ECOLOGY, BEHAVIOR AND BIONOMICS

Emergence and Pupal Mortality Factors of *Anastrepha obliqua* (Macq.) (Diptera: Tephritidae) along the Fruiting Season of the Host *Spondias dulcis* L.

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Emergência e Fatores de Mortalidade Pupal de *Anastrepha obliqua* (Macq.) (Diptera: Tephritidae) no Período de Frutificação do Hospedeiro *Spondias dulcis* L.

RESUMO – A emergência e os fatores de mortalidade pupal de *Anastrepha obliqua* (Macq.) (Diptera: Tephritidae) durante a frutificação da planta hospedeira *Spondias dulcis* L. (Anacardiaceae) foram estudados no campo e no laboratório em Sertãozinho, SP. Nas duas condições experimentais, após os períodos de emergência, foram registrados os números de pupários fechados e abertos. Os números de moscas e parasitóides emergidos dos pupários foram registrados. Os pupários fechados foram analisados e, conforme o estado da pupa dentro do pupário, as mesmas foram classificadas em vivas (dormentes) e mortas. Os fatores de mortalidade considerados foram: dessecação, doenças e predação. Foram analisados 1204 pupários, sendo que de 53% emergiram adultos e 47% permaneceram fechados; do total de pupários fechados, 25,3% eram pupas em estado de dormência e 21,7% eram pupas mortas por predadores, doenças e dessecação. Das pupas em estado de dormência, 17,8% eram moscas e somente 0,2% completaram o estágio pupal; 7,5% continham parasitóides, sendo que 4,7% deles emergiram. O parasitismo inicial foi de 8,6% e após a emergência das pupas em dormência aumentou para 15,5%. A ação predatória em condições naturais foi acentuada, especialmente quando o tempo de exposição foi prolongado. Em condições de laboratório, a dessecação foi o principal fator de mortalidade pupal. O parasitismo também contribuiu significativamente para a mortalidade pupal enquanto que, as doenças provocadas por patógenos (fungos e bactérias), parecem ter sido menos significativas. Predadores e parasitóides atuaram efetivamente no controle populacional dessa mosca-das-frutas. Entretanto, os fatores que regulam o estado de dormência, ainda devem ser determinados. A estimativa do estado de dormência, assim como a dos fatores bióticos e abióticos que atuam no estágio pupal são importantes para o entendimento das estratégias adaptativas de *A.obliqua* e seus parasitóides, como também para o desenvolvimento de métodos eficientes de controle em regiões tropicais.

PALAVRAS-CHAVE: Insecta, mosca-das-frutas, estágio pupal, bioecologia.

ABSTRACT - The emergence and pupal mortality factors of *Anastrepha obliqua* (Macq.) (Diptera: Tephritidae) along the fruiting season of the host plant, *Spondias dulcis* L. (Anarcadiaceae), were studied in Sertãozinho, SP, Brazil, under field and laboratory conditions. Eclosed and uneclosed puparia were recorded in two experimental conditions. The number of emerged flies and parasitoids were determined in the eclosed puparia. The uneclosed puparia were inspected and classified into living (dormant) and dead. The following pupal mortality factors were considered: disease, desiccation, predation and parasitism. Out of the total of 1,204 puparia analyzed, 53% emerged and 47% remained uneclosed. Out of the uneclosed puparia, 25.3% contained dormant pupae and 21.7% showed no signs of emergence. Among the dormant pupae, 17.8% were flies, 0.2% of which emerged; 7.5% were parasitoids, 4.7% of them emerged. The initial parasitism was 8.6%, increasing to 15.3% after the emergence of dormant pupae. Predatory activity (natural condition), especially when time of exposure was long, and desiccation (laboratory condition) were the predominant causes of pupal mortality. Variation in mortality caused by parasites and pathogens (bacteria and fungi) seems to play a minor role. Control by predators on fruit fly population is significant. However, the factors, which regulate

induction, maintenance and termination of dormancy, are still to be determined. An estimate of the dormancy and of the biotic and abiotic pupal mortality factors are essential to understand the adaptive strategies of *A.obliqua* and its parasitoids and to develop effective methods of control in tropical regions.

KEY WORDS: Insecta, fruit fly, pupal stage, bioecology.

In Brazil, there are two economically important genera of fruit flies: *Anastrepha* Schiner and *Ceratitis* MacLeay (Diptera: Tephritidae). The West Indian fruit fly or Antillean fruit fly *Anastrepha obliqua* (Macquart) and the South American fruit fly *Anastrepha fraterculus* (Wiedemann) are widely distributed throughout the country and may cause severe damage to fruit orchards (Malavasi *et al*. 1980, Bressan & da Costa Teles 1991).

Optimum integration of the available techniques for the control of fruit flies cannot be performed without knowing their population dynamics. When it comes to dealing with data, we can observe that most of the information about the fluctuation of fruit fly has been based on adult trapping. However, these data represent only part of the population. Accurate information about the size of the population entering in each of the successive developmental stages is required to carry out studies about population dynamics. The family Tephritidae comprises species with different life history strategies, ranging from polyphagous multivoltine to monophagous univoltine (Bateman 1972). As a result, the best control strategy for each species must take into account its phenology and also host characteristics.

Knowledge of pupal stage parameters will be important for the development of integrated control techniques. Information about the mortality factors during the pupal stage of *Ceratitis capitata* (Wiedemann), *Bactrocera* (= *Dacus*) tryoni (Froggatt), *Rhagoletis pomonella* (Walsh) and *Rhagoletis cerasi* (Linnaeus) has been tabulated by Bateman (1974) in a review on the biology of these groups. Despite the importance of *A. obliqua*, little is know about its ecology, phenology, and population biology.

In this study, by sampling fruits from time to time (i. e. weekly), the number of pupae and adults of *A. obliqua* during fruiting season and the mortality factors acting upon them could be determined.

Material and Methods

Study Site. The study was conducted in a small orchard located in Sertãozinho (21º 8' S and 47º 59' W), São Paulo, Brazil. This orchard is 555 m above sea level, in a tropical area. The highest annual temperature is 32ºC and the lowest is 16ºC. The annual precipitation mean is 1,447 mm. Wind is mostly SE-rooted from January to November (6 km/h) and NE-originated in December. The sun shines 2,660 h/year.

Host Phenology and Sampling Methods. The study was developed on *Spondias dulcis* L. tree (hog plum). The tree was about 9-m tall and 6-m canopy. In 1993, the flowering season of *S. dulcis* began at the end of January and the fruits were available from March to August (for about 26 weeks). Infested fruits were collected from the ground and transported to the laboratory in the 8th week (May 17) after the beginning of the fruiting season, 12th week (Jun 14), 14th week (Jun 24) and 19th week (Jul 30). For each week sample, infested fruits were placed in plastic trays (3 kg of fruit per tray) and kept at 26ºC and 70% R.H. Sand (5cm) lay was added to provide a pupation site for the larvae exiting the fruit.

Pupae Collection. As soon as mature larvae started leaving the fruits, they were recovered from plastic trays and transferred to cylindrical plastic containers (25cm high x 10cm diameter) linned with a 20 cm sand layer. The number of larvae obtained in each sampling depended on the abundance of ripe fruits. The date on which the larvae leave the fruit and pupate in the sand was taken as the beginning of the pupal period (date of pupation).

Study Under Field and Laboratory Conditions. *Field conditions* - To determine the dynamics of emergence of *A. obliqua* and its parasitoids, as well as the factors of pupal mortality under field condition, pupa of *A. obliqua* were separated in two experimental groups, A and B. Both experimental groups consisted of 16 containers, with 80 freshly formed pupae collected in several periods. The containers were buried in the locations where the fruits had been collected. After burying the containers in the soil, its wrappage was removed, remaining in the place only the cylinder-shaped block of the inferior extremity of the container. Containers were covered by organdy cloth to keep flies and parasitoids from escaping.

Pupae from group A were kept in these conditions 20 – 27 days which corresponds to the length of pupal development of the fly. Pupae from group B remained for 72 – 80 days after pupation date. Fly and parasitoids emergence was checked daily during the period of exposure of the groups. The emerged flies and parasitoids were counted and removed from the containers. After the periods of exposure the plastic wrappage of each container was put back, facilitating the withdrawall of the cylinder-shaped block.

Laboratory Conditions. To examine the emergence and the factors of pupal mortality in laboratory conditions, remaining fruit fly pupae of each sampling week constituted the group C. As in field studies, freshly formed pupae were placed in plastic cylindrical containers with a 20 cm sand layer. Containers were covered with organdy cloth to keep flies and parasitoids from escaping. The period of exposure was

42 – 53 days, corresponding to the mean of the periods of exposure of the groups A and B (Table 1). Fly and parasitoid emergence was recorded daily.

Eclosed and Uneclosed Puparia Identification. The cylinder-shaped blocks were removed and examined after exposure. For each group, we recorded the number of uneclosed and eclosed puparia which produced adults, flies and parasitoids and those that were damaged by predators or were missing.

The uneclosed puparia were inspected and dissected so that the state of development of fruit flies could be determined. For the puparia to be cut up, the ventral section of their caps were removed and slight pressure on their lateral suture was applied by means of pins. This procedure exposed only part of the ventral surface of pupa heads. The pupae were classified into living (dormant) and dead. The dormant pupa was characterized as a state of arrested development of the pupal stage (i.e. fruit fly pupa or parasitoid larva or imago alive within the puparium when no adult emergence had occurred after the periods of exposure). The dormant pupae were kept under laboratory conditions (25ºC and 70% R.H.) in plastic containers (7 cm high, 11 cm diameter), with a sand layer for about eight moths after pupation date. Containers were covered with organdy cloth and the emergence of flies and parasitoids was recorded daily. The following pupal mortality factors were considered: 1) Disease - number of puparia infected with fungi (pupae filled or covered with filamentous hyphae, or adult insects with a halo of spores on the surface surrounding them) and bacteria (pupae usually darkened in color; with dark fluids, distintegrated tissues and putrid odor); 2) Predation - number of damaged puparia (fragments of pupae and/or pupae destroyed at the soil) or missing; 3) Desiccation - number the undamaged puparia which contained dry insects, either a pupa or a fully-developed fly, and 4) Parasitism - number of emerged parasitoids / number of open puparia x 100.

Larval parasitoids were identified by Van Achterberg (Leiden, Rijksmuseum Van Naturlijke Historie, Netherlands) and pupal parasitoids by A.M. Penteado-Dias (Dept. of Ecology and Evolutive Biology, Federal University of São Carlos, Brazil. The identification of flies was based on Zucchi (2000), Jorge (1987) and White & Elson-Harris (1992).

The number of eclosed, uneclosed, dormant and dead pupae were submitted to analysis of variance by the F test and the means were compared by means of the Tukey test. Whenever necessary, the original data were transformed to $x^{1/2}$ or $(x + 0.5)^{1/2}$.

Results

Table 1 summarizes data on sizes sample, fruit and puparia numbers and the analysis of fruit fly emergence and pupal mortality factors. Sample size were variable because fruit abundance along the fruiting season was variable. Overall, the mean length of the pupal development was 19.3±0.6 days. The longest mean pupal period (23.1±0.7 days) was recorded for pupae obtained from fruits collected at the end of the fruiting season (i.e. fourth sample). For *A. obliqua* and its parasitoids, the period of adult emergence varied from four to six days.

There was no significant difference among groups A, B and C in terms of total number of eclosed and uneclosed puparia ($P<0.05$) (Table 2). The lowest number and percentage of eclosed puparia (14.5%) were observed in group A, followed by group C (15.3%). The highest number and percentage of eclosed puparia (23.2%) were registered in group B, including flies and parasitoids. In group A, the larval parasitoid *Doryctobracon areolatus* (Szèpligeti) (Braconidae) represented 7.4% of parasitism. Meanwhile, in group B, as the puparia were maintained in the soil for a long time (72 - 80 days after date of pupation), parasitism was higher than in groups A and C (12.1%). *D.areolatus* and *Opius bellus* Gahan (Braconidae) (larval parasitoids) and *Odontosema* sp. (Figitidae) and *Spalangia* sp. (Pteromalidae) (both pupal parasitoids) were recorded in this group. In group C, parasitism was very low comparing to group A; only larval parasitoid – *O. bellus* and *D.areolatus* – were registered in this group.

Out of a total of 1,204 puparia analyzed in the three groups, 53% were eclosed (48.5% flies and 4.5% parasitoids), 21,7% were dead and 25,3% entered dormancy (17,8% flies and 7.5% parasitoids) (Tables 1, 3 and 4). Parasitism (8.6%) was registered in eclosed puparia during the period of emergence (Tables 1 and 2). Parasitised and non-parasitised puparia can be easily distinguished, as it is shown in Figs.1E1 and 1E2. From uneclosed puparia (47%), 21.7% contained dead pupae with no signs of emergence. Flies and parasitoids were alive inside the puparia in a state of arrested development (Fig. 1A, 1B, 1C and 1D; Table 3). No significant differences (P£0.05) were observed between mean number of uneclosed puparia and dormant pupae for groups A, B and C. Nevertheless, the mean number of dead pupae was significantly higher at the group B ($P>0.05$). The highest percentage of dead pupae (28.3%) was observed in B. Percentages of dormant pupae below 10% were recorded in groups B and C. Out of the total puparia analyzed in group A, 43% were dormant and 11% were dead. From 305 dormant pupae (taking into account all experimental groups), a total of 215 puparia contained phanerocephalic fly pupae; 90 contained parasitoids at larval or imaginal stages (Fig.1A-D). Only 0.7% (2) out of 315 dormant fly pupae emerged during the mean dormancy period of 50.0±15.5 days after pupation date, while 18.7% (57) parasitoids stemming from fruit fly larvae emerged during a mean dormancy period of 90.0±27.3 days after pupation. After eight months from pupation date, 80.7% of the 315 dormant pupae presented no signs of emergence (Table 4). Pathogens (fungus and bacteria) caused mortality of fly and parasitoid in dormancy, especially in fruit fly pupae. Out of the total 1,204 puparia analyzed, 57.9% were emerged adults (flies and parasitoids), 42.1% were dead pupae and 15.5% were parasitised pupae (Tables 1, 3 and 4).

Significant factors that cause pupal mortality – parasitism and desiccation – were observed in the three groups ($P>0.05$) (Fig. 2). No significant differences in terms of pathogens and predators were observed between the groups ($P>0.05$). Desiccation was the predominant mortality factor in group

Table 1. Design of sampling program for measurement of *A. obliqua* emergence from fruit fly host plant *S. dulcis* from May to August 1993, Sertãozinho, SP.

Sample	Date of harvest	Number of fruits	Date of pupation	Group1	No. of pupae	Puparia (%)			Period of emergence	PD2	Period of exposure (days)
						Eclosed		Uneclosed			
						Frui fly	Parasitoid				
				A	240	15.4	0.4	84.2			20 - 27
1	May 17	255	May 25	B	240	58.4	4.1	37.5	Jun 12 - 16		72 - 80
				C	49	65.3	4.0	30.7		18.7±1.0	42 - 53
				Total	529	39.5	2.3	58.2			
				A	80	38.8	2.5	58,7			20 - 27
2	Jun 14	106	Jun 23	B	80	28.8	7.5	63.7	Jul 09 - 14		72 - 80
				C	53	73.6	7.6	18.8		17.7±0.4	42 - 53
				Total	213	43.7	5.6	50.7			
				A	80	58.7	5.0	36.3			20 - 27
3	Jun 24	139	Jul 06	B	80	48.8	15.0	36.2	Jul 21 - 26		72 - 80
				C	65	66.2	3.0	30.8		16.4±1.1	42 - 53
				Total	225	57.3	8.0	34.7			
				A	80	60.0	6.2	33.8			20 - 27
4	Jul 30	60	Aug 12	B	80	55.0	7.5	37.5	Sept 04 - 08		72 - 80
				C	77	79.2	1.3	19.5		23.1±0.7	42 - 53
				Total	237	64.5	5.1	30.4			
	Total	560			1204	48.5	4.5	47.0		19.3±0.6	

1- A and B – pupae maintened in the field and C in laboratory conditions.
2 - Mean pupal development.

C, whereas in group B - where puparia remained in the ground for a long time (72-80 days) - predation and parasitism have occurred (larval and pupal parasitoids) (Fig. 2).

Discussion

In tropical species the number of adult flies is low in the beginning of the fruiting season. Typically, a population

Table 2. Mean (±SEM) number of eclosed and uneclosed puparia, of *A. obliqua* collected from *S. dulcis*, percentage of parasitism and species of parasitoids, of pupae collected from fruits of *S. dulcis* and maintained under different conditions. Sertãozinho, SP, 1993.

Group[1]	Total	Number of puparia						Period of exposure (days)	Parasitism %	Species of parasitoids (%)
		Eclosed[2]		%	Uneclosed[2]		%			
A	480	43.7±4.9a	[4]	14.5	76.5±42.4a	[4]	25.4	20 - 27	7.4	*Doryctobracon areolatus (*Szepligeti) (2.7)
B	480	70.0±26.1a	[4]	23.2	50.0±14.3a	[4]	16.6	72 - 80	12.1	*D. areolatus* (4.0); *Opius bellus* Gahan (0.4); *Odontosema* sp.(0.6) and *Spalangia* sp. (2.1)
C	244	45.7±13.8a	[4]	15.3	15.2±2.0a	[4]	5.0	42 - 53	4.3	*O. bellus* (0.8) and *D.areolatus* (2.5)
Total	1204	47.0±9.5	[4]	53.0	47.2±15.5	[4]	47.0		8.6	All species (4.6)

[1]A - pupae maintained in the field for 20-27 days, B - pupae maintained in the field for 72-80 days, C - pupae kept under laboratory conditions.
[2]Original data (duly transformed for analysis).
Means followed by the same letter in each column do not differ using Tukey test ($P<0.05$).
Numbers in brackets refer to samples/Group and number in parentheses refer to the frequency of parasitoid species.

Table 3. Results of observations and dissections of fruit fly puparia, expressed by mean (±SEM) number and mean percentage of uneclosed puparia, and dormant and dead pupae of *A.obliqua* on host fruit *S. dulcis*. Sertãozinho, SP, 1993.

Group	Total	Number of puparia		Number of pupae			
		Uneclosed[1]	%	Dormant	%	Dead	%
A	480	76.5±42.4a [4]	54.0	61.5±46.2a [4]	43.0	15.51±4.6a [4]	11.0
B	480	50.0±14.3a [4]	35.4	9.5±8.6a [4]	7.1	40.5±8.6b [4]	28.3
C	244	15.7±2.0a [4]	10.6	5.0±1.9a [4]	3.9	10.2±3.4a [4]	6.7
Total	1204	47.2±15.5 [4]	47.0	25.2±16.0 [4]	25.3	22.1±5.1 [4]	21.7

[1]Original data (duly transformed for analysis).
Means followed by the same letter in each column do not differ using Tukey test (P<0.05).
Numbers in brackets refer to number of samples/group.

multiplies quickly, producing extremely high numbers of offspring. Normally, when the supply of host fruit declines, the population disintegrates (Bateman1972).

In our study, the duration of larval stage has increased along the fruiting season of host plant. This result can be explained by the ovipositing behavior of females during the exploration of the fruit (i.e. pattern of egg distribution among available fruits host) (Bressan Nascimento - submitted). Larvae of frugivorous tephritids (e.g. *A. obliqua*) which can survive to maturity in a given fruit can depend on fruit size, nutritional quality and condition, as well as on larval density. Larval density above certain point typically results in a reduction in body size, delays development or increases mortality (Peters & Barbosa 1977). The mean pupal period decreased from the first to the last sample. For *A. obliqua*, the mean duration of the pupal stage was 23.2± 0.1 days in laboratory (Teles da Silva *et al.* 1983). In field conditions the mean duration of the pupal stage was 9.8±0.3 days when the fruit flies were reared on *Spondias purpurea* L. and 14.3±0.4 days on *Averrhoa carambola* L. (Bressan 1987).

The population of adults of *A. obliqua* during the fruiting of the host *S. dulcis* is sustained by the emergence of flies and by the action of biotic and abiotic factors on the pupal stage. Some puparia showed no sign of emergence due to predation, disease or desiccation. It was found that some parasitised or non-parasitised pupae were in a state of arrested development. As we could not employ a fully experimental procedure to establish adequate distinction between diapause and quiescence, we used the general term dormancy to include both possibilities (Denlinger 1986). The condition of strict diapause grades almost indistinctly to quiescence or aestivation and certain states of arrested development are yet to be classified. The state of arrested morphogenesis (known as diapause) allows many insects to maintain their population throughout unfavorable seasons (Danilevskii 1965, Huffaker & Messenger 1976) or it may be similar to those of polymodal emergence strategy ("bethedging"), approached by Masaki (1982) in his review of summer diapause.

Lees (1955) discussed diapause and quiescence in several hymenopterous and dipterous parasitoids. Among parasitic

Table 4. Total number of dormant pupae of *A.obliqua* and dormant fruit fly parasitoids, mean length of dormancy period, percentage of emergence and mortality of dormant pupae.

Dormant pupae			Mean length of dormancy (days)	Emergence of adults %	Mortality %	Parasitism %
Insects	Number	%				
Fruit fly	215	17.8	50.0±15.5 [2]	0.2	17.7	
Parasitoids	90	7.5	90.5±27.3 [57]	4.7	2.7	
Total	305	25.3		4.9	20.4	15.5

Numbers in parenthesis refer to number of adult flies and parasitoids emerged from dormant pupae.

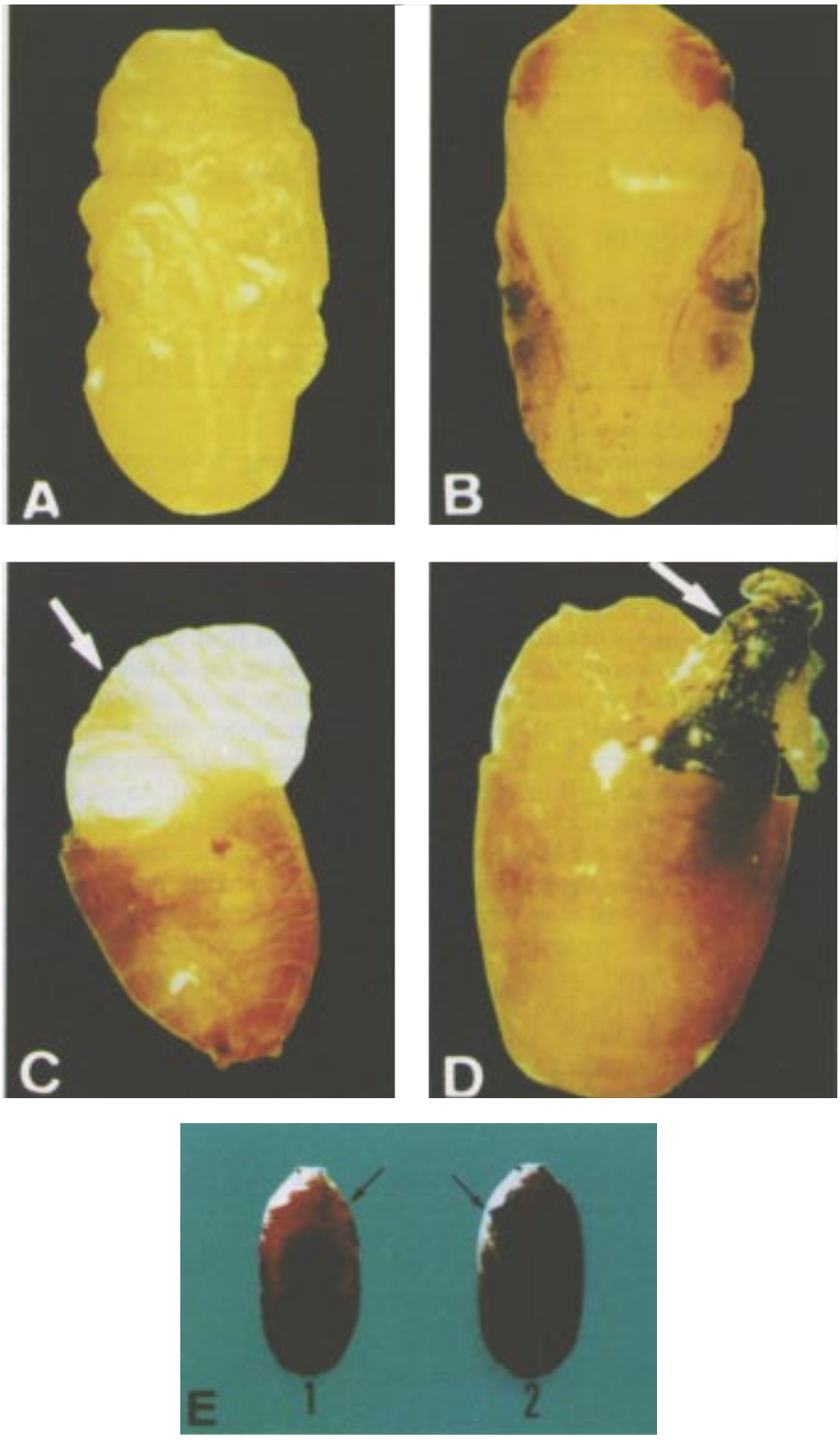

Figure 1. Characterization of the puparium of *A.obliqua*. A to D – Stadia of arrested development of pupal stage (A and B - fruit fly pupae; C – *D. areolatus* larva [arrow]; D – *Spalangia* sp. adult [arrow]; E1 – fruit fly puparium, fly compound eyes [arrow], E2 - parasited puparium, parasitoid compound eyes [arrow].

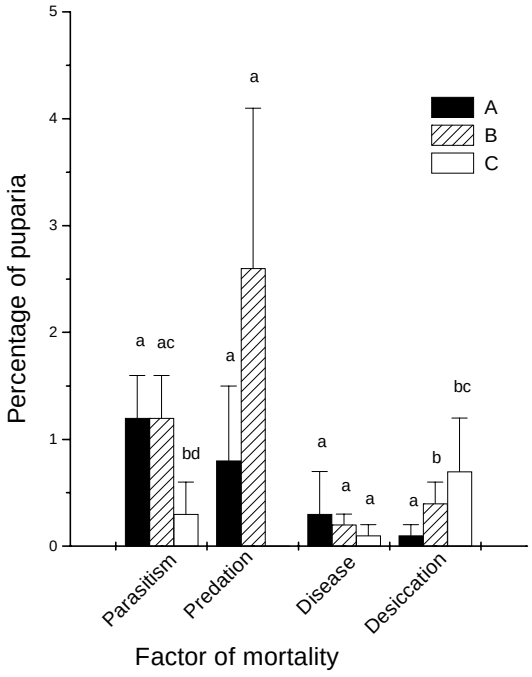

Figure 2. Mean (±SEM) percentage of factors of pupal mortality of *A. obliqua* under field conditions (groups A and B; n= 4) and laboratory conditions (group C; n= 4), during the fruiting season of *S. dulcis* L., Sertãozinho, SP. Means followed by the same letter are not significantly different (P<0.05) using t test.

Hymenoptera, developmental arrests of one sort or another are recorded in every stage of development, including eggs, all developmental instars, and in adults of a few species (Doutt 1959, Aluja *et al.* 1998). Considering the mean lifetime of fruit *flies C. capitata*, *Bactrocera dorsalis* Hendel, *B. curcubitae* (Coquillett), *B. tryoni* (Froggatt) and *B. oleae* (Gmelin), we notice that higher death rates in the pupal stage can be associated with prolonged periods of arrested development (Messenger & Flitters 1954, Bateman & Sonleitner 1967, Paiva & Silva 1974). Denlinger (1986) indicated that dormancy in the tropics implies increased vulnerability to parasites, predators, and pathogens. In tune with the data provided by previous authors, our results accounted for high percentages of mortality in puparia that were in a state of arrested development. For example, only a small proportion (0.2%) of dormant flies emerged. We speculate that the breaking of the puparia for inspection of the pupae's state of development, as well as the long-time development, favoured the colonization of the pathogens.

The main mortality factor of dormant pupae was fungal infection. Nevertheless, other biotic and abiotic factors that regulate populations, such as predation, parasitism, disease and desiccation were found in non-dormant puparia. *A. obliqua* parasitism, caused by the larval parasitoids *D. areolatus* and *O. bellus* and the pupal parasitoids *Spalangia* sp. and *Odontosemia* sp., seems to be relatively constant. A native larval complex and pupal parasites attack most species of fruit flies (Aluja 1994, Canal & Zucchi 2000). Some of these parasites exist in low densities in native hosts. These findings have been based on adult trapping or on samples of fruit taken from the host plant. In Mexico *D. areolatus* had a pattern of decreasing parasitism during the fruiting periods of individual trees as the season changed from rainy to dry (Sivinski *et al.*1997). In reality, the results of this work show that emergence of dormant pupae and of parasitoids can be better evaluated if observed for a large period. After seven days from the beginning of the emergence, it is common practice to get rid of uneclosed puparia, considering that the insects have died. This practice may certainly underestimate the percentage of parasitism and percentage of emergence of different species of fruit flies.

The soil inhabiting stages of the fruit fly, like the mature larva, pupa and teneral adult, are more liable to being aimed at by biotic and abiotic factors (Bateman 1972, Wharton *et al.* 1981, Aluja *et al.* 1990). Predators and pathogens may contribute to the decrease in the fruit fly population size. The mortality caused by predators is important for regulating fruit fly densities (Bateman 1972), especially for fruit flies whose pupation period is long. In the data provided by Bateman & Sonleitner (1967) and Bateman (1974), a similar pattern of pupal predation was observed in relation to *B. tryoni*, *B. dorsalis* and *B. oleae*. Among soil predators, ants have particular importance. They have been observed carrying of mature larvae, pupae, and newly emerged adults (Bateman 1972, Bressan & Teles 1990). Bateman (1972) appointed Staphylinidae, Carabidae, Chrysopidae, Pentatomidae and Dermaptera (earwigs) as predators of the larvae and pupae in Tephritidae. The influence of abiotic factors - such as soil moisture observed during desiccation - was the most important component of pupal mortality in laboratory conditions. Bateman (1974) pointed out that there is a connection between soil moisture and the pupal mortality of *B. tryoni* throughout long and dry periods.

The data available in this work seem to show that predation (natural condition) - especially when time exposure is long - and desiccation (laboratory condition) were the predominant causes of pupal mortality. Considerable variation occurs in mortality caused by parasitoids whereas pathogens (bacteria and fungi) seem to play a minor role. Predatory control on fruit fly population is significant.

Finally, our results seem to imply that an important regulation process occurs during the pupal stage of *A. obliqua*. Arrests of pupal stage developments of flies and parasitoids suggest the presence of developmental adaptation (e.g. not all individuals entered dormancy). In the present study, out of a total of 1,204 puparia analyzed, 25.3% entered dormancy and 53% did not. At the beginning of the season, dormant pupae emergence could be invoked to explain population explosion that exists in tropical species, however migration can satisfactorily contribute to this phenomenon. Although we have not determined the factors that regulate dormancy induction, maintenance and termination, an estimate of this phenomenon is essential for understanding the phenological strategies of *A.obliqua* and its parasitoids. This knowledge is also required for stablishing effective strategies of insect

management, specifically in predicting timing of dormancy, migration, development and reproduction of pests and beneficial species; in selecting well-adapted species or biotypes of natural enemies for use in biological control; and in manipulating cultural practices to reduce pest damage. Predators and parasitoids could be used in the future control of *A. obliqua*, though we emphasize the need for more ecological knowledge.

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