Influence of male nutritional conditions on the performance and alimentary selection of wild females of *Anastrepha obliqua* (Macquart) (Diptera, Tephritidae)

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ABSTRACT. Influence of male nutritional conditions on the performance and alimentary selection of wild females of *Anastrepha obliqua* (Macquart) (Diptera, Tephritidae). The behavior of *A. obliqua* females is regulated by endogenous and exogenous factors and among these the presence of males. Experiments were carried out to investigate whether the presence of males and their nutritional condition may affect the behavior of self-selection feeding and the performance of *A. obliqua* females. Females were sorted in groups containing yeast-deprived females and males, and non-yeast-deprived females and males. The females were maintained apart from the males by a transparent plastic screen. Several yeast and sucrose combinations were offered to the females in a single diet block or in separate blocks. Ingestion, egg production, longevity and diet efficiency were determined. The non-yeast-deprived males positively influenced the females performance when the latter were fed with yeast and sucrose in distinct diet blocks. Performance was better in the groups without males and with yeast-deprived males where the females could not select the nutrient proportions (yeast and sucrose in a single diet block).

KEYWORDS. Feeding behavior; fruit flies; longevity; presence of males; production egg.

RESUMO. Influência do estado nutricional do macho na performance e seleção alimentar de fêmeas selvagens de *Anastrepha obliqua* (Macquart) (Diptera, Tephritidae). O comportamento das fêmeas de *Anastrepha obliqua* é regulado por fatores endógenos e exógenos, e entre estes últimos pode estar a presença do macho. Experimentos foram realizados para investigar se a presença do macho e seu estado nutricional alteram o comportamento de auto-seleção alimentar e a performance das fêmeas de *A. obliqua*. Grupos com fêmeas, fêmeas e machos privados de lêvedo e fêmeas e machos não privados de lêvedo foram montados, permanecendo as fêmeas separadas dos machos por uma divisória plástica transparente. Várias combinações de lêvedo e sacarose foram oferecidas em um único bloco de dieta ou em blocos separados para as fêmeas. Ingestão, produção de óvulos, longevidade e eficiência das dietas foram medidas. Os machos não privados de lêvedo influenciaram positivamente a performance das fêmeas quando estas foram alimentadas com lêvedo e sacarose em blocos distintos de dieta. Nos grupos em que as fêmeas não puderam selecionar as proporções de nutrientes (lêvedo e sacarose em um único bloco de dieta), a performance foi melhor para os grupos sem machos e com machos privados de lêvedo.

PALAVRAS-CHAVE. Comportamento alimentar; longevidade; moscas-das-frutas; presença do macho; produção de ovos.

As highly adapted animals with great evolutionary diversity, the insects are considered important subjects for studies concerning nutrition and feeding behavior. Although they have developed morphological, physiological and behavioral means to guarantee acquisition and utilization of nutrients, the insects are constantly facing more immediate problems when food quality varies not only in space but also in time. In addition, the insects needs are not constant: they vary as concerns growth, development and reproduction (Simpson & Simpson 1990; Simpson *et al.* 1995).

All organisms exhibit a series of behaviors that function as bridges between the organism physiological needs, a variety of phylogenetic limits and the environment where they live. These behaviors are highly adapted standards which optimize the reproductive success of the performing individual (Yuval & Hendrichs 2000). These principles are very well illustrated in the behavioral analysis of the Tephritidae family members in general.

The genus *Anastrepha* (Schiner, 1868) is known in the neotropical region mainly because it infests a great number of fruit trees, a lot of them of commercial value (Malavasi *et al.* 2000).

The female behavior is regulated by several external factors such as temperature, predator avoidance, spatial, temporal, seasonal distribution of resources and by internal factors mainly appetite for proteins and search for oviposition (Yuval & Hendrichs 2000), and still in agreement Aluja *et al.* (2001) copulation, presence of males and social context.

A number of studies about the alimentary behavior of *A. obliqua* (Macquart, 1835) females were carried out with virgin females (Message & Zucoloto 1989; Fontellas & Zucoloto 1999; Cresoni-Pereira & Zucoloto 2001a,b). Based in Aluja *et al.* (2001) hypothesis the male presence without copulation can influence through emission of pheromones some aspects of the diet selection of *A. obliqua* females. In *A. obliqua*, as well as in most of Tephritidae, the sexual pheromone is released by the male (Aluja *et al.* 2000). Endogenous and exogenous factors control pheromone production, liberation and perception (Lima & Della-Lucia 2001).

When purified components of the usual diet are offered separated, some insects ingest the nutrients in a proportion that somehow resynthetizes the original diet and is very much superior to it. Other insects ingest two or more natural foods in proportions that guarantee a more favorable balance of nutrients than any of these foods in isolation (Waldbauer & Friedman 1991). This behavior is called alimentary self-selection.

The alimentary self-selection was already observed in a number of insects (Waldbauer & Friedman 1991), including laboratory *Ceratitis capitata* (Wiedemann, 1824) (Cangussu & Zucoloto 1995) and wild *A. obliqua* (Cresoni-Pereira & Zucoloto 2001b). Only females were used in the latter studies. Considering the hypothesis that the females behavior can be mediated by the presence of males, diet selection by *A. obliqua* females is an interesting aspect to be investigated under these conditions.

The aim of this study was to investigate the influence of the presence and nutritional condition of the males on food selection and performance of *A. obliqua* females.

MATERIAL AND METHODS

Wild *A. obliqua* adults were obtained from "cajá-manga" (*Spondias venulosa*) (Engler, 1876) infested fruit (Campinas Agronomic Institute Experimental Farm, Ribeirão Preto).

The infested fruit was collected and placed in plastic boxes (60x40x10cm), with approximately 5cm sand. After drying totally the pulp, the fruits were taken off and the pupae were sift out from the sand, washed in running water and placed in acrylic boxes (11x11x3cm) with sterile sand in the bottom.

The boxes with the pupae and the experimental boxes were maintained at 29 ± 1°C on average in a wooden muffle covered with a glass lid, at 70 to 80% relative humidity and a 12 hours light/12 hours dark photoperiod with 400 lux fluorescent lamps. The acrylic boxes (11x11x3cm) were diagonally divided by a transparent perforated plastic surface. Each side of the box had three lateral holes (1cm diameter) where the diets and water were offered. Water was offered using small cotton stopped glass tubes. The diets were offered in pieces (400 mg each) speared on a pin stuck into a cork.

As they began to emerge, the flies were allocated to three groups: group F, boxes with 8 females each; group FM, boxes with 8 females and 8 yeast (6.5g) and sucrose (11.0g) fed males; and group FMS, boxes with 8 females and 8 sucrose (11.0g) fed males. FM and FMS females and males were separated by the plastic screen. The females were fed according to the below mentioned treatments. In group F, the females were maintained in one half of the box, the other half remaining empty during the experiment in order that all the females had the same space. Group F boxes were maintained in a separate room from the FM and FMS boxes. This procedure was adopted to avoid the FM and FMS males pherormone action on group F virgin females.

Six treatments were prepared and repeated six times for each group (F, FM and FMS). The diets for each treatment were: agar 2.5g, distilled water 100ml, Nipagin 1.5ml (20% solution), yeast 6.5g and sucrose according to each treatment: control (CTL) – 11.0g, treatment 1 (T1) – 5.0g, treatment 2 (T2) – 19.5g, treatment 3 (T3) – 27.0g, and treatment 4 (T4) – 35.0g. The control diet containing 11.0g sucrose was the amount used in other *A. obliqua* studies conferring good performance when consumed in the same yeast diet block (Fontellas & Zucoloto, 1999). The last treatment referred to in this study as SS offered to groups F, FMS and FM was a combination of yeast and sucrose similar to the control treatment but in separate blocks: yeast only (6.5g) and sucrose only (11.0g), simultaneously. The objective was to determine, through ingestion, whether the females select the proportions which produce the best performance in the above mentioned parameters.

The above mentioned male diets consisted of a control diet for the non-deprived males and a sucrose diet (the same composition of the control diet with the exception of yeast) for the yeast-deprived males.

Thus, the different groups (F, FMS and FM) were submitted to different treatments (SS, CTL, T1, T2, T3 and T4). "Group FMS-SS" means "group with 8 females, submitted to the SS treatment (separate nutrients), maintained with 8 males fed with sucrose only", "group F-T1" means "group with 8 females, submitted to treatment 1, with no males", and so on. The comparisons were made between groups with the same treatment and between treatments of the same group.

The diets were prepared by heating in a conventional stove, then placed in Erlenmeyers (200ml), sterilized in autoclave, distributed in Petri dishes (90x12mm) and stored under refrigeration (10°C).

The parameters used were ingestion, egg production, longevity and diet efficiency.

Ingestion was daily determined through the formula (Cangussu & Zucoloto 1995): $I = \dfrac{MST - MSR}{N}$ as follows: I = ingestion (mg/female/day); MST = total dry matter (weight of the diet placed in boxes without flies and maintained under the same experimental conditions in order to control evaporation); MSR = remaining dry matter (weight of the diet placed in the experimental box) and N = number of living flies in the box.

The diets were withdrawn from the box after 24 hours, dried in muffles during additional 24 hours at 80 ± 1°C then weighted to determine ingestion.

Dead flies were daily removed from the box.

Egg production was determined as follows: the fly found dead in the box was removed, desiccated and had its eggs counted. The number of eggs deposited in the box was also counted, divided by the number of living flies in the box plus the removed fly. These numbers were then registered and summed as the flies died until the moment when only one fly was alive in the box, which was then discarded.

Longevity was determined counting the days the females lived in each box. Day 1 was the emergence day.

Diet efficiency was calculated considering egg production (number of eggs produced / diet ingestion) and longevity (days of life / diet ingestion).

Comparisons were made among groups for one treatment (for example, FxFMSxFM in relation to T1) and among all treatments for the same group (for example, SSxCTLxT1xT2 in the group F). Anova on Ranks and Multiple Comparison Tukey Test were apllied (α=0.05).

SigmaStat Program for Windows, version 2.03, Jandel Comporation was used to carry out the statistical tests.

RESULTS

Treatments 3 and 4 (T3 and T4) did not show significant differences in any of the parameters (ingestion, number of eggs and longevity). There wasn´t egg production in these groups and the results were not represented. The egg absence can be explained by low quantity of yeast in relation to sucrose in the T3 and T4 diets. Yeast quantity was insufficient to support egg production.

Table I shows data related to performance of all groups and treatments. Diet ingestion did not show significant difference when different groups (F, FMS e FM) were compared in relation to the same treatment. However, different treatments (SS, CTL, T1 and T2) showed some significant differences when they were compared in the same group. SS females in all groups (F, FMS and FM) ingested significantly less diet that CTL and T1 females, but they did not differ from T2.

In relation to egg production, different treatments showed significant differences in the each group. T1 was treatment that provided the highest egg production by female in all groups, althought in FMS group, T1 has not been different from SS and CTL. Comparing the same treatment in different groups, only T2 treatment in group FM was significantly different from F and FMS groups.

About longevity, only T1 treatment showed significant difference when compared to other treatments in group FMS. When comparison was made among different groups for the same treatment, only CTL and T2 treatments in the FM group showed difference in relation to other groups.

Analyzing these data it is difficult to detect any influence of the male presence or nutritional condition, based on differences that were found.

Table II shows diet efficiency for egg production and longevity. These informations can elucidate the found results. T1 and SS treatments provided the best results in relation to egg production in the same group (F or FMS or FM).

According to Table II, when diet efficiency for egg production of the same treatment was compared in different groups, CTL, T1, T3 and T4 did not showed significant difference among the groups. T2 showed significant difference between F x FM and FMS x FM, but this treatment provided few eggs by female (Table 1) and low efficiency for egg production. The most interesting result was that SS treatment only showed significant difference between F x FM and these groups are the best example of differences caused by male presence. In other studies about these topic, FMS group behaved like F group, because yeast diet deprivation for FMS males.

In relation to diet efficiency for longevity, CTL, T3, T4 and SS did not show significant differences among groups. T1 showed difference between F x FM. T2 showed difference between F x FM and FMS x FM.

The values for ingestion indicated in Table I and used to calculate diet efficiency (Table II) refer to total ingestion,

Table I. Ingestion of diets with different amounts of yeast and sucrose, egg production and longevity of *A. obliqua* females: in the absence of males (F), in the presence of males fed with sucrose only (FMS), and in the presence of males fed with yeast (6.5g) and sucrose (11.0g) (FM). The data represent mean SD. Proportions of yeast:sucrose in the diets with both nutrients: control-CTL (6.5g:11.0g), T1 (6.5g:5.0g) and T2 (6.5g:19.5g) and with separate nutrients: SS (6.5g yeast and 11.0g sucrose).

Groups	Treatments			
	SS	CTL	T1	T2
	Ingestion (mg/female/day)			
F	1,22±0,22a^{1}	2,16±0,47b^{1}	2,16±0,27b^{1}	1,12±0,11a^{1}
FMS	1,21±0,34a^{1}	2,09±0,30b^{1}	2,19±0,25b^{1}	1,19±0,13a^{1}
FM	1,03±0,11a^{1}	1,87±0,55b^{1}	2,72±0,51c^{1}	1,26±0,13a,b^{1}
	Number of eggs/female			
F	66,87±34,09a,b^{1}	48,86±26,21a^{1}	188,05±72,77c^{1}	19,35±5,79b^{1}
FMS	75,53±13,26a^{1}	60,61±19,81a,b^{1}	124,41±52,26a^{1}	19,93±13,72b^{1}
FM	92,58±15,02a^{1}	45,22±21,91a,b^{1}	154,05±56,63c^{1}	2,97±5,00b^{2}
	Longevity (days)			
F	152,16±19,22a^{1}	151,17±57,28a^{1}	140,67±31,34a^{1}	191±18,87a^{1}
FMS	150,16±16,64a^{1}	193,33±37,79b^{1}	95±45,12c^{1}	197,33±25a,b^{1}
FM	124,5±51,79a^{1}	87±19,56a^{2}	97±37,15a^{1}	106±38,17a^{2}

Means followed by different letters in the same line are significantly different (Tukey, $p < 0.05$). Means followed by different numbers in the same column are significantly different for the same treatment (Tukey, $p < 0.05$). The numbers for the SS treatment ingestion represent the yeast diet ingestion plus the sucrose diet ingestion.

including treatment SS. Fig. 1 shows the amounts of diets with yeast and sucrose ingested by females of all groups maintained in treatment SS. No differences were observed in each diet ingestion, nothwithstanding the presence or nutritional condition of the males. In the groups in which the nutrients were offered separately, group F yeast ingestion was almost twice groups FMS and FM ingestions (Fig. 1). Besides that, diet efficiency considering egg production was significantly higher in group FM, contributing to the hypothesis that the females made better utilization of the diet with separate nutrients when non-protein deprived males were present.

In general, when the nutrients were offered in a single diet, groups F had a better performance, coming closer to groups FMS than groups FM. When the nutrients were offered in separate diets (treatment SS), performance was better in group FM, when the diets efficiency was compared. One hypothesis would be that the male presence influence only occurs when they are fed with a protein source and can only be perceived when the females are able to select adequate proportions of the nutrients to be ingested.

DISCUSSION

A lot has been discussed about the importance of the nuptial presents as concerns the reproductive potential of the females; the adult diet is a key factor that can alter the relative importance of nutrient donations of males for the reproductive efficiency of females (Boggs 1990).

The males presence has already been indicated as a responsible factor for higher oviposition rates, as well as higher total fecundity in the fruit flies *Rhagoletis pomonella* (Walsh, 1867) (Opp & Prokopy 1986).

Variation in the quality of the nuptial present can affect *Pieris napi* (Linnaeus, 1758) females preference for the aminoacids present in the nectar (Mevi-Schültz & Erhardt 2004). Apparently, *P. napi* females are unable to evaluate the spermatophore quality before copulation (Wicklund *et al.* 1993); however, they are able to perceive the male presence, since when they are not available the females are forced to search alternative feeding sources (Mevi-Shültz & Erhardt 2004).

Yolk production followed by reabsorption is a widely difused phenomenon among the insects and it is common that the vitellogenesis begins in every oocyte but is completed in only some of them, possibly proportionately to the protein ingestion rate (Chapman 2004). Occasionally in this study, in groups with males, the expectation for copulation due to their presence may have caused a too long expectation for fecundation and oviposition and many eggs may have been reabsorbed, thus the number of eggs produced by group FM-SS females was inferior to that of group F-T1, the two best groups.

It is important to notice that though group FM-SS number of eggs was lower, probably due to the above mentioned reason, ingestion in this group was much inferior to group F-T1, what means less time foraging and diet utilization similar for both groups: diet efficiency for egg production was equal for both groups.

Fruit flies that do not produce eggs cyclically or synchronously seem to absorb oocytes only if not copulated or in response to adverse weather conditions, though it is possible that *Bactrocera oleae* (Gmelin, 1788) also behaves similarly when adequate hosts are not available (Fletcher 1987). In this study, though males were present, copulation did not occur and the eggs may have been reabsorbed.

Insects feed themselves when adults depend little of nuptial presents or larval reserves for reproduction, if alimentary resources are available. Two Coleoptera species, *Photinus ignitus* (Fall, 1927) and *Ellychnia corrusca* (Linnaeus, 1767) behave differently, the first does not feed itself when adult but the latter does. Experiments using radiation to observe destination of resources provided by the males showed that in *P. ignitus* the resources focus oocyte maturation while in *E. corrusca* the resources aim the somatic tissue (Rooney & Lewis, 1999). It is expected that in the species which feed themselves when adults, the benefit of the nuptial

Table II. Diet efficiency as concerns egg production and longevity of *A. obliqua* females: in the absence of males (F), in the presence of males fed with sucrose only (FMS) and in the presence of males fed with yeast (6.5g) and sucrose (11.0g) (FM). The data represent mean ± SD. Proportions of yeast:sucrose in the diets with both nutrients: control-CTL (6.5g:11.0g), T1 (6.5g:5.0g) and T2 (6.5g:19.5g) and with the separate nutrients: SS (6.5g yeast and 11.0g sucrose).

Groups	Treatments			
	SS	CTL	T1	T2
	Diet efficiency as concerns egg production			
F	54.33±25.68a,c^{1}	22.89±12.60b^{1}	90.44±40.89a^{1}	17.18±4.79b,c^{1}
FMS	65.41±12.97a^{1,2}	29.15±9.35b^{1}	58.58±29.03a^{1}	17.36±12.33b^{1}
FM	90.60±7.32a^{2}	23.12±7.40b^{1}	55.53±14.26c^{1}	2.08±3.34d^{2}
	Diet efficiency as concerns longevity			
F	133.55±51.97b,c^{1}	75.53±39.47a,c^{1}	66.24±17.94a^{1}	172.14±29.30b^{1}
FMS	133.87±40.06a,d^{1}	94.35±25.93c,d^{1}	43.66±21.36b^{1,2}	166.84±27.80a^{1}
FM	125.49±58.89a^{1}	50.26±20.38b,c^{1}	35.83±11.93b,c^{2}	84.48±33.75a,c^{2}

Means followed by different letters in the same line are significantly different for the same group(Tukey, $p < 0.05$). Means followed by different numbers in the same column are significantly different for the same treatment (Tukey, $p < 0.05$).

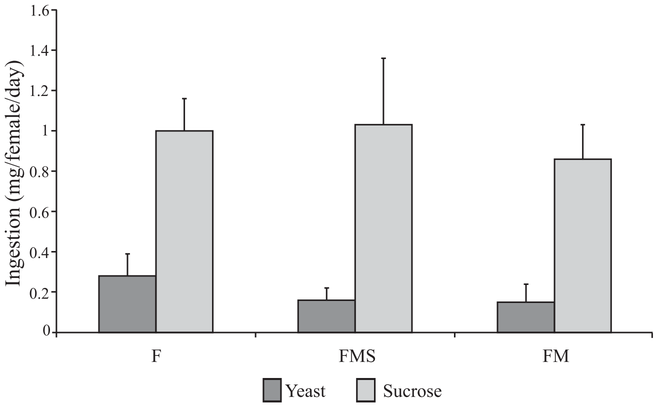

Fig. 1. Ingestion of diets with yeast (6.5g) and sucrose (11.0) by *A. obliqua* females: in the absence of males (F), in the presence of males fed with sucrose only (FMS), and in the presence of males fed with yeast (6.5g) and sucrose (11.0g) (FM). There was no significant difference as concerns diet ingestion among the groups. (Tukey, P > 0.05).

presents reflects directly on longevity, and this could indirectly promote higher egg production in insects as *A. obliqua* which continuously produce eggs and can live long.

The number of oocytes in experiments with *Anastrepha ludens* (Loew, 1873) and *A. obliqua* was high when the females were simultaneously submitted to volatile fruit and male pheromones; counting was low when no chemical stimuli were present and was intermediate when only one type of stimulus was present (Aluja *et al.* 2001a). An interpretation consistent with these results, particularly for *A. obliqua*, is that volatile fruit and male pheromones independently make egg production easier and these facilitating effects can be additive or synergistic in nature. However, as the combinations volatile fruit/pheromones could not be replicated due to the limitations in space and fruit availability, the authors could not discard an alternative interpretation that unknown differences among the rooms the experiment was carried out have generated those standards (Aluja *et al.* 2001a).

All the groups may have reached their maximum reproductive potential along the time, however the methodology did not allow us to daily accompany oviposition in order to observe whether variations occurred in the oviposition peaks in relation to the treatments. *A. obliqua* females are highly plastic and long-living in order to adequate their egg distribution within physiological limits according to the availability of feeding resources.

Female insects can use the nuptial present nutrients to produce more eggs (Vahed 1998). As an alternative, hormonal substances present in the sperma or in the nuptial present can trigger oviposition of more eggs (Eberhard & Cordero 1995). In this study, the presence of males without direct contact with the females and without copulation could have had its effect diluted by time within each experimental group.

Chemically modulated responses can have the effect reduced by habituation due to continuous exposition to the stimulus. The females may have habituated to the experiment conditions presenting their maximum reproductive potential: along the time, despite the male presence, the environment became equal for all the females: eight females confined in half a box with the same food.

Mangan (2003) working with *A. ludens* observed that copulation with well fed males guaranteed a higher production of eggs as compared with copulation with precariously fed males. The same author observed that the presence of males (fed with any diet) lessened ovarian maturation as compared with females non exposed to males.

A comparison between laboratory and wild *A. ludens* has shown that oviposition was inhibited by the constant presence of males in wild females cages as compared with females exposed only once to males aiming at copulation. Frequent exposition to males (24h exposition, each 2 or 3 days) significantly reduced the number of ovipositions and the number of eggs/oviposition. Forced contact between males and females during ovarian maturation influences egg production more than the adults diet (Mangan, 2003).

Though it is known that copulation produces benefits for reproduction in many fruit flies, most of the studies emphasized the effect of factors as adult diet, host stimulus and female density on the ovarian development of the *Anastrepha* species (Fontellas & Zucoloto 1999, Jácome *et al.* 1999; Cresoni-Pereira & Zucoloto 2001a,b; Aluja *et al.* 2001a).

Considering recent literature and the data from this study, it is convenient to investigate the role of copulation on *A. obliqua* females egg production and longevity. The current studies have emphasized the males performance, particularly the comparison of wild, laboratory and sterile (irradiated) males as a function of their applicability in handling programs, and *C. capitata* has been the most studied species (Yuval *et al.* 1998; Field & Yuval 1999; Taylor & Yuval 1999; Aluja *et al.* 2001b; Hendrichs *et al.* 2002; Maor *et al.* 2004).

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