ECOLOGY, BEHAVIOR AND BIONOMICS

The Presence of the Sexual Partner and Nutritional Condition Alter the *Anastrepha obliqua* MacQuart (Diptera: Tephritidae) Protein Discrimination Threshold

CARLA CRESONI-PEREIRA AND FERNANDO S. ZUCOLOTO

Depto. Biologia - FFCLRP-USP. Av. Bandeirantes, 3900, 14040-901, Ribeirão Preto, SP

Neotropical Entomology 34(6):895-902 (2005)

Presença e Estado Nutricional do Parceiro Sexual Alteram Limiar de Discriminação Protéica por *Anastrepha obliqua* MacQuart (Diptera: Tephritidae)

RESUMO - A quantidade mínima de proteínas que *Anastrepha obliqua* MacQuart pode detectar na sua fonte alimentar é variável, mas as causas dessa variação ainda são pouco conhecidas. Neste trabalho, foi testado se o estado nutricional e a presença do parceiro sexual, sem contato direto, alteram o limiar de discriminação protéica em *A. obliqua*. Indivíduos de cada sexo foram agrupados como se segue: (i) recém-emergidos, (ii) privados de fonte protéica (levedo de cerveja) por 18 dias, (iii) não-privados de levedo por 18 dias, (iv) privados mantidos na presença de parceiros sexuais igualmente privados de levedo, (v) privados mantidos na presença de parceiros não-privados, (vi) não privados mantidos com parceiros privados e (vii) não-privados mantidos com parceiros não-privados. Os parceiros sexuais foram separados entre si por uma divisória de plástico transparente com pequenos furos. Não só a presença do macho, como também seu estado nutricional, alteraram o limiar de discriminação das fêmeas. O limiar da fêmea foi, portanto, determinado pelo seu próprio estado nutricional mais o reconhecimento do estado nutricional do macho. O limiar de discriminação dos machos foi mais alto para os indivíduos não-privados do que para os indivíduos privados. A ocorrência de respostas na ausência de contato direto entre machos e fêmeas indicou que eles devem se utilizar de algum mecanismo químico para reconhecimento mútuo do estado nutricional do parceiro sexual.

PALAVRAS-CHAVE: Seleção de dietas, mosca-das-frutas, proteína, comportamento alimentar

ABSTRACT - The minimum protein amount that *Anastrepha obliqua* MacQuart can detect in its alimentary source is variable, though the causes of such variation are not very well known. In this study, the authors tested whether the sexual partners nutritional condition and presence devoid of direct contact alter the *A. obliqua* protein discrimination threshold. Male and female insects were assigned to groups as follows: (i) newly emerged, (ii) deprived of protein source (yeast) during 18 days, (iii) non-yeast-deprived during 18 days, (iv) yeast-deprived in the presence of equally yeast-deprived sexual partners, (v) yeast-deprived in the presence of non-yeast-deprived partners, (vi) non-yeast-deprived with yeast-deprived partners and (vii) non-yeast-deprived with non-yeast-deprived partners. The sexual partners were maintained apart by a transparent plastic screen with small holes. Not only the males presence but also their nutritional condition have altered the females discrimination threshold, particularly when the females were deprived and when non- deprived females cohabited with deprived males. Therefore, the females threshold was determined by their own nutritional condition in addition to recognition of the males nutritional condition. The males discrimination threshold was higher for non-deprived subjects than for the deprived ones. The occurrence of responses in the absence of direct contact between males and females has shown that they may use a chemical mechanism for mutual recognition of the sexual partner nutritional condition.

KEY WORDS: Diet selection, fruit fly, feeding behavior

The adults of the fruit fly *Anestrepha obliqua* MacQuart, before becoming sexually active, go through a maturation period where they need to be regularly fed with carbohydrates and water to survive and with a protein source to promote egg maturation (Aluja 1994). Proteins are particularly important for *A. obliqua*: wild females do not produce eggs if they do not ingest proteins in the adult phase (Ferro & Zucoloto 1990); the production and liberation of pheromones by the males is impaired by the absence of proteins in the adult´s diet (Ferro & Zucoloto 1989); protein deprivation during adulthood changes the females discrimination threshold as concerns this nutrient (Cresoni-Pereira & Zucoloto 2001); larvae do not develop with artificial diets without proteins (Message & Zucoloto 1980); a protein hydrolysate is the most attractive food utilized in fly-traps to catch this and other species of fruit flies (Nascimento *et al.* 2000). Proteins in general are the feeding constituent that can most limit growth and fecundity.

Due to the importance of proteins to the *A. obliqua* adults, aspects related to this nutrient acquisition and utilization by the flies are highly interesting targets in the study of these insects. Several studies have investigated the relationship between the production of eggs by virgin and copulated female insects (Boggs 1990, Blay & Yuval 1997, Fadamiro & Baker 1999, Mangan 2003). There are hypotheses that the males could, through nuptial presents, increase the females nutritive reserves and this would result in benefits to reproduction (Boggs 1990). Nutrients transferred by the males during copulation would be responsible for the increased fecundity (Fadamiro & Baker 1999). Factors transmitted by the males can play a role in reproduction inducing or increasing oviposition, maybe through hormonal effects (Fadamiro & Baker 1999).

Aluja *et al.* (2001) have for the first time hypothesized that the simple presence of the males in the same environment, lacking direct contact, could affect the feeding behavior of *A. obliqua* females, which could increase or decrease food ingestion as a consequence of the co-specific male presence. Therefore, the aim of this study was to test whether the presence of sexual partners and their nutritional condition alter the protein discrimination threshold of *A. obliqua* individuals. The discrimination threshold is the smallest amount of a particular nutrient or compound that can be detected by the insect in a given volume of diet (Cresoni-Pereira & Zucoloto 2001) and it is an important process in the food selection behavior.

Material and Methods

Wild *A. obliqua* adults were collected from infested fruits of *Spondias lutea* and *Spondias venulosa*. The infested fruits were collected and placed in plastic boxes with approximately 5 cm sand. After the pulp is completely dry, the fruits were removed and the pupae were separated from the sand with a screen, washed with running water, and placed in acrylic boxes containing sterilized sand. The boxes with the pupae and the experimental boxes were maintained in a wooden incubator with glass lid at 29 ± 1°C mean temperature, 70% to 80% relative humidity, and a 12h-light / 12h-dark photoperiod using 400 lux fluorescent lamps. As soon as they started to emerge, the flies were randomly allocated to acrylic boxes, according to each experimental group. The acrylic boxes were diagonally divided by a transparent perforated plastic surface. The boxes moieties had three lateral orifices (1cm diameter) to offer water and the diets. Water was offered through small glass test tubes with cotton lids. The solid diets were offered in pieces using pins stuck on corks.

The experimental diets were made of: agar (Zetec, São Paulo) 2.5 g, distilled water 100 ml, sucrose (Sigma, São Paulo) 11.0 g, Nipagin (Merck®) 1.5 ml, and different amounts of brewer´s yeast (Macroflora, São Paulo). The daily ingested amounts were obtained using the formula

$I = \dfrac{MST - MSR}{N}$: I = ingestion, MST = total dry matter (total weight of the diet placed in boxes without flies and maintained in the same experimental conditions to control evaporation); MSR = remaining dry matter (total weight of the diet placed in the experimental box), and N = number of living flies inside the box (Cangussu & Zucoloto 1995). The diets taken from the boxes after 24h were placed in a kiln during 24 more hours, in a 80 ± 1°C temperature in order to dry, and were then weighted to calculate ingestion.

Every day the dead flies were removed from the boxes. The newly emerged flies were allocated into groups: (i) newly emerged, (ii) deprived of protein source (yeast) during 18 days, (iii) non-yeast-deprived during 18 days, (iv) yeast-deprived in the presence of equally yeast-deprived sexual partners, (v) yeast-deprived in the presence of non-yeast-deprived partners, (vi) non-yeast-deprived with yeast-deprived partners and (vii) non-yeast-deprived with non-yeast-deprived partners. Females were tested in all the groups (i-vii), while males were tested only in the female presence (iv-vii).

All the boxes were provided with a transparent plastic perforated division to separate males from females and females from other groups, in such a way that in every group each moiety contained only eight individuals. Newly emerged females were assigned to two groups: groups with eight females (half of the box remained empty) and groups with 16 females (eight in each side of the screen, but only one of the sides was tested).

The newly emerged flies were tested in the three first days after emergence. The deprived flies were fed with the sucrose diet (11.0 g) during 18 days and were then tested from de 19th to the 21th days. The non-deprived flies were fed with the sucrose diet (11 g) and yeast (6.5 g) during 18 days and then tested from de 19th to the 21th days. In the test, two diets were concomitantly offered: sucrose diet and sucrose plus yeast diet. The yeast amount initially used in the test was 0.7 g /100 ml diet for the newly emerged flies and deprived females groups, and 1.6 g / 100 ml diet for the non-deprived flies group (Cresoni-Pereira & Zucoloto 2001). Ingestion was measured and the yeast amount was increased or reduced according to the results. The males threshold was also evaluated using the same procedure. The data were compared by the tests of Tukey or Wilcoxon, through the SigmaStat for Windows, 2.03 version, by Jandel Corporation.

Results

The results have shown that the groups with females in the absence of males did not differ from the results found for that same situation in other studies (Cresoni-Pereira & Zucoloto 2001), nor have differed between groups with eight and 16 females in the box. The threshold found for newly emerged females, in boxes with eight and with 16 insects, was yeast 0.7 g / 100 ml diet. For the non-deprived females, the threshold was yeast 1.6 g / 100 ml diet (Fig. 1). As the eight and 16 female groups did not show different thresholds when newly emerged or when non-deprived, the 16 females group was not repeated for the yeast-deprived females. The threshold found for deprived females was yeast 0.7 g / 100 ml diet (Fig. 2).

Females kept with males have shown altered thresholds. Non-yeast-deprived females in the presence of non-deprived males have shown the same threshold as females in the absence of males (Figs. 1 e 3). However, non-deprived females in the presence of deprived males have shown a discretely higher threshold (Figs. 1 e 3).

Yeast-deprived females have shown thresholds higher than the initially tested, independently of the males nutritional *status* (Figs. 2 e 3). In this case, there are again evidences that the visual contact may not be important. The fact the females are deprived and wild indicates that their eggs are not ready to fecundation. Apparently, the greater the protein need the higher the threshold.

The males were also tested with the females present. The threshold was higher for the non-deprived males than for the deprived males (Figs. 4 e 5).

The yeast amounts in the diet found as thresholds for the different groups were statistically compared (Figs. 3 and 6). In the non-deprived females group, statistical differences were found between the 1.6 g quantity of yeast (FF, F and FM groups threshold) and 1.8 g of yeast (FMS group threshold) (Fig. 3). In deprived females group, statistical differences were found among all yeast quantities found as threshold (0.7 g to F group; 1.2 g to FF group and 1.5 g to FMS group) (Fig. 3).

To males group, statistical differences were found among the yeast quantities found as threshold (Fig. 6) to all groups (non-deprived males and deprived males).

Discussion

The discrimination threshold has already been found for carbohydrates in *A. obliqua* females (Fontellas & Zucoloto 1999) and for the brewer´s yeast in *C. capitata* females (Cangussu & Zucoloto 1995) and *A. obliqua* females (Cresoni-Pereira & Zucoloto 2001). In the latter study, the females presented a discrimination threshold considered high since the *C. capitata* females used by Cangussu & Zucoloto (1995), considered autogenous, presented a much lower threshold. In these studies, males have not been used. Changes in the threshold can occur mediated by external factors (Lima 2001). In the present study, the quantities found as threshold to the groups were significantly different (Fig. 3 and 6), so we accepted that the threshold was modified not only when the males were present, but also in relation to the nutritional *status* of the sexual partner.

In the case of non-deprived females, it is possible that the threshold has not been altered because the female feeding itself is already sufficient, independently of any contribution on the part of the males. When the male is deprived, there

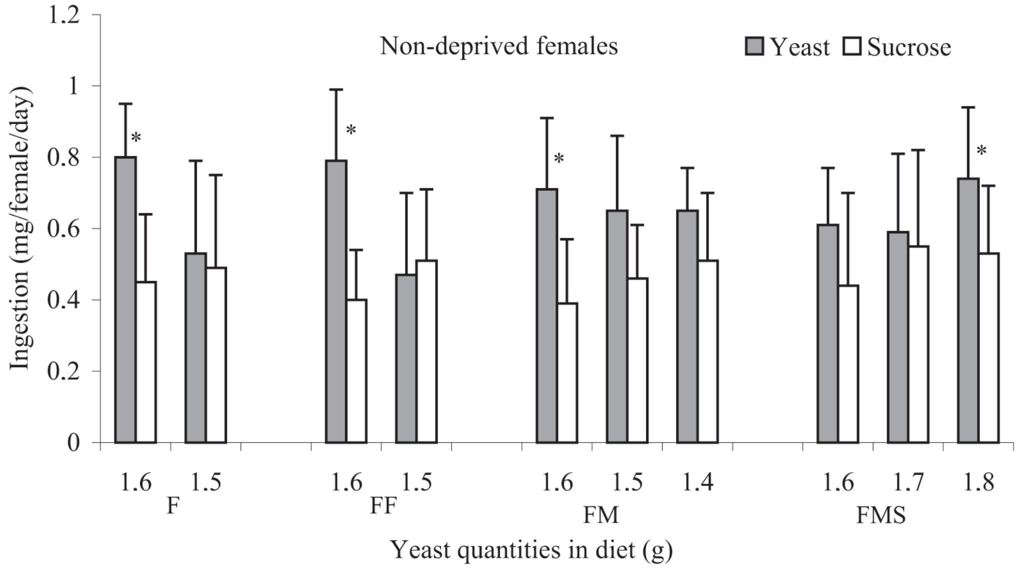

Figure 1. Ingestion of sucrose containing diets (11 g) and of diets containing different amounts of yeast by non-deprived *A. obliqua* females fed with yeast diets (6.5 g) and sucrose (11.0 g) during 18 days. The asterisk indicates significant difference the two diets ingestion (threshold) (Wilcoxon, $P < 0.05$). F - 8 females; FF - 16 females; FM - 8 females and 8 non-deprived males, FMS - 8 females and 8 deprived males.

Figure 2. Ingestion of sucrose containing diets (11 g) and diets containing different amounts of yeast by deprived *A. obliqua* females fed with sucrose diets (11.0 g) during 18 days. The asterisk indicates significant difference in the two diets ingestion (threshold) (Wilcoxon, $P < 0.05$). F - 8 females: FM - 8 females and 8 non deprived males; FMS - 8 females and 8 deprived males.

is a small amplification in the threshold that can be related to the detection by the females of the nutritional *status* of the males, that can contribute with a little or no protein material.

During the experimental period, the non-deprived females attained sexual maturity: their eggs were ready to be fertilized and would not need increments from the males for the initial ovipositions. The non-deprived females living with deprived males cannot count on nuptial presents of nutritive value, and they must invest in their own feeding as a means to obtain nutrients that guarantee successful reproduction. It is of the most importance to be able to recognize food with the necessary nutrients, thus a small rise occurs in this group threshold when compared to the group of non-yeast-deprived females living with also non-deprived males. It is also interesting to observe how the females can perceive the nutritional environment provided by the males without physical contact. Aluja *et al.* (2001) have shown that *A. obliqua* females are able to regulate oviposition considering the availability of resources and this is a characteristic of the species which use ephemeral hosts. Perhaps the same type of mechanism is involved when the acquisition of nutrients for reproductive maintenance is concerned, considering the female and male nutritional *status* itself. Nutrients deriving from the males can contribute for egg production only in species that emerge with few or no eggs with yolk (Boggs 1990). This is the case for wild *A. obliqua* flies that emerge with immature ovaries and need

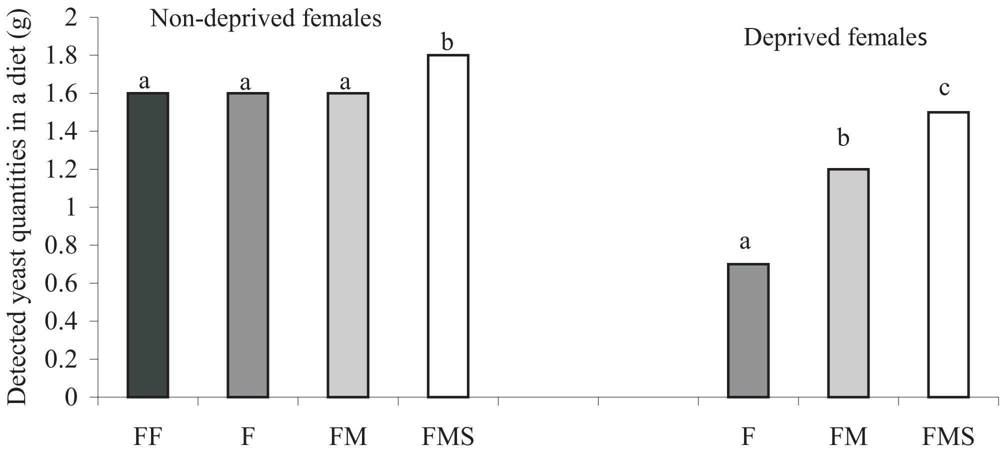

Figure 3. Comparison between the yeast amounts perceived in the diets (discrimination threshold) by *A. obliqua* females, in different groups. Different letters indicate significant difference between the bars (Tukey, $P < 0.05$). FF - 16 females; F - 8 females; FM - 8 females and 8 non-deprived males; FMS - 8 females and 8 deprived males.

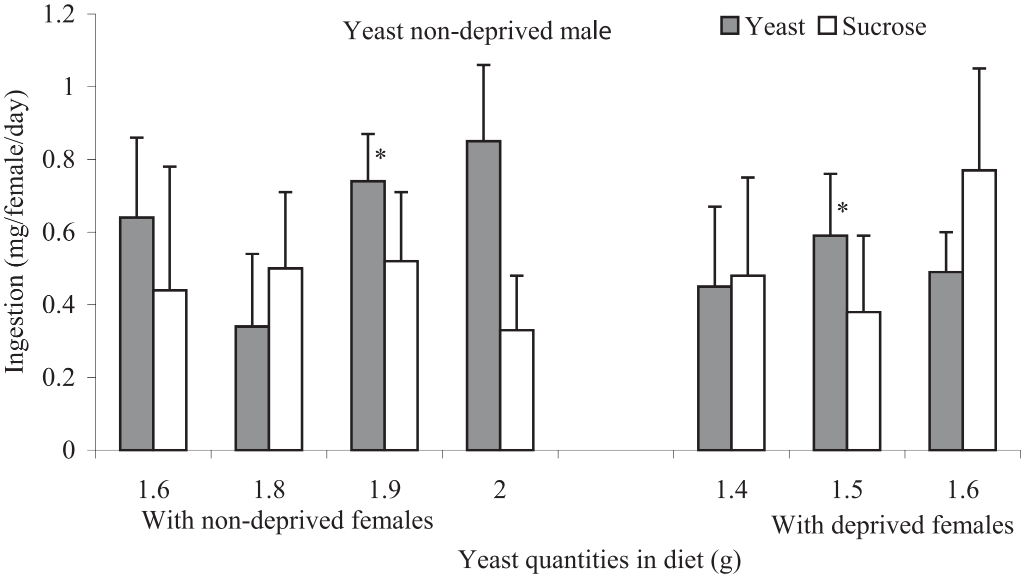

Figure 4. Ingestion of sucrose containing diets (11 g) and diets containing different yeast amounts by non-deprived *A. obliqua* males fed with yeast diets (6.5 g) and sucrose (11.0 g) during 18 days, accompanied by non-yeast-deprived and yeast-deprived females. The asterisk indicates significant difference in the two diets ingestion (threshold) (Wilcoxon, P < 0.05).

an exogenous protein source to produce eggs (Message & Zucoloto 1980).

The deprived females living with males in any nutritional *status* showed higher threshold. This increase observed in both groups could be explained by the nutritional *status* of the (yeast-deprived) females and this would make impossible the eggs production. Not even the possibility of a nuptial present from non-deprived males would be sufficient to supply the protein needs to produce eggs. The fact that the threshold is higher than the one for deprived females in the absence of males offers evidences that the females behavior is widely based on the nutritional environment. The females can, in a way or another, detect the nutritional *status* of the male. It is possible that this is done through chemical signs, such as the pheromone composition.

The results found for newly emerged females repeat those found by Cresoni-Pereira & Zucoloto (2001). When males are not present, the nutritional environment, in addition to the feeding source, is totally unknown to the females. No protein resources can be anticipated coming from the males, thus any amount of protein food that can be acquired is advantageous, even though it is not possible to compensate its dilution in the food due to the volumetric factor (limit for compensation).

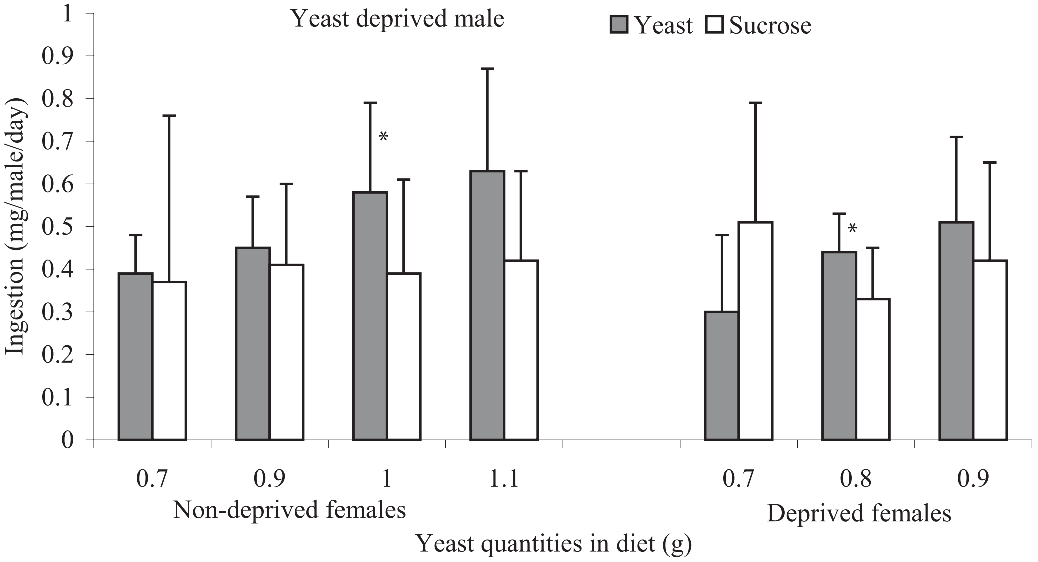

Figure 5. Ingestion of sucrose containing diets (11 g) and diets containing different yeast amounts by deprived *A. obliqua* males fed with sucrose diets (11.0 g) during 18 days, accompanied by non-yeast-deprived and yeast-deprived females. The asterisk indicates significant difference in the ingestion of the two diets (threshold) (Wilcoxon, P < 0.05).

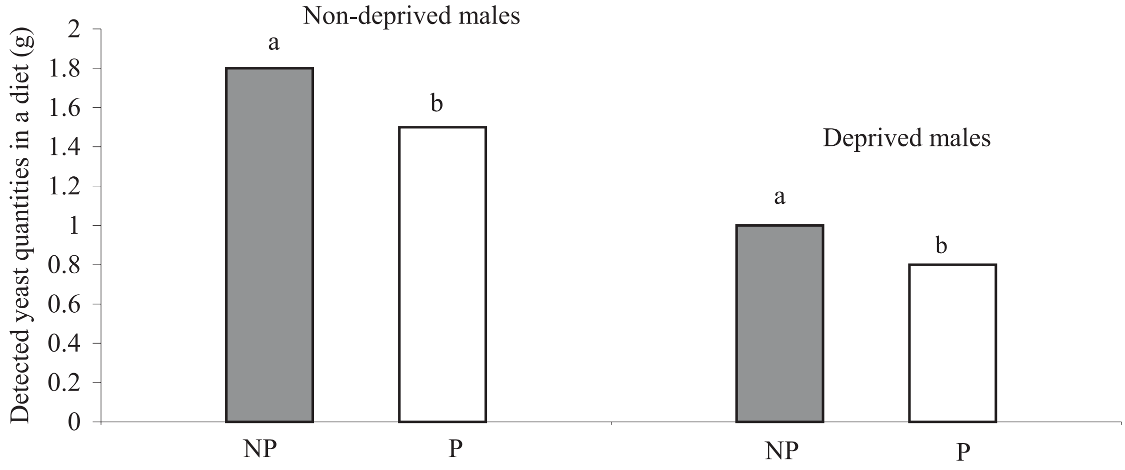

Figure 6. Comparison of the yeast amounts perceived in the diets (discrimination threshold) by *A. obliqua* males, in different groups. Different letters indicate significant difference between the bars (Tukey, $P < 0.05$). NP - non-yeast-deprived females; P - deprived females.

Morgante *et al* (1983) also argue that, in the copulation systems with *leks* formation, the females of several species of fruit flies are able to select their partners. Sometimes that selection is not based only on visual aspects as male size (Mangan 2003). Wild *C. capitata* females actively select and discriminate in favor of males which produce pheromones with the adequate composition (Heath *et al.* 1994) and which adequately carry out the court, sound, visual and tactile behaviors (Eberhard 2000). An adequate composition of pheromones and even the performance in court reflect the nutritional *status* of the male, as mentioned below.

The exact recognition mechanism of such male characteristics by the females is not yet known, however we dare to hypothesize that it is via odour since no physical contact between males and females occurred in our experiments, and the visual hypothesis is discarded since this kind of stimulus was similar for all the groups where males were present, in spite of the nutritional *status*. Cangussu & Zucoloto (1997) also proposed that the odour exhaled by females fed with proteins was responsible for the males preference for these females.

It has been hypothesized that the females preferences for males may be based on quality, on resources controlled by the males, on the males court exhibition that the females use as indicative of the male genetic quality, or on a combination of factors (Gwynne 1988, Whittier & Kaneshiro 1995). The females preferences provide direct benefits as expanded survival and success as concerns reproduction or indirect benefits as gametes that improve the offspring quality or attractiveness. Apparently, the females do not discriminate males when size variation is concerned. No benefits for the offspring were observed as a result of the females choice. The female choice may be based in direct benefits for the female itself in the form of fecundity. These benefits can result from variation among males in their ability to maximize fertilization, or from the variation concerning nutrients and/or sexual peptides transferred to the females during copulation (Whittier & Kaneshiro 1995).

There is information that the males pheromones of many tephritids species contain certain compounds that imitate the food and the host smell (Robacker & Warfield, 1993), acting as phagostimulants. Feeding intensification would bring direct benefits that could only be incremented by the nuptial present by itself insufficient as exogenous protein source. This seems to be supported by results obtained with deprived females.

Males of all groups showed tendency to a threshold higher than the one initially tested. Studies with several tephritids (Ferro & Zucoloto 1989, Shelly & Dewire 1994, Blay & Yuval 1997) showed that nutrient deprived males were inferior concerning activities such as provision of nuptial presents, development of the salivary gland responsible for pheromones production, pheromones emission, quantity and intensity of court signalization, partners acquisition, sperm reserve restoration, and ability to induce a refractory period in the females (periods post-copulation when the female is not yet receptive to another copulation).

Many interesting interactions are found in studies carried out with females and males of several species considering the nutritional *status*. It is important to remember that all these experiments are carried out with the occurrence of copulation. Protein in the males diet increases egg maturation when compared to males fed only with sugar, but the presence of males fed with any diet lessens maturation when compared with females not exposed to males (Mangan 2003).

C. capitata males fed with proteins which copulate with females also fed with proteins were significantly heavier than those which copulate with females fed with sucrose, and this suggests a relation between the nutritional *status* of the female and its grade of exigency when selecting a partner (Field & Yuval 1999). Protein fed males which copulated with females fed with sucrose weighted less than the protein fed males which copulated with females also fed with proteins, because they transferred more sperm than the others. The results suggest that when the females are inadequately nourished, selectivity is loosened and they accept smaller partners (Field & Yuval 1999).

The tests have shown that the sexual partners presence and their nutritional condition can affect the discrimination threshold of *A. obliqua* insects consequently altering the ingested amounts of diet. That alteration in food selection and ingestion can bring benefits to the individuals, particularly in this case as concerns reproduction, since the protein source has been proven to be of the utmost importance for this species. The exact mechanisms of influence of the sexual partners and their nutritional condition must be further investigated.

Acknowledgements

We are grateful to Ana Paula dos Santos and Laércio Massocato for the technical assistance. This research is financed by FAPESP.

Literature Cited

Aluja, M. 1994. Bionomics and management of *Anastrepha*. Annu. Rev. Entomol. 39: 155-178.

Aluja, M., F. Díaz-Fleischer, D. Papaj, G. Lagunes, & J. Sivinski. 2001. Effects of age, female density, and the host resource on egg load in *Anastrepha ludens* and *Anastrepha obliqua* (Diptera, Tephritidae). J. Insect Physiol. 47: 975-988.

Blay, S. & B. Yuval. 1997. Nutritional correlates of reproductive success of male Mediterranean Fruit flies (Diptera, Tephritidae). Anim. Behav. 54: 59-66.

Boggs, C.L. 1990. A general model of the role of male-donated nutrients in female insect's reproduction. Amer. Natur. 136: 598-617.

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

Cangussu, J.A. & F.S. Zucoloto. 1997. Effect of protein sources on fecundity, food acceptance and sexual choice by *Ceratitis capitata* (Diptera, Tephritidae). Rev. Bras. Biol. 57: 611-618.

Cresoni-Pereira, C. & F.S. Zucoloto. 2001. Dietary self-selection and discrimination threshold in wild *Anastrepha obliqua* females (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, 1176p.

Eberhard, W. 2000. Sexual behavior and sexual selection in Mediterranean fruit fly, *Ceratitis capitata* (Dacinae, Ceratidini), p.459-489. In M. Aluja & A.L. Norrbom, Fruit flies (Tephritidae): Phylogeny and evolution of behavior. CRC Press, Boca Raton, Florida, 1281p.

Fadamiro, H.Y. & T.C. Baker. 1999. Reproductive performance of female European corn borer *Ostrinia nubilalis*: Effects of multiple mating, delay in mating and adult feeding. J. Insect Physiol. 45: 385-392.

Ferro, M.I.T. & F.S. Zucoloto. 1989. Influência da nutrição protéica no desenvolvimento da glândula salivar de machos de *Anastrepha obliqua* MacQuart, 1835 (Diptera, Tephritidae). Científica 17: 189-193.

Ferro, M.I.T. & F.S. Zucoloto. 1990. Effect of the quantity of dietary aminoacids on egg production and layings by *Ceratitis capitata* (Diptera, Tephritidae). Braz. J. Med. Biol. Res. 23: 525-531.

Field, S.A. & B. Yuval. 1999. Nutritional status affects copula duration in the Mediterranean fruit fly, *Ceratitis capitata* (Insecta Tephritidae). Ethol. Ecol. Evolution 11: 61-70.

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

Gaskin, T., P. Futerman & T. Chapman. 2002. Increased density and male-male interactions reduce male longevity in the medfly, *Ceratitis capitata*. Anim. Behav. 63: 121-129.

Gwynne, D.T. 1988. Courtship feeding and the fitness of female katydids (Orthoptera, Tettigoniidae). Evolution 42: 545-555.

Heath, R.R., N.D. Epsky, B.D. Dueben, A. Guzman & L.E. Andrade. 1994. Gamma radiation effects on production of four pheromonal components of male Mediterranean fruit flies (Diptera, Tephritidae). J. Econ. Entomol. 87: 904-909.

Lima, I.S. 2001. Semioquímicos das moscas-das-frutas, p.121-126. In E.F. Vilela & T.M.C. Della-Lucia (eds.), Feromônios de insetos: Biologia, química e emprego no manejo de pragas. Holos Editora, Ribeirão Preto, 206p.

Mangan, R.L. 2003. Adult diet and male-female contact effects on female reproductive potential in Mexican fruit fly (*Anastrepha ludens* Loew) (Diptera, Tephritidae). J. Econ. Entomol. 96: 341-347.

Message, C.M. & F.S. Zucoloto. 1980. Valor nutritivo do lêvedo de cerveja para *Anastrepha obliqua* (Diptera, Tephritidae). Ci. Cult. 32: 1091-1094.

Morgante, J.S., A. Malavasi, R.J. Prokopy. 1983. Mating behavior of wild *Anastrepha fraterculus* (Diptera, Tephritidae) on a caged host tree. Fla. Entomol. 66: 234-241.

Nascimento, A.S., R.S. Carvalho & A. Malavasi. 2000. Monitoramento populacional, p.109-112. In A. Malavasi & R.A. Zucchi (eds.), Moscas-das-frutas de importância econômica no Brasil: Conhecimento básico & aplicado. Holos Editora, Ribeirão Preto, 327p.

Robacker, D.C. & W.C. Warfield. 1993. Attraction of both sexes of Mexican fruit fly, *Anastrepha ludens*, to a mixture of ammonia, methylamine and putrescine. J. Chem. Ecol. 19: 2999-3016.

Shelly, T.E. & T.S. Whittier. 1993. Effect of sexual experience on the mating success of males of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera, Tephritidae). Proc. Haw. Entomol. Soc. 86: 141-154.

Shelly, T.E. & A.M. Dewire. 1994. Chemically mediated success in male oriental fruit flies, *Bactrocera dorsalis* (Diptera, Tephritidae). Ann. Entomol. Soc. Am. 87: 375-382.

Whittier, T.S. & K.Y. Kaneshiro. 1991. Male mating success and female fitness in the Mediterranean fruit fly (Diptera, Tephritidae). Ann. Entomol. Soc. Am. 84: 608-611.

Whittier, T. S. & K. Y. Kaneshiro. 1995. Intersexual selection in the Mediterranean fruit fly: Does female choice enhance fitness. Evolution 49: 990-996.

Received 22/VI/04. Accepted 20/VI/05.