concentration, the females ingesting bigger amounts of diets with 5% sucrose than with 20% (Tab. IV).

Table IV. Consumption of wet diets with two different concentrations by females of *A. obliqua*. Results represent the average \pm SD between them. There has been a statistical difference for the diets ($P < 0.05$).

Sucrose concentration (%)	Consumption ($\mu\text{l}/\text{female}/\text{hour}$)
5	3.05 \pm 0.64
20	1.12 \pm 0.32

Discrimination threshold

In this experiment, the value of discrimination threshold was established for each carbohydrate. Discrimination threshold is here understood to be the value for the minimum concentration of a nutrient that flies can discriminate in their diet. The

categorisation of high or low threshold is relative. When we say the discrimination threshold is high, this means that flies can discriminate very tiny concentrations of the nutrient in their diet.

The control diet was composed of 100 ml of distilled water, 2.0 g agar-agar, 1.5 ml nipagin. The experimental diet was composed of 100 ml of distilled water, 2.0 g agar-agar, 1.5 ml nipagin and one carbohydrate in different concentrations.

The discrimination threshold for each carbohydrate was considered to be the concentration immediately inferior to the one that showed a difference in ingestion in relation to the control diet (CANGUSSU & ZUCOLOTO 1995). The two diets were placed within the same box at the same time in order to measure ingestion. Twelve newly hatched females were placed in each box. In the experiment, the same routine was followed for a period of three days, during which time the replacement and weighing of diets were done according to the same system as the one used in the first phase of the investigation.

Ten replications were done for each concentration.

The results were analysed by means of test-t, for a significance level of 5%.

Analysis showed that the discrimination threshold values for each carbohydrate are: starch: 0.5 g; fructose: 0.3 g; glucose: 0.2 g; maltose: 0.5 g and sucrose: below 0.1 g.

When diets are prepared with carbohydrate concentrations inferior to those mentioned above, flies, in general, are not able to discriminate between a diet with the nutrient and another containing only water and agar-agar.

DISCUSSION

According to DADD (1985), to analyse the nutritive value of a carbohydrate, it is necessary to consider three factors: 1) if it is fagostimulating; 2) if the insect has digestive enzymes to reduce polysaccharides; and 3) if the insect can metabolise monosaccharides. With artificial diets, chiefly for the larvae of holometabolic insects, it is also necessary to take account of the diet density due to the presence of a certain carbohydrate in it (ZUCOLOTO 1993).

Sucrose and brewer's yeast are highly fagostimulating nutrients for most insects (SHARP & CHAMBERS 1984), as are all carbohydrates and brewer's yeast for *A. obliqua* (Macquart, 1835). Research for *A. suspensa* (Loew, 1862) has shown that, apparently, several amino acids present in hydrosoluble brewer's yeasts and casein are active components and are partially responsible for the amount of protein they consume (SHARP & CHAMBERS 1984). In an investigation on nymphs of *Locusta migratoria*, it was also found that the presence of brewer's yeast in a diet seems to have a relevant role in regulating ingestion of that diet (SIMPSON & ABISGOLD 1985). This can be a possible explanation for the results found for ingestion of control I, in experiment 1 that, in spite of being an inefficient diet for egg production, was consumed in high amounts. A hypothetical explanation for the high ingestion of that diet, in similar mounts to the carbohydrate and the brewer's yeast diets, however yielding a poor production of eggs and low survival rate, is that flies do not use proteins efficiently as a source of energy to substitute carbohydrates (CANGUSSU & ZUCOLOTO 1992). Probably, there is no advantage for the flies to use proteins to get energy. Some species of polyphagous insects feed on a wide variety of sugar sources

in nature (CHRISTENSON & FOOTE 1960; BATEMAN 1972), a fact that seems to point to an absence of selective pressure to use proteins as a source of energy (CANGUSSU & ZUCOLOTO 1992).

In relation to ingestion of maltose, the results differ from those found by ZUCOLOTO (1992) for *C. capitata* (Wiedemann, 1824). The results obtained by this author indicated that the maltose, despite have been similarly ingestion as outhar carbohydrate tested, did not exhibit adequate results for egg production and efficiency. The glucose (the final product of maltose digestion) yielded superior results to those obtained with maltose. Although in general an enzyme that digests maltose also digests sucrose (α -glucosidase), there is the possibility that sucrose be digested by a β -fructodidase. The possible explication found by the author is that, *C. capitata* flies may have β -fructodidase to digest sucrose and lower activity of enzyme α -glucosidase to digest maltose, (BURSELL 1970 *apud* ZUCOLOTO 1992). This does not seem to happen with *A. obliqua*, as this species showed good ingestion and efficiency results with sucrose as well as with the other carbohydrates tested.

Still in comparison with the results found for *C. capitata* (ZUCOLOTO 1992), it was observed that the diet containing starch was the least ingested by those flies and there was no production of eggs either. Woweever, in this work, we found that starch also has produced positive results in relation to ingestion and egg production, in the same way as with the other carbohydrates tested. This leads us to conclude that, for *A. obliqua*, starch is also a highly nourishing food. Analysis of data from several studies shows that the carbohydrates with the highest nutritive value are the ones found in natural sources. The principal ones are: glucose, fructose, sucrose, maltose and, for some species, starch (GALUN & FRAENKEL 1957; CANDY 1985; DADD 1985; REINECKE 1985; HSIAO 1985; WALDBAUER & FRIEDMAN 1991; ZUCOLOTO 1992; ALUJA 1994). Adults, chiefly females of *A. obliqua*, feed preferentially on pollens and nectars. Nectars supply the energy demands by means of simple sugars. Pollens have starch and also supply the demands for protein, salts and vitamins (BARBIER 1944 *apud* HAGEN *et al.* 1984). The starch diet, as well as the other carbohydrates, also approximates the effects of natural diets for females. Maybe, because of this, starch has produced adequate results for *A. obliqua*.

According to investigations by ZUCOLOTO (1992) and CANGUSSU & ZUCOLOTO (1995), *C. capitata* does not necessarily require a protein source to produce eggs, at least in the first 15 days after they emerge. This investigation shows that the same was not observed to happen with *A. obliqua*. It seems that these two fruit fly species have one disadvantage in relation to this aspect: they require a source of protein in the adult phase to produce eggs. The same was found to happen with *A. suspensa* (SHARP & CHAMBERS 1984).

In relation to efficiency parameters, the sucrose diet produced the lowest results, as compared to the other carbohydrates. This same characteristic was found by MCEWEN & LIBER (1995) with the moth *Prays oleae*. However, in relation to survival, it could be seen that all *A. obliqua* specimens, fed on sucrose were alive at the end of the experiment. Perhaps, if the analysis had covered all the reproductive span of the flies, the efficiency results might have favoured the sucrose diet, as they would have lived longer, and so laid more eggs. In ZUCOLOTO's (1992) investigation

of *C. capitata*, the results for the sucrose diet, in relation to egg production, were fairly positive. This difference may be related to the biology of the two species. *C. capitata* starts producing eggs earlier than *A. obliqua*. Perhaps this characteristic would favour *C. capitata* highly in relation to the species of the *Anastrepha*. Early ovipositing lessens the risks for *C. capitata* to become a prey before ovipositing, besides their nutritional requirements in the adult phase for egg production being less pressing than for the species of the *Anastrepha*. Considering the fact that both genera inhabit similar niches, those characteristics are relevant as to competition between those flies (ZUCOLOTO 1992). The starch diet yielded opposite results to those found with sucrose. The starch diet supplied the best numerical results in relation to ingestion and egg production, but the females that ingested starch had a survival rate inferior to the ones that ingested sugars. Relating the high mortality observed, it can be presumed that the metabolic cost for starch ingestion is high. We do not know if this characteristic is a "strategy" of those insects' biology, a biological mechanism insects of shorter longevity use to produce a bigger amount of eggs in order to compensate for their shorter life spans (Zucoloto's supposition). Future research may confirm this hypothesis.

In experiment 2, with dry diets, a bigger ingestion of diets with lower nutrient content was not observed to happen. Ingestion results are found to vary. SALAMA (1967) *apud* FOSTER (1995), states that the type of sugar and its content affect ingestion by mosquitoes. FRIEND *et al.* (1988), also investigating mosquitoes, concluded that the more concentrated sugar is, the more flies ingest it. This may have happened with the *A. obliqua* in this study.

Another possibility, that may explain the non-compensation of food, is associated to metabolic costs, as described by JACOME *et al.* (1995), that is, to ingest big amounts of less concentrated diets might not be compensatory. The energy gained from this operation might not be big enough to compensate for the energy spent in the job of ingesting and digesting the dry food. HENDRICKS *et al.* (1993a), investigating *Rhagoletis pomonella*, and LOPEZ *et al.* (1996), investigating moth *Helicoverpa zea*, discuss another possibility as related to salivation. They found that salivation is relevant to facilitate ingestion of dry diets. Production of saliva involves metabolic water that facilitates ingestion but this process also consumes energy.

Contrary to the results found for dry diets, with wet diets it was possible to observe a higher ingestion of diets with lower sucrose concentration. These results are similar to the ones found by SHARP & CHAMBERS (1984), for *A. suspensa* fed on wet diets, that showed that the flies ingested a bigger amount of diets containing 8% sucrose, and smaller amounts of diets with 2%, 4%, 16%, and 32% of sucrose. NESTEL *et al.* (1985), working on *C. capitata* fed on wet diets, found a bigger ingestion of 2% sucrose diets than of 8% and 16%. NAYAR & SAUERMAN (1974), working on flies fed on 5%, 10% and 25% sucrose diets, verified a bigger ingestion of the least concentrated diet. However, in relation to caloric compensation, this does not seem to have happened. Those researches also showed that compensation is not total. Increase of ingestion is not big enough to compensate for dilution. Besides that, no direct evidence has been observed up to now that insects self-regulate ingestion for caloric sake, as it seems to happen with rats (SIMPSON & ABISGOLD 1985).

When measuring the caloric gain of flies ingesting 5% sucrose diets, we verified that they did not actually achieve the same caloric gain as the flies fed on 20% sucrose diets did. The calculation of caloric gain was based on the information that each gram of sucrose releases four calories.

Independently of occurring caloric compensation or not, it is probable that ingestion of wet diets does not require as much energy as dry diets do. A possible explanation is that the volume of wet diet ingested is determined by the interaction between the oral receptors' excitatory input and the abdomen inhibitory input, in a similar way to what happens with mosquitoes (OWEN & MCCLAIN 1981).

Anastrepha obliqua is a polyphagous insect and feeds on several natural sources (honeydews, nectars, pollens, etc.), apparently being excited by the carbohydrates present in them (GOTHILF *et al.* 1971; EVANS 1963 *apud* TSIROPOULOS 1980). The principal sugars in those sources are: fructose, glucose and sucrose, among others, whereas maltose occurs occasionally in low concentrations (AUCLAIR 1963; HAGEN *et al.* 1984). Sugars from nectar vary as to caloric content and their perception by insects depends on the concentration of each sugar or of their mixture (MITCHEL 1981). Nectar from extrafloral nectaries contains chiefly fructose, glucose and sucrose, besides seven other sugars (BENTLEY 1977 *apud* HAGEN *et al.* 1984). The honeydews excreted by Homoptera also normally contain sucrose, glucose and fructose (MAURIZIO 1975).

The discrimination threshold for starch being similar to the one found for maltose suggests that either the starch content in those insects' diets is also low, or that it is not phagostimulating.

In comparison with results obtained in this phase, it can be noted that the highest discrimination threshold was the one for sucrose, followed by glucose and then fructose. These findings seem to confirm the possibility of a relationship between availability of the nutrient in nature and the refinement of sensorial mechanisms to discriminate those carbohydrates. BINDER (1996) has also found out that the most frequent floral carbohydrate is sucrose. This finding, as already stated, coincides with the high discrimination threshold for this carbohydrate; flies are able to discriminate the presence of this nutrient in diets even when its concentration is not enough to guarantee their survival.

GOTHILF *et al.* (1971) observed the effect of several salts and sugars on chemoreceptors of *C. capitata*. Those researchers found that the mere contact of the tip of a sense bristle with a sugar solution is enough to cause the proboscis to extend. Of the sugars tested, the ones that caused the highest electric discharges were: fructose, glucose and sucrose. Maltose is among the ones that caused the least stimulation. There is no register for starch (the authors used sugars only). In spite of the fact that the research mentioned investigated another species of flies, it is very plausible to think that the chemical perception mechanisms are similar in the two species. Perhaps this characteristic is related to the biology of the species that makes it possible for the flies to discriminate very low concentrations of nutrients in their diets.

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