ECOLOGY, BEHAVIOR AND BIONOMICS

Longevity and Fecundity of Four Species of *Anastrepha* (Diptera: Tephritidae)

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Longevidade e Fecundidade de Quatro Espécies de Moscas-das-Frutas do Gênero *Anastrepha* (Diptera: Tephritidae)

RESUMO - Estudos sobre longevidade e fecundidade de moscas-das-frutas são importantes para o entendimento de seus aspectos demográficos e para orientar a implantação de estratégias de manejo integrado. Neste trabalho estudou-se a longevidade de adultos de *Anastrepha fraterculus* (Wiedemann), *A. sororcula* (Zucchi), *A. zenildae* (Zucchi) e *A. obliqua* (Macquart). Avaliou-se, também, o padrão reprodutivo ao longo da vida das espécies *A. sororcula* e *A. obliqua* e a fecundidade, aos dezoito dias de vida, das quatro espécies. A longevidade de *A. zenildae* foi semelhante à de *A. sororcula* e maior que de *A. fraterculus*, seguida de *A. obliqua.* Não diferiu estatisticamente entre os sexos, exceto para *A. obliqua.* O decréscimo da sobrevivência ocorreu mais rapidamente em *A. obliqua,* seguida de *A. fraterculus* e de *A. sororcula*, que foi semelhante a *A. zenildae*. A maior média de óvulos aos 18 dias de vida foi de *A. obliqua*, seguida por *A. fraterculus, A. zenildae* e *A. sororcula*. O padrão reprodutivo ao longo da vida diferiu entre as espécies avaliadas. *A. obliqua* apresentou período reprodutivo mais longo, teve mais de um pico de oviposição e maior produção diária e total de ovos. As diferenças observadas nos padrões de sobrevivência e de produção e postura de ovos das espécies de *Anastrepha* refletem estratégias que podem estar associadas à estabilidade do ambiente e/ou à capacidade diferencial de resposta a ambientes instáveis. Assim, pode-se sugerir a existência de estratégias de sobrevivência semelhantes entre *A. obliqua* e *A. fraterculus* e entre *A. sororcula* e *A. zenildae*.

PALAVRAS-CHAVE: Demografia, *Anastrepha obliqua, A. sororcula, A. fraterculus, A. zenildae*

ABSTRACT - Studies on fruit fly longevity and fertility are important to understand their demographic aspects and to orient implantation of integrated management strategies. This study investigated the longevity of adult *Anastrepha* species *A. fraterculus* (Wiedemann), *A. sororcula* (Zucchi), *A. zenildae* (Zucchi) and *A. obliqua* (Macquart). The reproductive pattern was also assessed throughout the life of the species *A. sororcula* and *A. obliqua* and fertility at eighteen days of life of the four species. *A. zenildae* longevity was similar to *A. sororcula,* longer than *A. fraterculus* and followed by *A. obliqua*. No statistical difference between the sexes was observed, except for *A. obliqua*. The decrease in survival occurred fastest in *A. obliqua* followed by *A. fraterculus* and *A. sororcula*, which was similar to *A. zenildae*. The highest mean of eggs at 18 days of life was for *A. obliqua*, followed by *A. fraterculus*, *A. zenildae* and *A. sororcula*. The reproductive pattern over the lifespan differed among the species assessed. *A. obliqua* presented a longer reproductive period, with more than one oviposition peak and greater daily and total egg production. The differences observed in the survival patterns and egg production and oviposition in the *Anastrepha* species reflect strategies that may be associated with environmental stability and/or differential response capacity to unstable environments. Thus the existence of similar survival strategies can be suggested between *A. obliqua* and *A. fraterculus* and between *A. sororcula* and *A. zenildae*.

KEY WORDS: Demography, *Anastrepha obliqua*, *A. sororcula*, *A. fraterculus, A. zenildae*

The main biological aspects to be studied in economically important species include data for demographic analysis. Demography is defined as the study of populations and the processes that shape them (Carey 1993). Formal demography is based on four aspects of the populations: size (number of organisms within the population), distribution (arrangement of the population in a given time and space), structure (distribution of the population by age and sex) and change (total growth and decline of the population or one of its structural units). The parameters that can be studied include immature survival and duration of the life cycle of immature, adult survival and fertility, population growth rates, mean generation time and age distribution (Carey 1989).

Knowledge of demographic aspects of fruit flies is important because some species are extremely damaging pests for Brazilian and world fruit crops (Malavasi *et al.* 1980, Prokopy & Roitberg 1984, Norrbom & Kim 1988, Nascimento *et al.* 1993). Demographic studies enable strategies of life cycles of different species to be compared and the dynamics of species distribution in different host plants to be better understood. They further supply basic data on birth and death rates for the development of population growth prediction models. These studies are also important for the implantation of integrated management strategies, techniques that include biological control and the use of sterile insects. Both procedures use mass rearing and depend on basic biological data such as birth, death, longevity and fertility rates for success (Levins & Wilson 1980, Carey *et al.* 1988).

The demographic parameters of the populations can be affected by several factors. Four facts on fruit flies have been studied for their effects on demographic parameters: mass rearing, body size, adult nutrition and larvae host (Carey 1989). Regarding mass rearing, in most of the species studied, the flies reared in laboratory have higher fertility rates, reproduce earlier and have a life cycle shorter than wild flies (Carey 1989, Joachim-Bravo & Zucoloto 1998). Body size has been considered a factor that affects survival and fertility of *Ceratitis capitata* (Wiedmann)*, Bractocera dorsalis* (Hendel) and four species of *Anastrepha* (Krainacker *et al.* 1989, Liedo *et al.* 1992, Sivinski 1993). Natural resources used as food by adults and physical factors, such as temperature, affect certain demographic parameters, such as survival and fertility (Hendrichs *et al.* 1993, Jacome *et al.* 1999, Perez *et al.* 2000, Taufer *et al.* 2000). Larvae hosts greatly influence the demographic parameters of several fruit fly species, because as the insects have complex nutritional requirements, the nutrients for adults are available in the sources of natural foods, in the synthesis of substances by symbionts and also in reserves of previous development stages (Fontellas & Zucoloto 1999). Influences of larvae hosts on *C. capitata* demographic parameters have already been reported (Carey 1984, Krainacker *et al.* 1987) and on some *Anastrepha* species (Celedonio-Hurtado *et al.* 1988).

The objective of the present study was to investigate the female fertility and male and female longevity of four *Anastrepha* species: *A. fraterculus* (Wiedmann), *A. sororcula* (Zucchi), *A. zenildae* (Zucchi) and *A. obliqua* (Macquart). These demographic parameters are important to compare the life histories of these species and to support the implantation of integrated management strategies that include biological control and mass rearing of sterile insects.

Material and Methods

The *Anastrepha* species were obtained from infested fruits (guava and mango) from different regions of Bahia state: *A. fraterculus* obtained from guava from the regions of Jequié and Juazeiro, *A. sororcula* obtained from guava collected in the region of Santo Amaro da Purificação, *A. zenildae* obtained from guava from the region of Itaparica and *A. obliqua* obtained from mango from the region of Itaparica.

After collection the fruits were kept separately on sand-filled trays to obtain pupa. After emergence the flies obtained from the different fruits and the different regions were kept separately to be used in the experiments. Fly identification, based on wing analysis and female ovipositor, was performed by specialists from the Bahian Agricultural Development Corporation (EBDA-Salvador). The males were identified presumed the same as the females with the same origin. There was no more than one species of *Anastrepha* per fruit or per region in any batch of fruit used in this study. All the specimens were donated to EBDA-Salvador.

The populations were kept in the laboratory as follows: water and an artificial diet (6.5g Brewer's yeast, 11 g sugar, 2 g agar, 1 g citric acid, 1 ml nipagin and 100 ml distilled water) were offered daily to the adults (Zucoloto *et al.* 1979). At the weekends, a saturated sucrose solution was offered to avoid diet change. The adults were kept in plastic pots (15 x 20 cm) with an opening to place the flies, and a perforated lid. For the oviposition, spheres of colored agar covered with 'parafilm' were placed inside the pots and periodically removed to collect the eggs.

To assess the adult longevity, fifteen recently-emerged flies of each sex from the collected fruits were placed individually in plastic pots (12 x 15cm) and fed on a saturated sucrose solution and water *ad libitum*, both offered in glass tubes covered with cotton. All the individuals were observed daily until their death.

For female fertility assessments, fifteen couples of recently-emerged flies were placed individually in plastic pots (12 x 15 cm) and kept as described previously. In addition to the sucrose solution a diet based on brewer's yeast was also offered to permit egg production. At eighteen days of life, the females were fixed and the eggs counted. This period was chosen because according to Sales (2000) the pre-oviposition period in *A. fraterculus* can vary from seven to 30 days, and thus 18 would be the intermediary period; it has also been reported for *A. obliqua* that after this same period the females began oviposition (Fontellas & Zucoloto 1999). For *A. obliqua* and *A. sororcula* collected in higher amounts, the fertility was assessed throughout life and the eggs laid daily on agar balls were counted during all the fly life. Thirty-five *A. sororcula* females and 50 *A. obliqua* females were used.

The data were analyzed using the Mann-Whitney test for comparison among two samples and the Kruskal-Wallis test to compare more than two samples at 5% significance (Siegal 1956).

Results

The three species collected from guava, *A. zenildae* and *A. sororcula* had similar longevity (Kruskal-Wallis $P > 0.05$) (Fig. 1) but differed from *A. fraterculus* that presented lower

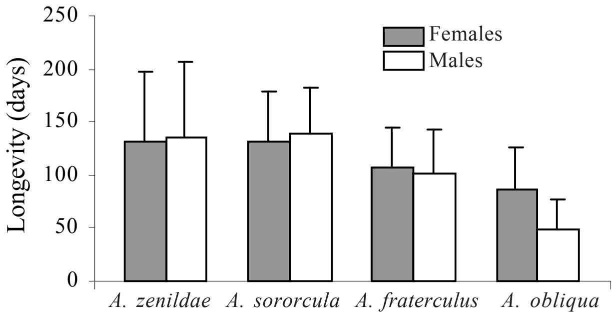

Figure 1. Mean longevity of 15 females and 15 males of the four species. The longevity differed statistically for both sexes, and *A. zenildae* = *A. sororcula* > *A. fraterculus* > *A. obliqua* (Kruskal-Wallis at 5%). There was no statistical difference in longevity among males and females for *A. zenildae* (P = 0.9999), *A. sororcula* (P = 0.4624) and *A. fraterculus* (P = 0.4363); in *A. obliqua* the female longevity was higher than that of the males (P = 0.0068), Mann-Whitney at 5%.

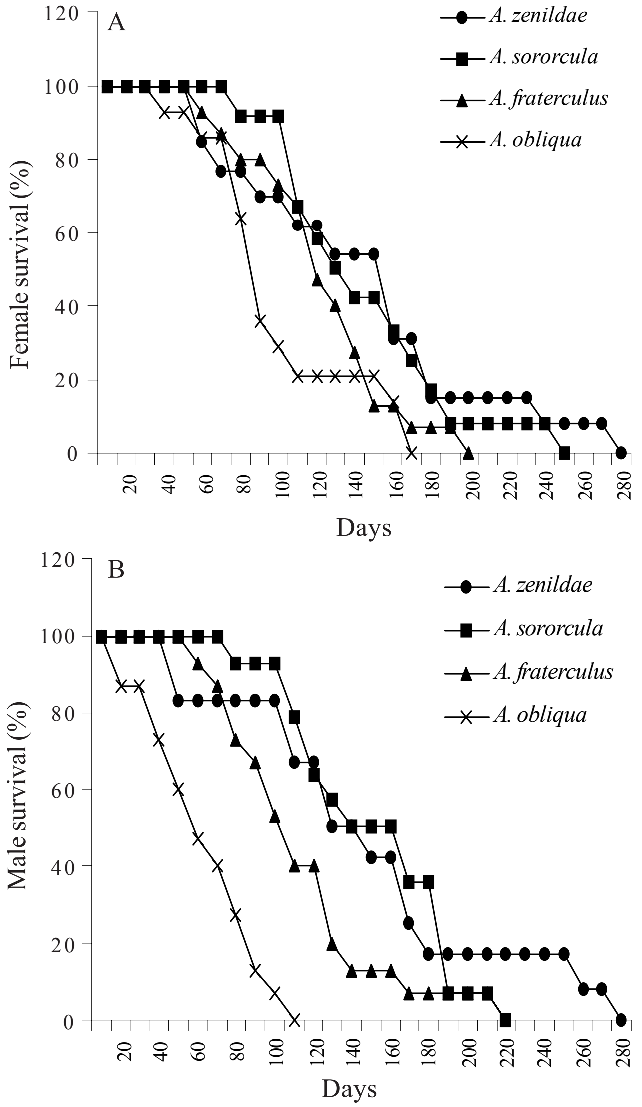

Figure 2. Survival curve of females (A) and males (B) of four *Anastrepha* species.

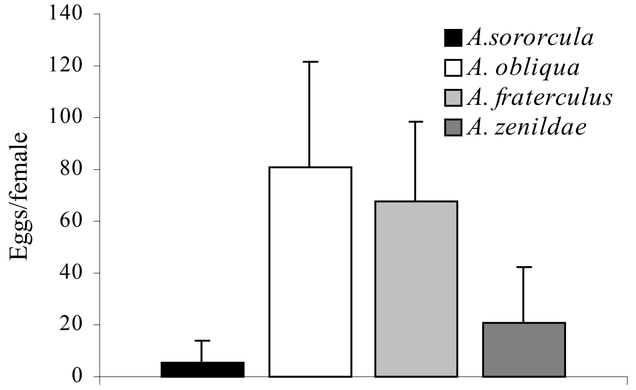

Figure 3. Mean number of eggs in 15 females of four *Anastrepha* species at 18 days of life. *A. obliqua* > *A. fraterculus* > *A. zenildae* > *A. sororcula* (Kruskal-Wallis, P < 0.05).

longevity (Kruskal-Wallis P < 0.05). There was no statistical difference in the longevity among the sexes in any of the species (*A. zenildae* P = 0.9999, *A. sororcula* P = 0.4624 and *A. fraterculus* P = 0.4363, Mann-Whitney test). *A. obliqua*, obtained from mango, presented lower longevity compared with the other species (Kruskal-Wallis P < 0.05). Furthermore, the females of this species had higher longevity than the males (Mann-Whitney P = 0.0068).

The female survival curve (Fig. 2A) showed that some *A. zenildae* females lived up to 265 days, some *A. sororcula* lived up to 240 days and some *A. fraterculus* lived at most 190. Survival decreased faster also in *A. fraterculus*, and on the 115th day 50% of the female had died. In *A. sororcula*, 50% of the females were dead on the 120th day but in *A. zenildae* only on the 140th day 50% of the females were dead. Regarding the males (Fig.2B), some from the *A. zenildae* species also had higher longevity (265 days) and some *A. fraterculus* and *A. sororcula* males lived up to 210 days. On the 100th day, only 50% of the *A. fraterculus* males were alive. For the *A. zenildae* and *A. sororcula* species this reduction to 50% occurred on the 120th and 130th days, respectively. In adult *A. obliqua* that were obtained from mango, some females lived up to 160 days and some males lived up to 100 days. On the 50th and 80th days, 50% of the males and females, respectively, had died.

The data on eggs counted at the 18th day of life of the female (Fig. 3) showed significant differences among the four species studied. *A. obliqua* presented the greatest number of eggs, followed, respectively, by *A. fraterculus*, *A. zenildae* and *A. sororcula* (Kruskal -Wallis, P < 0.05).

Regarding fertility throughout life, the assessed species, *A. sororcula* and *A. obliqua,* differed significantly in the quantity of eggs produced and oviposited (Fig. 4). *A. sororcula* laid 79.7 ±17.93 eggs/female throughout life while *A. obliqua* laid 274.0 + 132.37 eggs/female, differing statistically (Mann-Whitney P = 0.0004).

The two species differed also in several other aspects of reproductive pattern (Fig. 4). The reproductive period was shorter for *A. sororcula*. Oviposition started between the 14th and 16th day but up to the 23rd day, 43% of the females still

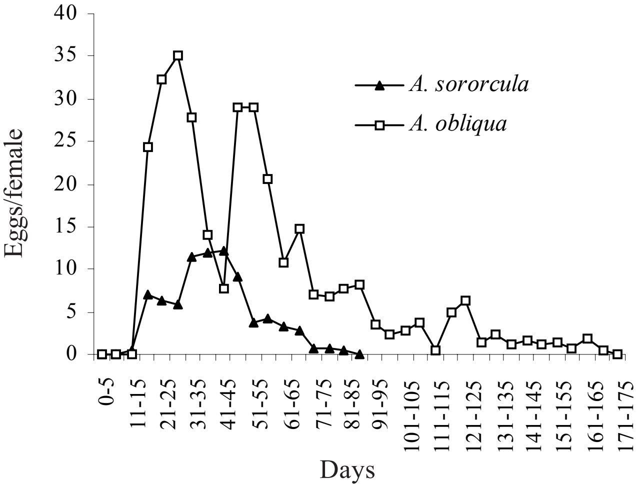

Figure 4. Fertility throughout the life of *A. sororcula* obtained from guava and *A. obliqua* obtained from mango.

had not laid eggs. The maximum time for oviposition was 67 days and the mean was 55.0 ± 9.16 days. The oviposition was longer in *A. obliqua* and there was a more similar distribution pattern of eggs among the females. These began ovipositing on the 16th day, and on the 17th day 100% of the females had already oviposited. The maximum time for oviposition was 149 days and the mean 85.8 ± 39.65 days. The oviposition peak also differed for both species. *A. sororcula* presented oviposition peak between 31 and 45 days and *A. obliqua* presented two oviposition peaks, one between 21 and 25 days and the other between 45 and 55 days.

In 58% of the laying period, *A. sororcula* laid one to five eggs per day (Fig. 5) and in only 1% of the period this oviposition increased from six to eleven eggs, which was the maximum daily production. *A. obliqua* oviposited from one to five eggs in 39% of the total oviposition period and oviposited more than 10 eggs daily in 21% of the period.

The comparison of the percentages of females that oviposited different quantities of eggs were compared (Fig. 6), indicated that the fraction of females that did not oviposit, thus belonging to the class called here ‘without oviposition’ in *A. obliqua,* fell from 100% (at 10 days of age) to 20% at 30 days of age. This change was more gradual for *A. sororcula*, reaching less than 20% only on the 45th day. After the 45th day the ‘without oviposition’ class in *A. sororcula* began to increase again and at the end of the egg laying period (around the 75th day) about 70% of the females belonged to this class, that is, after 75 days most of the females had already stopped oviposition. In *A. obliqua* a new increase of the fraction of females in the ‘without oviposition’ class began after the 30th day and remained in the range of 50-60% up to the end of the oviposition period. Only *A. obliqua* females laid more than ten eggs a day. This fraction, although small, maximum of 12-15% of the females in the period up to 60 days and less than 10% in the period after 60 days, remained constant throughout the oviposition period.

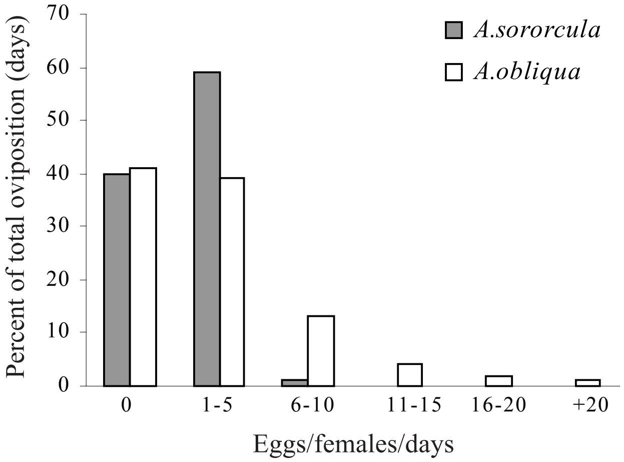

Figure 5. Frequency of distribution of the daily levels of oviposition by the *A. sororcula* and *A. obliqua* females throughout their lives.

In many cases the flies oviposited on several consecutive days, followed by periods without egg production. This behavior was observed much more frequently in *A. sororcula* at the end of the oviposition period, while in *A. obliqua* this occurred throughout the reproductive period.

Some similarities in the oviposition pattern of the two species were detected: oviposition was concentrated in the first weeks of the oviposition period (Fig 4). No eggs were laid in approximately 40% of the total period of oviposition and up to five eggs were oviposited during most of the remaining period (Fig. 5).

Discussion

The results of the present study showed that (1) *A. sororcula*, *A. zenildae* and *A. fraterculus* presented some differences in the demographic parameters assessed, although they came from host fruits of the same species; (2) longevity and fertility were similar – great longevity and low fertility at 18 days for *A. sororcula* and *A. zenildae* obtained from guava; (3) *A. fraterculus* presented the least longevity and greatest fertility at 18 days compared with the other species obtained from guava; (4) *A. obliqua* obtained from mango presented the least longevity and greatest fertility at 18 days compared with the other species studied; (5) males and females from the three species obtained from guava presented similar longevity amongst themselves; (6) *A. obliqua* males had shorter longevity than the females of the same species; (7) the reproductive pattern of *A. obliqua* throughout its life was different from *A. sororcula* mainly because it was longer, had more than one oviposition peak and had greater daily and total egg production.

The species obtained from guava (*A. obliqua*, *A. sororcula* and *A. fraterculus*) although they fed at the immature stage on the same host species and were maintained in the adult stage with the same treatment (sucrose solution) showed different survival patterns. These results can obviously be discussed in function of the quality of the hosts from which they were obtained, because they were fruits obtained from different regions and that can differ quantitatively and/or qualitatively from the nutritional point of view. However, these results can also be attributed to biological strategies characteristic of the

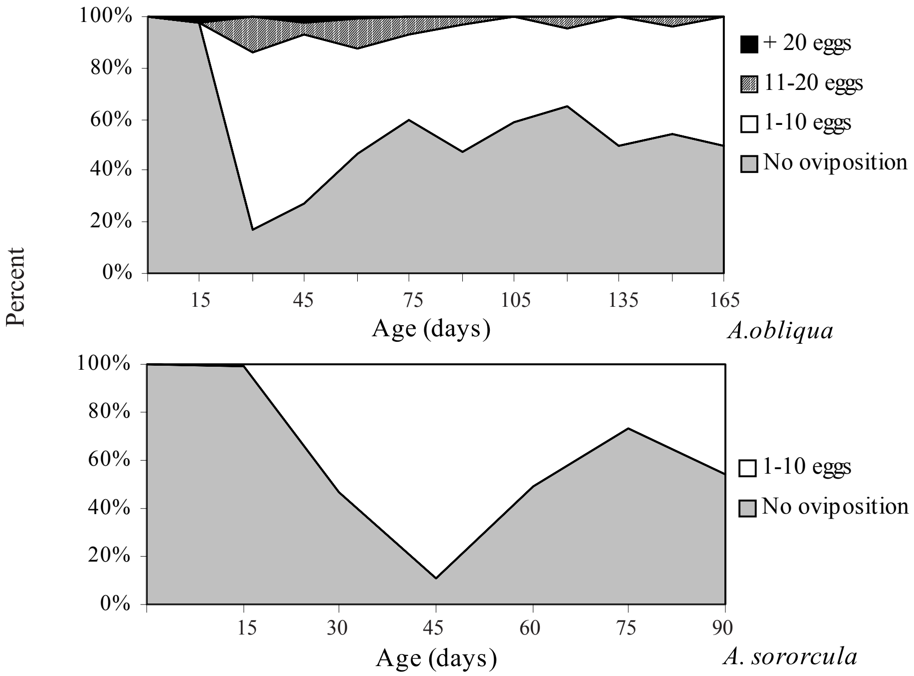

Figure 6. Percentage of *A. sororcula* and *A. obliqua* females that had not started oviposition (without oviposition) and that oviposited different quantities of eggs by age: 1 to 10 eggs, 11 to 20 eggs and more than 20 eggs.

different species, that may not depend exclusively on a single host as the species under study.

A. zenildae and *A. sororcula* did not differ significantly in longevity and had similar survival patterns, but differed from *A. fraterculus*, that lived less. Male and female longevity and the survival pattern of *A. fraterculus* females that had reduced their population to 50% in the 15th week, were similar to those reported by Salles (1992). The survival pattern of the males was different. In the study by Salles the males decreased their population by 50% in the 18th week, and these had a more rapid decrease (50% in the 14th week). There were also differences regarding maximum longevity, and this was greater for the adults in the present study. However, Lima *et al.* (1994) reported mean longevity in adult *A. fraterculus* greater than that obtained here. *A. obliqua* longevity, from mango, was similar to that obtained by Carvalho *et al.* (1998) although in the present study some females presented higher values. For the *A. zenildae* species, these are the first reports of longevity in the laboratory. The differences detected showed that longevity and adult survival patterns can be influenced by the experimental conditions and also can vary according to the population studied. However, in spite of these differences, generally hight longevity can be observed under laboratory conditions for both males and females.

The fertility of the species studied also presented interesting differences. *A. obliqua* was the species that most produced eggs in the first 18 days of life compared to the others whereas *A. sororcula* had the least production in 18 days. *A. fraterculus* and *A. zenildae* produced eggs in intermediate quantity in this period. Although the results presented statistical differences, the fertility pattern of *A. fraterculus* was more similar to *A. obliqua* and the pattern of *A. zenildae* to that of *A. sororcula*.

Several factors affect insect fertility. In addition to intrinsic factors – life histories and phylogenetic restrictions of each species – that determine potential minimum and maximums and the general fertility patterns, environmental factors also influence egg production. Quality of the food received, both in the larval and adult phase are among the most important factors (Slansky & Scriber 1985). Similarly to other insect, species, the ingestion of a protein source at the larval phase is determinant for egg production in fruit flies (Zucoloto 1987, 1988; Message & Zucoloto 1989; Chan *et al.* 1990). As fruits are poor amino acid sources (Bateman 1972) some authors believe that these species meet their needs with the help of symbionts or by ingesting microorganisms found in the fruit (Courtice & Drew, 1984, Hendrichs *et al.* 1993). The need to ingest proteins in the adult stage for ovule production is a controversial point (Zucoloto 2000). According to some authors most of the tephritides are anautogenous (require proteins in the adult stage) (Tsiropoulo 1977, Tsitsipis 1989).

Studies on the female *C. capitata*, reared in the laboratory, showed that they can produce eggs ingesting only sucrose in the adult phase but egg production increases with protein ingestion (Ferro & Zucoloto 1990, Cangussu & Zucoloto 1997). Regarding the *Anastrepha* species studied here, at least for *A. obliqua*, Braga & Zucoloto (1981) reported that the ingestion of proteins in the adult phase is necessary for egg production. Furthermore, the ingestion in the adult phase of natural foods or artificial diets with greater protein concentration increases fertility (Perez *et al.* 2000, Pereira 2001). However, when the concentration of protein exceeds the ideal concentration the effect can be damaging (Pereira 2001). A study with *A. serpentina* also showed that ingestion of foods with a greater quantity of protein made the females more fertile (Jacome *et al.* 1999). In the present study, as all the species received the same food (containing protein) in the adult stage, it is probable that the different results were due to differentiated life strategies and/or quality of the host fruit.

Marked differences were reported between egg production throughout the life and the oviposition patterns of *A. obliqua* and *A. sororcula*. The first had a longer oviposition period, greater egg production and shorter mean pre-oviposition period. These results for *A. obliqua* are similar to those reported by Liedo *et al.* (1992) in a comparative study of this species with *A. ludens* and *A serpentina*. The latter had greater longevity as did *A. sororcula* and *A. zenildae* in the present study, and lower egg production.

An interesting aspect when the relationship between longevity and fertility is analyzed is that there seems to be an inverse relationship between these two parameters. The species that presented greater quantity of eggs at 18 days were those that had lower longevity. The same was observed when the egg production throughout life was compared with the longevity of the species analyzed. These results are inserted in the life histories of the species and are part of the strategies of energy allocation that several animal species use. Such strategies can be influenced by the environmental conditions in which they live. However, the results of this study showed that, even in laboratory conditions, there is a great variation in some aspects of the life history of the different *Anastrepha* species. Within this context similar survival strategies can be suggested between *A. obliqua* and *A. fraterculus* and between *A. sororcula* and *A. zenildae*. According to data from Liedo *et al.* (1992), corroborated by this study, *A. obliqua* can be characterized as a species with high capacity to colonize because it presents a short life cycle and a very intense reproduction period.

Longevity and fertility of an insect are determined by the genetic characteristics of its species and by the environmental conditions to which it is submitted. In nature, according to Salles (2000), longevity of adult fruit flies can also depend on the possibility of infesting hosts. Fertility and oviposition patterns are not only influenced by momentary nutrition and the physiological condition of the insect but can also vary according to the availability of hosts. Thus when the survival patterns and egg production and oviposition are compared in the four *Anastrepha* species, the differences observed reflect strategies that can be associated to environmental stability and/or a differential capacity to respond to unstable environments. One of the most important aspects is the availability of hosts and the flexibility of the species to use varied hosts.

Acknowledgments

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