

# Ecological Evidence for Diapause in Four Native and One Exotic Species of Larval-Pupal Fruit Fly (Diptera: Tephritidae) Parasitoids in Tropical Environments

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**ABSTRACT** We provide ecological evidence for the existence of diapause in 4 native and an exotic species of larval-pupal fruit fly (Diptera: Tephritidae) parasitoids inhabiting tropical environments. We worked in central Veracruz, Mexico, in perturbed tropical deciduous and subdeciduous forests and in diversified agroecosystems during 4 yr (1993–1997). The native parasitoid species *Doryctobracon areolatus* (Szépligeti), *Utetes (B.) anastrephae* (Viereck) (Hymenoptera: Braconidae), *Aganaspis pellenaroi* (Brethes), *Odontosema anastrephae* Borgmeier (Hymenoptera: Eucolidae), and the introduced species, *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) all exhibited diapause. Importantly, none of the 6 *Anastrepha* species serving as hosts for these parasitoids entered diapause. The larval-pupal parasitoids *Doryctobracon crawfordi* (Viereck) (Hymenoptera: Braconidae; native) and *Aceratoneuromyia indica* (Silvestri) (Hymenoptera: Eulophidae; introduced) and the pupal parasitoids *Coptera haywardi* (Hymenoptera: Diapriidae; native), and *Pachycrepoides vindemiae* (Rondani) (Hymenoptera: Pteromalidae; introduced) did not exhibit diapause even though they were collected in the same region and at the same time of year. Importantly, in diapausing species not all populations exhibited the phenomenon and, furthermore, in those that did, patterns were polymodal (proportion of a given population entering diapause fluctuated between 0.4 and 100% depending on species). All diapausing individuals dissected from fly pupae were 3rd instars. Diapause lasted up to 11 mo (depending on the particular species) and was predominantly observed in fly pupae collected between the months of September and December (time of year when temperature and rainfall drops and days become shorter). Based on observations on tree fruiting phenology, we conclude that diapause is an effective mechanism allowing parasitoids to bridge periods during which fruit fly hosts (i.e., larvae) are scarce or not available. We discuss our findings in light of their ecological and practical implications.

**KEY WORDS** diapause, parasitoids, fruit flies, Tephritidae, Braconidae, Eulophidae

INSECTS LIVING in both tropical and temperate zones must cope with seasonal environments. Through much of the tropics the most apparent annual cycle is the amount of rainfall. Although attenuated if contrasted to regions at higher latitudes, seasonal variation in the tropics can also be measured in daylength and temperature (Schwerdtfeger 1976). Despite the importance of such abiotic factors, seasonal differences in the abundance of tropical insects is mainly caused by changes in biotic elements of the environment (Denlinger 1979, 1986). For example, resource availability (i.e., suitable hosts), has been identified as the principal reason for population fluctuations in fruit flies of the genus *Anastrepha* (Celedonio et al. 1995, Aluja et al. 1996).

Diapause is a means of coping with environmental changes. Tauber et al. (1983, 1986) defined diapause as “a hormonally-mediated state of low metabolic activity, associated with reduced morphogenesis, in-

creased resistance to environmental extremes, and altered or reduced behavioral activity. It occurs during a genetically determined stage of metamorphosis and generally in response to token environmental cues that precede unfavorable conditions.” Diapause (also referred to as “dormancy”) enables insects to circumvent adversity and synchronize emergence with their hosts (Denlinger 1986; Tauber and Tauber 1976, 1981; Masaki 1980). Diapause induction, maintenance, and termination is triggered principally by temperature and photoperiod but availability and quality of food, physiological status of the host, humidity, population density, or host type also play a role (Tauber and Tauber 1976; Tauber et al. 1983, 1986; Hodek 1983; Taylor and Spalding 1986; Vinogradova 1986). Even though better studied in Temperate Zone insects, diapause is also very common in insects inhabiting tropical environments (Young 1982, Denlinger 1986).

Diapause in fruit fly (Diptera: Tephritidae) parasitoids has been repeatedly reported in temperate zones (e.g., AliNiazee 1968, 1985; Carl 1968; Prokopy 1968; Cameron and Morrison 1974; Maier 1981; Hoffmeister 1990, 1992; Gut and Brunner 1994) but has not been well studied in tropical environments. There are 2

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Table 1. General description of study sites

Site	Altitude, m	Northern latitude	Western longitude	Climate type	Mean annual rainfall, mm	Mean annual temp, °C
La Mancha	35			Aw <sub>2</sub> <sup>n</sup>	1,128	25.9
Playa Oriente	119			Aw <sub>1</sub> (w <sup>n</sup> )(i')	1,234	25.4
Rinconada	323			Aw <sub>0</sub> (w <sup>n</sup> )(i')g	916	24.9
Apazapan	347			Aw <sub>1</sub> (w <sup>n</sup> )(i')g	1,250	25.5
Jalcomulco	380			Aw <sub>2</sub> (w <sup>n</sup> )i	1,107	24.5
San Pedro	932			(A)C(m)a(i')g	1,823	18.8
Llano Grande	950			(A)C(m)aig	1,250	25.0
Monte Blanco	1,050			(A)C(m)(w <sup>n</sup> )big	1,750	20.0
Tejeria	1,000			(A)C(fm)a	1,600	21.0
Teocelo	1,000			(A)C(m)a(i')g	2,108	19.5
Cosautlan	1,298			(A)C(m)a(i')g	2,000-2,500	19.0
Xalapa	1,440			C(fm)w <sup>b</sup> (i')g	1,514	17.9

Classification of Köppen modified by Garcia (1981). Group A: Warm, humid. Mean annual temperature between 22 and 26°C and that of the coldest month >18°C. Aw, Warm subhumid with rainfall during summer. Precipitation of the driest month less than 60 mm. Proportion of winter rainfall between 5 and 10.2%. Aw<sub>0</sub>, The driest of the warm subhumid. Rainfall during summer. Total precipitation <43.2 mm. Proportion of winter rainfall between 5 and 10.2%. Aw<sub>1</sub>, Intermediate between Aw<sub>0</sub> and Aw<sub>2</sub>. Total precipitation between 43.2 and 55.3 mm. Proportion of winter rainfall between 5 and 10.2%. Aw<sub>2</sub>, The warmest of the warm-subhumid. Rainfall during summer. Total precipitation >55.3 mm. Proportion of winter rainfall between 5 and 10.2%. Subgroup (A)C: Semiwarm. The warmest of the temperate climates. Mean annual temperature >18°C and of coldest month lower than 18°C. It is subdivided into 2 subtypes: (A)C(fm), Humid semi-warm. The warmest of temperate climates type C. Mean annual temperature over 18°C and of coldest mo <18°C. Rainfall all year long. Precipitation during driest month over 40 mm. Proportion of winter precipitation <18%. (A)C(m), Humid semi-warm. The warmest of temperate climates type C. Mean annual temperature over 18°C and of coldest month <18°C. Summer rains influenced by monsoon. Proportion of winter precipitation <18%. Precipitation of driest month lower than 40 mm. Other symbols: a, Warm summer. Temperature of the hottest month >22°C. b, Long and cool summer. Mean annual temperature between 5° and 12°C and temperature of hottest month between 6.5° and 22°C. i, Isothermal type of annual oscillation of the mean monthly temperatures (<5°C). Corresponds to the difference of the mean monthly temperature of the warmest month with respect to the coldest month. (i'), Little interannual oscillation in the mean monthly temperatures (oscillations between 5 and 7°C). g, Pattern of annual temperature Ganges type (i.e., warmest month always before June). (w), Proportion of winter precipitation <5% with respect to the lower total. <sup>n</sup>, Midsummer drought (i.e., short, rain-deficient period occurring in the middle of the rainy season).

early references to probable diapause in fruit fly parasitoids inhabiting tropical environments. Pemberton and Willard (1918a, b) reported "hibernation" in *Biosteres* (= *Diachasma*) *tryoni* (Cameron) and in *Opius fullawayi* (Silvestri). Darby and Knapp (1934) discovered that a few individuals of *Doryctobracon* (= *Opius*, *Diachasma*) *crawfordi* (Viereck) parasitizing *A. ludens* "seemed to remain in a quiescent state of suspended development" and presumed it was diapause. Some individuals emerged 7 mo after pupation. Clausen et al. (1965) reported larval diapause in *Diachasmimorpha* (= *Biosteres*) *longicaudata* Ashmead variety *novacaledonicus*, a widely distributed species introduced to the American Continent from Asia, and in *Opius formosanus* Fullaway, *O. compensans* Silvestri (both species are junior synonyms of *D. longicaudata*) and *Opius watersi* Cameron (= *Diachasmimorpha dacustii*) as well (the latter 3 records apparently based on reports by Christenson 1953 and Marucci 1952). Maximum length of diapause was 12, 15, and 9 mo for *D. longicaudata*, *O. formosanus*, and *O. watersi*, respectively. Ashley et al. (1976) indicate that diapause in *D. longicaudata* was effected by cool temperatures and low levels of moisture content in the pupating medium.

Our objective was to document the existence of diapause in native and exotic parasitoids of fruit flies in the genus *Anastrepha* living in tropical environments in the State of Veracruz, Mexico. The same species of parasitoids had been previously reported in another State of Mexico (Chiapas) by Aluja et al. (1990) but these authors did not report the existence of diapause. In addition, we wanted to document the

occurrence of diapause within various habitats and describe differences in environmental factors that have been reported to select for diapause. Distribution, relative abundance, ecology, and some aspects of the bionomics of these parasitoids are described elsewhere (Sivinski et al. 1997, 1998; López et al. 1999).

## Materials and Methods

**Study Sites.** Our study was divided into field and laboratory components. In the case of insects held under field conditions, parasitized fruit fly larvae were collected from infested fruit in the field. Resulting pupae were then kept in situ in protected enclosures until fly or parasitoid emergence. For laboratory studies, infested fruit was collected in the field, and parasitized pupae were kept in the laboratory until fly or parasitoid emergence. Infested fruit was collected in 12 sites located in central Veracruz, Mexico: La Mancha, Playa Oriente, Rinconada, Apazapan, Jalcomulco, San Pedro, Llano Grande, Monte Blanco, Tejería, Teocelo, Xalapa, and Cosautlán. Exact location (latitude, longitude), altitude, mean annual temperature and rainfall and climate type are described in Table 1. Fruiting phenologies of those fruit fly hosts most likely to harbor parasitoids are shown in Fig. 1.

**Fruit Collection Methods. Study Under Laboratory Conditions.** Fruits harboring parasitized and unparasitized fruit fly larvae (i.e., infested) were collected in the field and transported to the laboratory in Xalapa. There, fruits were weighed and placed in plastic trays. This is described in detail in Sivinski et al. (1997) and López et al. (1999).

HOST, MONTH	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
<i>Spondias purpurea</i> L.												
<i>Ximenia americana</i> L.												
<i>Mangifera indica</i> L.												
<i>Spondias mombin</i> L.												
<i>Psidium guajava</i> L.												
<i>Tapirira mexicana</i> Marchand												
<i>Psidium sartorianum</i> (Berg.) Nduz												
<i>Citrus sinensis</i> (cultivar Corriente) (L.) Osbeck												

Fig. 1. Fruiting phenology of most important fruit fly hosts in Central Veracruz, Mexico. Fruit fly larvae developing in these hosts are in turn attacked by various species of larval-pupal parasitoids.

**Study Under Field Conditions.** Infested fruits were collected from the ground and placed in plastic trays (2 kg of fruit per tray), which in turn were placed over a plastic washbowl. Soil (5 cm) was added to provide a pupation site for larvae exiting the fruit. Washbowls were protected from rainfall with corrugated fiberglass. The washbowls were placed in the locations where fruit had been collected. To keep predators away Tangle-Trap Insect Trap Coating (Tanglefoot, Grand Rapids, MI) was applied to the rim of the washbowls.

**Pupal Processing Under Field and Laboratory Conditions.** *Field Conditions.* Fruit fly pupae were recovered from washbowls and placed in 500-ml plastic containers with 200 ml of soil (100–200 pupae per container). Soil used was always from the site where fruit had been collected. Containers were covered with organdy cloth to keep flies and parasitoids from escaping. Between 5 and 8 containers (number depended on availability of pupae) were placed in “emergence cages.” Fly and parasitoid emergence was checked once a week until the last individual emerged (9 mo in some cases). All adults (live and dead) and pupal cases were removed weekly and brought back to the laboratory for identification. We tried to mimic natural moisture conditions by wetting the soil and leaf litter in protected containers (emergence cages) every time there was natural rainfall. A hygrothermograph was placed adjacently to record ambient temperature and relative humidity.

*Laboratory Conditions.* As in field studies, pupae were placed in 500-ml plastic containers. After most insects had emerged, the few remaining pupae were transferred to 50-ml containers. Vermiculite instead of soil was used to cover pupae. Vermiculite was moistened weekly and parasitoid and fly emergence recorded once a week. All containers were kept under ambient conditions in a room protected from rainfall but with no control over other environmental factors.

**Parasitoid and Fly Identification.** Parasitoids were identified by Robert Wharton (Texas A&M University, College Station, TX) and Lubovir Masner (Canadian Bureau of Land Resources). Flies were identified by Vicente Hernández-Ortíz (Instituto de Ecología, A.C., Xalapa, Veracruz). Voucher specimens were placed in the Texas A&M University and Instituto de Ecología, A.C. permanent insect collections.

**Measurement of Environmental Conditions.** *Field.* During the 1995–1996 season during which we maintained diapausing parasitoids in the field, we placed 3 hygrothermographs in situ to monitor temperature and relative humidity. The hygrothermograph (Ota Keiki Seisakusho, Type MN-5, Tokyo) was placed inside a wooden frame to protect it from rainfall and theft. Sites were Llano Grande (under a *Spondias mombin* L. canopy), and Tejería [under canopies of *Psidium guajava* L. and *Citrus sinensis* L. (Osbeck) trees]. We also consulted temperature and rainfall records during the last 10 yr in 3 representative sites: La Mancha (35 m, 19° 35' North latitude and 96° 22' West longitude), Jalcomulco (380 m, 19° 20' North latitude and 96° 45' West longitude) and Teocelo (1,000 m, 19° 24' North latitude and 96° 58' West longitude). Data bases used belong to the Servicio Meteorológico Nacional, Servicio Meteorológico y Climatológico del Estado de Veracruz, and Comisión Federal de Electricidad, División Hidrométrica Golfo.

Results

**Environmental Conditions Prevalent During Study.** We only provide detailed information on the most representative sites. La Mancha: Precipitation peaks during July and remains high until September. Temperature is quite regular throughout the year. Apazapan: peak temperature and rainfall is observed during the months of May and July, respectively (Fig. 2 A and B). Llano Grande: patterns are very similar to those observed in Apazapan. Measurements taken during 1996 in situ in Llano Grande coincided with the 10 yr averages recorded at the weather station in Jalcomulco (Fig. 3A). Tejería: mean temperature also peaks at this site in May. However, temperatures are slightly lower than those of sites located at lower elevations (e.g., Llano Grande). Peak rainfall in Teocelo (a site near Tejería) occurred 1 mo earlier than in Apazapan and Jalcomulco (Fig. 3B). Xalapa (ambient): peak temperature is reached during May. However, temperatures recorded in the room where pupae were kept during May of 1995 were 4 degrees higher than the 10 yr average (Fig. 4A). Nevertheless, on a yearly basis temperature in Xalapa is significantly lower than in all the other sites described before (Table 1). Xalapa (Laboratory): Temperatures were

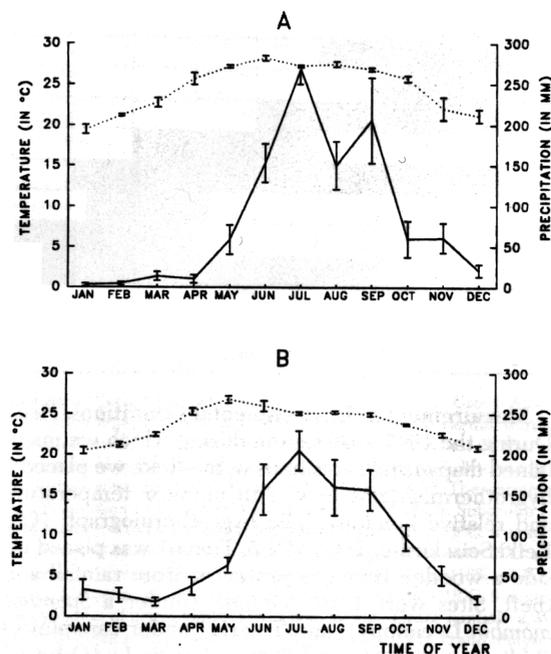


Fig. 2. (A) Temperature (.....) and rainfall (—) in La Mancha (6 yr average). (B) Temperature (.....) and rainfall (—) in Apazapan (10 yr average).

uniform, with an average of 26°C (Fig. 4B). Variations in average daylength in the study region are also depicted in Fig. 4B. Days were longest during May to

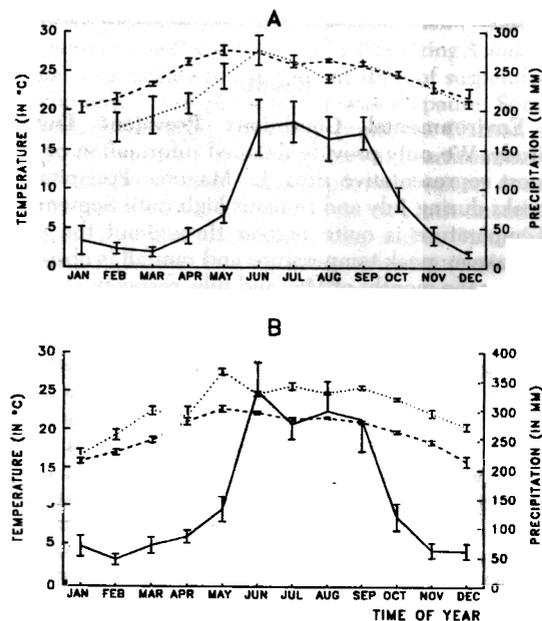


Fig. 3. (A) Temperature in Llano Grande during 1996 (.....) and temperature (---) and rainfall (—) in Jalcomulco (site close to Llano Grande) (10 yr average). (B) Temperature in Tejería during 1996 (.....) and temperature (---) and Rainfall (—) in Teocelo (site close to Tejería) (10 yr average).

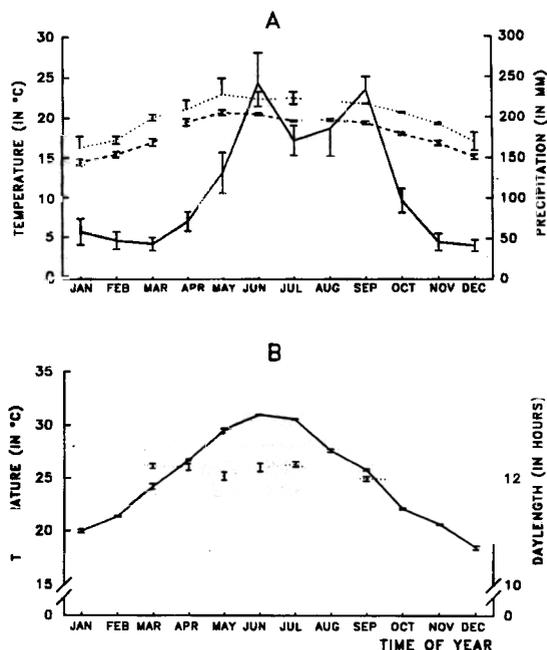


Fig. 4. (A) Temperature outside laboratory in Xalapa during 1995 (.....) and temperature (---) and rainfall (—) in Xalapa (10 yr average). (B) Temperature inside laboratory in Xalapa during 1995 (.....) and mean average daylength (in hours) in the study region (—).

July. Importantly, they started to become shorter during July–August.

**Occurrence of Diapause.** Fruit fly pupae that contained diapausing parasitoid larvae (3rd instars in all cases) could be distinguished from nondiapausing larvae because of their smaller size. This is particularly obvious at the end of the diapausing period. To illustrate this, we present a picture contrasting nondiapausing and diapausing parasitoid individuals in larval and prepupal stages and showing pupal cases containing diapausing and nondiapausing parasitoids (Fig. 5).

Of 10 species collected in the field (see López et al. 1998 for details), only the larval-pupal parasitoids *Doryctobracon areolatus*, *Utetes anastrephae* (Braconidae), *Aganaspis pellenaroi*, *Odontosema anastrephae* (Eucolilidae) (all native) and *D. longicaudata* (Braconidae) (introduced) exhibited diapause (Table 2). The larval-pupal parasitoids *D. crawfordi* (Braconidae) (native) and *Aceratoneuromyia indica* (Eulophidae) (introduced) and pupal parasitoids *Coptera haywardi* (Diapriidae) (native) and *Pachycrepoides vindemiae* (Pteromalidae) (introduced) did not exhibit diapause even though they were collected in the same region and at the same time of year. Furthermore, not all populations of a particular species entered diapause (Table 2) and when such was the case, diapause patterns were polymodal exhibiting a series of peak emergences (Figs. 7–9). Diapausing individuals were most commonly recorded during September and December and at sites >1,000 m above sea level, with mean annual temperatures under 20°C and rain-

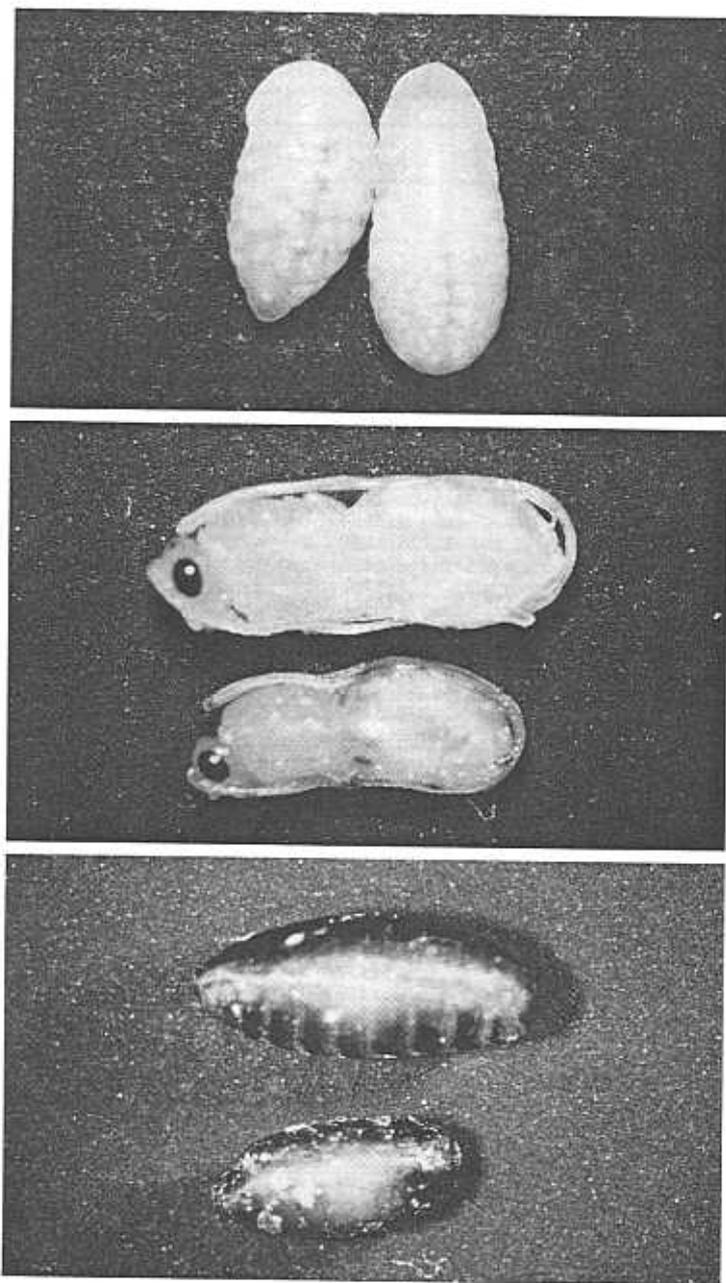


Fig. 5. Picture of diapausing and nondiapausing *D. areolatus* individuals in larval and prepupal stages and showing pupal cases containing diapausing and nondiapausing parasitoids. Note the marked difference in size.

fall >1,500 mm (Table 3). The longest diapause periods (11 mo) were recorded in *Doryctobracon areolatus* stemming from fruit fly larvae that had developed in *Spondias mombin*, and *Aganaspis pellenaroi* and *Utetes anastrephae* stemming from fruit fly larvae that had developed in *Psidium guajava* and *S. mombin*, respectively. This contrasts sharply with mean generation times recorded under laboratory conditions (Table 4). The shortest diapause period was recorded in *Diachasmimorpha longicaudata* (Table 2). Overall

(taking into account all fruit fly hosts and study sites), *D. areolatus* was the species with the highest proportion of individuals entering diapause (Table 2). We find it noteworthy that none of the *Anastrepha* species serving as hosts of the parasitoids entered diapause (*alveata* Stone, *fraterculus* (Wiedemann), *ludens* (Loew), *obliqua* (Macquart), *serpentina* (Wiedemann) and *striata* Schiner).

To illustrate parasitoid emergence schedules we have selected a few representative cases between 1993

Table 2. Proportion of parasitoid individuals that entered diapause according to fruit fly host plant from which parasitoids stemmed

Study period; parasitoid species; fruit fly larval host plant	Proportion entering diapause <sup>a</sup>						Length of diapause period, mo	
	Lab <sup>b</sup>	N <sup>c</sup>	Total Pupae <sup>d</sup>	Field <sup>e</sup>	N	Total Pupae	Min.	Max
1993-1994								
<i>Doryctobracon areolatus</i>								
<i>Spondias purpurea</i>	0	15	919	—	—	—	—	—
<i>Ximenia americana</i>	0	7	22	—	—	—	—	—
<i>Mangifera indica</i>	0	1	364	—	—	—	—	—
<i>Spondias mombin</i>	45.98	1,044	4,026	—	—	—	7	10
<i>Tapirira mexicana</i>	84.21	57	578	—	—	—	7	8
<i>Psidium guajava</i>	42.11	76	3,300	—	—	—	7	9
<i>Citrus sinensis</i>	95.65	23	1,464	—	—	—	3	7
<i>Aganaspis pellenaroi</i>								
<i>Psidium guajava</i>	64.60	113	3,300	—	—	—	5	9
<i>Citrus sinensis</i>	0	1	1,464	—	—	—	—	—
<i>Utetes (B.) anastrephae</i>								
<i>Spondias mombin</i>	2.10	144	4,026	—	—	—	10	10
<i>Tapirira mexicana</i>	12.12	33	578	—	—	—	7	9
<i>Diachasmimorpha longicaudata</i>								
<i>Spondias mombin</i>	80.00	5	4,026	—	—	—	7	7
<i>Tapirira mexicana</i>	0	15	578	—	—	—	—	—
<i>Psidium guajava</i>	16.14	378	3,300	—	—	—	5	6
<i>Citrus sinensis</i>	7.61	92	1,464	—	—	—	3	—
1994-1995								
<i>Doryctobracon areolatus</i>								
<i>Spondias purpurea</i>	0	340	1,233	—	—	—	—	—
<i>Spondias mombin</i> 1 <sup>f</sup>	8.30	265	910	—	—	—	9	11
<i>Spondias mombin</i> 2	62.10	620	2,287	—	—	—	6	11
<i>Psidium guajava</i>	0	3	2,128	—	—	—	—	—
<i>Citrus sinensis</i>	33.33	15	2,031	—	—	—	7	8
<i>Aganaspis pellenaroi</i>								
<i>Psidium guajava</i>	11.11	9	2,128	—	—	—	11	11
<i>Citrus sinensis</i>	33.33	3	2,031	—	—	—	9	9
<i>Utetes (B.) anastrephae</i>								
<i>Spondias mombin</i> 1	0.36	273	910	—	—	—	11	11
<i>Spondias mombin</i> 2	11.18	716	2,287	—	—	—	6	11
<i>Spondias purpurea</i>	0	13	1,233	—	—	—	—	—
<i>Diachasmimorpha longicaudata</i>								
<i>Mangifera indica</i>	0	34	880	—	—	—	—	—
<i>Spondias mombin</i> 2	0	4	2,287	—	—	—	—	—
<i>Psidium guajava</i>	9.52	21	2,128	—	—	—	6	6
<i>Citrus sinensis</i>	20.00	70	2,031	—	—	—	4	4
1995-1996								
<i>Doryctobracon areolatus</i>								
<i>Ximenia americana</i> 1	0	26	181	—	—	—	—	—
<i>Ximenia americana</i> 2	0	19	123	—	—	—	—	—
<i>Spondias mombin</i>	33.32	1,891	10,650	41.54	337	1,704	4	9
<i>Psidium guajava</i> 1	52.63	19	1,512	0	4	673	6	10
<i>Psidium guajava</i> 2	—	—	—	100.00	1	143	6	6
<i>Psidium sartorianum</i>	—	—	—	5.55	18	750	8	8
<i>Aganaspis pellenaroi</i>								
<i>Psidium guajava</i> 1	43.48	69	1,512	9.10	55	673	6	9
<i>Psidium guajava</i> 2	—	—	—	57.14	7	143	7	7
<i>Psidium sartorianum</i>	—	—	—	52.94	34	750	6	7
<i>Utetes (B.) anastrephae</i>								
<i>Spondias mombin</i>	3.62	2,127	10,650	25.52	145	1,704	4	10
<i>Psidium sartorianum</i>	—	—	—	26.87	67	750	2	8
<i>Odontosema anastrephae</i>								
<i>Psidium guajava</i>	45.45	11	1,512	—	—	—	—	—
<i>Diachasmimorpha longicaudata</i>								
<i>Spondias mombin</i>	—	—	—	27.27	33	1,704	4	4
<i>Psidium guajava</i> 1	39.53	86	1,512	20.00	25	673	4	4
<i>Psidium guajava</i> 2	—	—	—	85.71	7	143	6	6
<i>Psidium sartorianum</i>	—	—	—	30.77	26	750	3	3
<i>Citrus sinensis</i>	—	—	—	42.24	116	656	2	3
1996-1997								
<i>Doryctobracon areolatus</i>								
<i>Ximenia americana</i>	0	312	712	—	—	—	—	—
<i>Spondias mombin</i>	38.05	933	5,116	—	—	—	7	11
<i>Psidium guajava</i>	62.96	81	10,756	—	—	—	6	10
<i>Psidium sartorianum</i>	42.86	7	226	—	—	—	6	6

Table 2. (Continued)

Study period; parasitoid species; fruit fly larval host plant	Proportion entering diapause <sup>a</sup>					Length of diapause period, mo		
	Lab <sup>b</sup>	N <sup>c</sup>	Total pupae <sup>d</sup>	Field <sup>e</sup>	N	Total pupae	Min	Max
<i>Citrus sinensis</i>	100.00	9					4	
<i>Aganaspis pellenaroi</i>								
<i>Psidium guajava</i>	68.21	1,186					6	10
<i>Utetes (B.) anastrephae</i>								
<i>Spondias mombin</i>	1.32	1,668		—		—	6	11
<i>Ximenia americana</i>	0	48		—		—		—
<i>Psidium guajava</i>	0	5		—		—	—	—
<i>Psidium sartorianum</i>	0	4		—		—	—	—
<i>Diachasmimorpha longicaudata</i>								
<i>Psidium guajava</i>	30.88	136		—		—	5	6
<i>Citrus sinensis</i>	9.80	51		—		—	3	4
<i>Odontosema anastrephae</i>								
<i>Psidium guajava</i>	87.50	8					8	10

<sup>a</sup> Value may represent an underestimate since some diapausing individuals died from unknown causes.

<sup>b</sup> Proportion of parasitoid individuals entering diapause that stemmed from fruit collected in the field and transported to the laboratory. After larvae pupated, pupae were kept, under ambient conditions, in moist vermiculite until fly adult or parasitoid emerged.

<sup>c</sup> Refers to the total number of parasitoids (diapausing and nondiapausing individuals) that emerged from pupae that the sampled fruit, in that particular tree, had yielded (total pupae in next column).

<sup>d</sup> Refers to total number of pupae collected from fruit sampled in each particular tree. These pupae contained unparasitized flies and diapausing and nondiapausing parasitoids.

<sup>e</sup> Proportion of parasitoid individuals entering diapause that stemmed from fruit collected in the field and placed in plastic washbowls over moist soil. After larvae pupated, pupae were kept in the field in a protected enclosure until either adult flies or parasitoids emerged. Natural soil moisture conditions were mimicked by wetting the soil every time there was natural rainfall.

<sup>f</sup> Numbers after a plant species name refer to individual tree identification number (on occasion we sampled from 2 different trees of the same species).

and 1995. We first summarize data by parasitoid species (Figs. 6-9). With the exception of *Doryctobracon crawfordi*, which never exhibited diapause (Fig. 6), information on diapausing species is divided into the following 2 parts (Figs. 7-9): (1) Incidence of diapause according to the week of the fruiting period during which the infested fruit were sampled. We did so to ascertain if diapausing parasitoids were more

common if they had developed in fruit fly larvae stemming from fruit collected at the end of the fruiting period. Even though this proved to be true in some cases (e.g., *D. areolatus* and *U. anastrephae* stemming from *S. mombin* [Figs. 7A and 8A, respectively] and *A. pellenaroi* stemming from *P. guajava* [Fig. 9A]), there was no clear overall trend (different patterns also illustrated in Figs. 7A and 8A). (2) Emergence sched-

Table 3. Proportion of parasitoid individuals that entered diapause when exposed to different environmental conditions and times of year

Abiotic factor	Incidence of diapause (% individuals entering diapause) in each parasitoid species				
	<i>D. areolatus</i>	<i>U. anastrephae</i>	<i>A. pellenaroi</i>	<i>O. anastrephae</i>	<i>D. longicaudata</i>
Altitude					
0-500	1.43 (3,148)	0 (314)	0 (15)	0 (4)	0 (7)
500-1,000	39.63 (4,211)	6.01 (3,494)	52.94 (34)	—	18.49 (119)
1,000-1,500	58.59 (198)	12.12 (33)	43.49 (269)	—	18.80 (686)
Rainfall					
500-1,000	0 (9)	—	—	0 (2)	—
1,000-1,500	23.31 (7,314)	5.44 (3,786)	36.73 (49)	30.43 (69)	0 (4)
>1,500	54.27 (234)	14.54 (55)	43.49 (269)	17.54 (741)	54.54 (11)
Temp, °C					
15-20	47.00 (100)	7.27 (55)	23.08 (13)	0 (62)	—
20-25	36.18 (4,804)	5.85 (3,590)	45.52 (290)	41.67 (12)	20.19 (748)
25-30	1.77 (2,653)	0 (196)	0 (15)	0 (2)	0 (3)
30-35	—	—	—	—	—
Time of year					
Jan.-Feb.	—	—	—	—	0 (2)
Mar.-Apr.	—	—	—	—	—
May.-Jun.	1.23 (163)	0 (5)	—	0 (1)	—
Jul.-Aug.	2.34 (3,424)	0.26 (387)	4.17 (24)	0 (3)	13.33 (15)
Sep.-Oct.	46.86 (3,668)	6.16 (3,327)	44.76 (248)	45.45 (11)	18.99 (637)
Nov.-Dec.	58.14 (43)	26.87 (67)	54.76 (42)	—	28.36 (275)

Numbers in parenthesis represent total number of parasitoids (diapausing and nondiapausing) collected under each environmental condition and time of year.

Table 4. Comparison of generation times of non-diapausing parasitoids reared under laboratory conditions, collected in field and kept under laboratory conditions or collected in the field and kept under field conditions

Fly host plant species/ Parasitoid species	Generation times (range in days) under varying rearing conditions		
	Laboratory	Field/Laboratory	Field/Field
<i>Spondias purpurea</i>			
<i>Doryctobracon areolatus</i>	21–26 (26.1 ± 0.4)	20–28 (22.1 ± 0.1)	—
<i>Utetes anastrephae</i>	11–20 (26.1 ± 0.4)	16–22 (22.1 ± 0.1)	—
<i>Spondias mombin</i>			
<i>Doryctobracon areolatus</i>	21–25 (24.9 ± 0.28)	29–37 (21.7 ± 0.2)	20–29 (25.3 ± 1.4)
<i>Diachasmimorpha longicaudata</i>	16–21 (24.9 ± 0.28)	—	17–26 (25.3 ± 1.4)
<i>Utetes anastrephae</i>	11–20 (24.9 ± 0.28)	20–28 (21.7 ± 0.2)	19–26 (25.3 ± 1.4)
<i>Citrus sinensis</i>			
<i>Aganaspis pellenaroi</i>	25–32 (24.4 ± 0.3)	40–55 (17.7 ± 0.3)	—
<i>Diachasmimorpha longicaudata</i>	16–21 (24.4 ± 0.3)	35–48 (17.7 ± 0.3)	24–38 (21.4 ± 0.3)
<i>Doryctobracon areolatus</i>	21–25 (24.4 ± 0.3)	30–39 (17.7 ± 0.3)	—
<i>Doryctobracon crawfordi</i>	21–26 (24.4 ± 0.3)	38–50 (17.7 ± 0.3)	31–38 (21.4 ± 0.3)
<i>Psidium guajava</i>			
<i>Aganaspis pellenaroi</i>	25–32 (24.1 ± 0.2)	26–41 (19.6 ± 0.3)	31–48 (24.6 ± 1.3)
<i>Diachasmimorpha longicaudata</i>	16–21 (24.1 ± 0.2)	23–39 (19.6 ± 0.3)	24–34 (24.6 ± 1.3)
<i>Doryctobracon areolatus</i>	21–26 (24.1 ± 0.2)	22–33 (19.6 ± 0.3)	20–31 (24.6 ± 1.3)
<i>Doryctobracon crawfordi</i>	21–26 (24.1 ± 0.2)	27–47 (19.6 ± 0.3)	33–35 (24.6 ± 1.3)
<i>Odontosema anastrephae</i>	38–49 (24.2 ± 0.3)	80–91 (18.7 ± 0.3)	—
<i>Psidium sartorianum</i>			
<i>Aganaspis pellenaroi</i>	25–32 (24.4 ± 0.3)	—	65–83 (20.8 ± 0.3)
<i>Diachasmimorpha longicaudata</i>	16–21 (24.4 ± 0.3)	—	28–40 (21.4 ± 0.3)
<i>Doryctobracon areolatus</i>	21–25 (24.4 ± 0.3)	—	28–40 (21.4 ± 0.3)
<i>Utetes anastrephae</i>	11–20 (24.4 ± 0.3)	—	20–35 (21.4 ± 0.3)

Numbers in parenthesis refer to mean temperature ± SE at which parasitized pupae were maintained.

ules of diapausing parasitoids according to species of fruit from which parasitized fruit fly larvae were collected (Figs. 7–9). The 2nd set of figures illustrates the diapause history of all parasitoid species collected in representative fruit fly host plant species (Figs. 10–12). Figs. 10 and 11 represent data obtained from infested fruit (containing parasitized larvae) which was collected in the field and transported to the laboratory (see *Materials and Methods* section for details). In contrast, Fig. 12 illustrates emergence schedules of parasitoids kept in the field throughout the entire pupal period. Emergence schedules look nearly identical in both cases. Transporting parasitized larvae to the laboratory and exposing them to lower temperatures than they would normally experience in the field, did not change diapause schedules.

We find it noteworthy that in diapausing species not all populations exhibited the phenomenon (Tables 2 and 3). Furthermore, in those populations that did

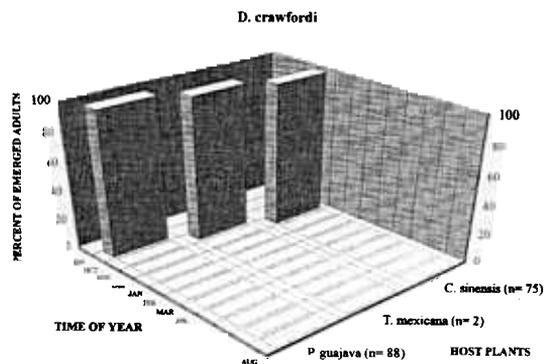


Fig. 6. Emergence schedules of *Doryctobracon crawfordi* collected during 1993 from fruit fly infested *Psidium guajava*, *Tapirira mexicana*, and *Citrus sinensis* fruit. No diapausing individuals were recorded.

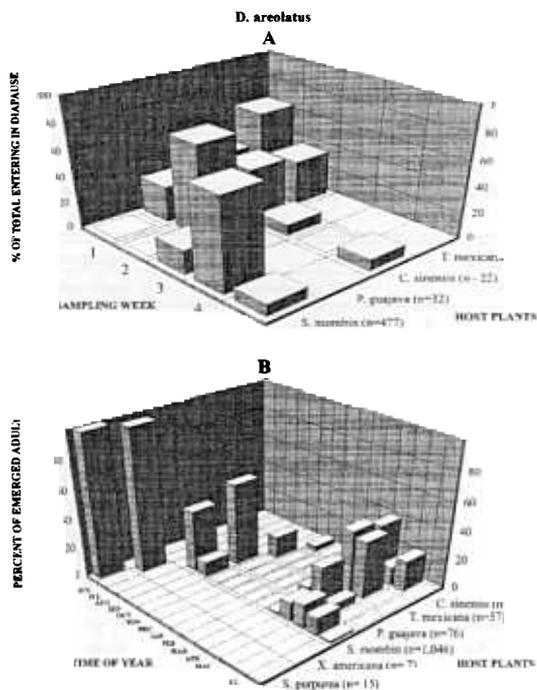


Fig. 7. Diapause history of *Doryctobracon areolatus* during 1993. (A) Incidence of diapause according to week when fruit was sampled. (B) Emergence schedules of individuals stemming from 6 different fruit species.

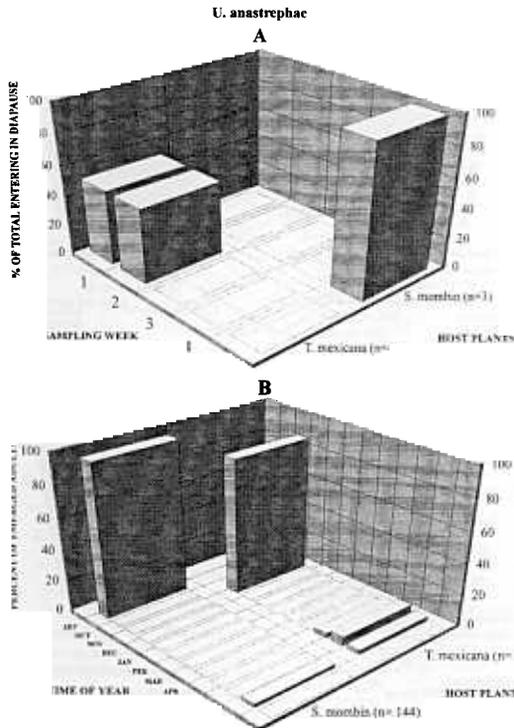


Fig. 8. Diapause history of *Utetes anastrephae* during 1993. (A) Incidence of diapause according to week when fruit was sampled. (B) Emergence schedules of individuals stemming from 2 different fruit species.

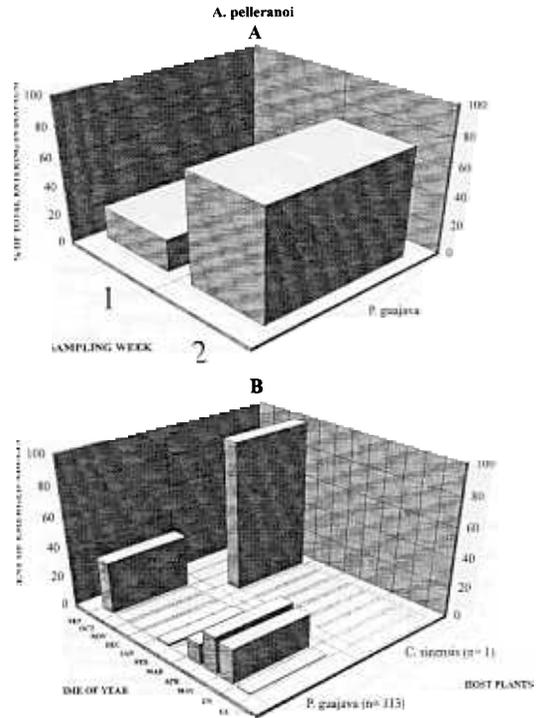


Fig. 9. Diapause history of *Aganaspis pellenaroi* during 1993. (A) Incidence of diapause according to week when fruit was sampled. (B) Emergence schedules of individuals stemming from 2 different fruit species.

exhibit diapause, the proportion of individuals entering this state fluctuated between 0.4 and 100% and emergence patterns were polymodal (Figs. 7–12).

Of the 9 parasitoid species kept in colonies under laboratory conditions, nondiapause generation times varied between 9 and 49 d depending on the species. Such developmental periods are roughly equivalent to those exhibited by parasitoids collected in the field but which did not enter diapause (Table 4). In the laboratory, only *D. areolatus* and *U. anastrephae* exhibited diapause. This, only during the months of December–February. Interestingly, not only did 3rd instar larvae enter diapause but we have circumstantial evidence that adults also entered a reproductive diapause. We base our evidence on the fact that starting in mid-October *D. areolatus* females showed little interest in foraging for fruit and when landing on a fruit, rarely oviposited. This fact is reflected in a significant drop in parasitized larvae.

### Discussion

Our discovery of widespread diapause in fruit fly parasitoids living in a tropical environment is an important step toward understanding the phenology of these insects. This phenomenon has been largely unappreciated by ecologists and entomologists interested in fruit fly biological control in the tropics. There

have been only a few reports of diapause in tropical fruit fly parasitoids, and many of these are anecdotal and scattered among the older literature (e.g., Pemberton and Willard 1918a, b; Darby and Knapp 1934). The failure to note diapause may be caused by the common practice of discarding pupae from which neither flies or parasitoids had emerged within a “reasonable period,” with the assumption that the insects within had died (J.S., unpublished data). If so, previously reported levels of parasitism may typically be underestimated.

Not all parasitoid species in Veracruz exhibited diapause, and in those that did, only certain populations contained diapausing individuals. For example, *D. areolatus* collected in Apazapan from *Spondias purpurea* L. infested by *Anastrepha obliqua* and in Llano Grande from *Ximenia americana* L. infested by *A. alveata* never entered diapause. In contrast, the same species collected in Llano Grande from *Spondias mombin* infested by *A. obliqua* or in Tejeria from *Citrus sinensis* (infested by *A. ludens*) and *Psidium guajava* (infested by both *A. striata* and *A. fraterculus*) did diapause. Interestingly, *D. crawfordi* did not diapause in the Veracruz sites, but appeared to exhibit diapause in another region of Mexico (central Morelos State; Darby and Knapp 1934). These differences may be the result of different patterns of fruit abundance at various times and places (see review by Vinogradova 1986; Ando 1983). For example, *S. purpurea* and *X.*

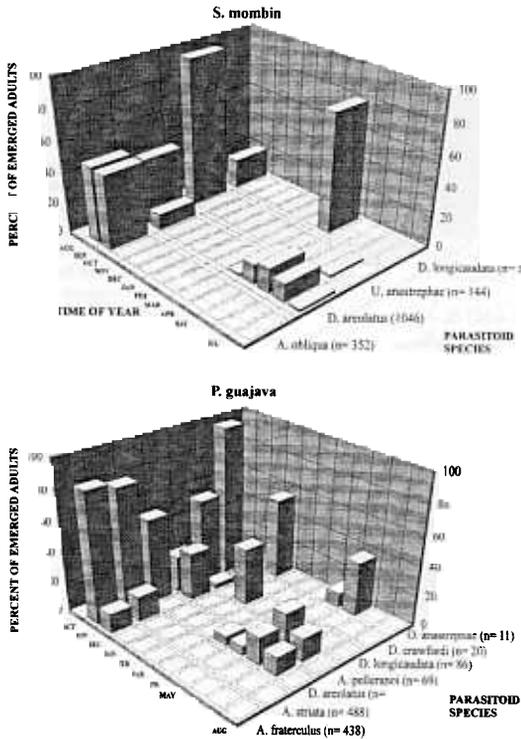


Fig. 10. Diapause history of parasitoids collected from *Spondias mombin* and *Psidium guajava* fruit during 1993 and 1995, respectively. Fruit fly pupae were transported to the laboratory and kept under environmental conditions different than those prevalent in site from which they stemmed.

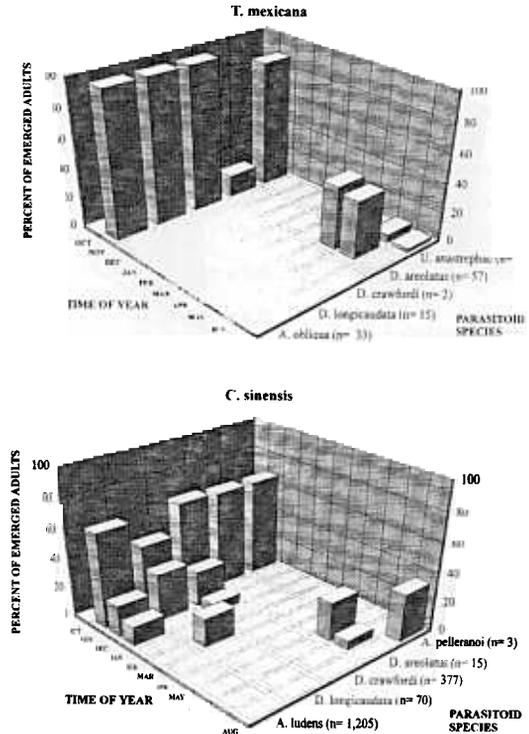


Fig. 11. Diapause history of parasitoids collected from *Tapirira mexicana* and *Citrus sinensis* fruit during 1993 and 1994, respectively. Fruit fly pupae were transported to the laboratory and kept under environmental conditions different than those prevalent in site from which they stemmed.

*americana* bear fruit early in the year, before other trees. Thus, a generalist parasitoid, such as *D. areolatus*, developing in fruit fly larvae in these fruits is likely to find other infested fruit fly hosts after its emergence as an adult. However, later in the year, fruits infested by fruit fly larvae become scarcer, and in some cases, because of irregular fruiting, may not be available at all (Fig. 1). Entering diapause under these circumstances would allow parasitoids to emerge in times of relative host predictability and abundance. This might account for the large proportion of diapausing *D. areolatus* emerging from late fruiting species such as *Tapirira mexicana* L. and *C. sinensis*. In general, those parasitoids that develop in fruit in the autumn months, before the winter's scarcity of fruits (see Fig. 1 for details) and the drastic drop of fruit fly populations, are more likely to enter diapause.

Figure 13A illustrates the yearly fluctuation in fruit fly numbers (14 species of the genus *Anastrepha*) in an area where we found the occurrence of parasitoid diapause to be widespread (Tejería/Monte Blanco) (data from Piedra and Zuñiga 1993). Note that fly population levels are very low from October to June. If we analyze diapause schedules of various species of parasitoids living in this region (Figs. 7–12), it becomes clear that diapausing individuals start to emerge (i.e., break diapause) at precisely the time of year

when fly populations become abundant (see Table 3 and Fig. 13A for details). In general, fly populations are low when fly larval hosts are scarce or not present (Fig. 1). The only exception to all the above is *D. crawfordi* and its preferred host *A. ludens*. This fly species is present almost throughout the year (with the exception of May) (Fig. 13B). Its host plants (mainly *Citrus* spp. in our study sites) are only absent during May and June (Fig. 1). Not surprisingly, the only parasitoid species we found not to enter diapause (*D. crawfordi*), parasitizes preferentially larvae of *A. ludens*. Given the basically continuous supply of hosts, there appears to be no need for this parasitoid species to enter diapause in our study region.

Even within diapausing populations, not all individuals entered diapause. Intrapopulation variability is well illustrated by *D. areolatus* collected during 1993 from *S. mombin* at the Llano Grande site (Fig. 10). Here, 46% of the population entered diapause and 54% did not. This diapause dimorphism may reflect different individual experiences of the environment or different estimations of risk by particular individuals. It is also possible that balancing selection would favor the coexistence of both diapause and competition. If competition for hosts increases, the advantages to diapause increase as well. However, as more individuals diapause the potential for competition declines and

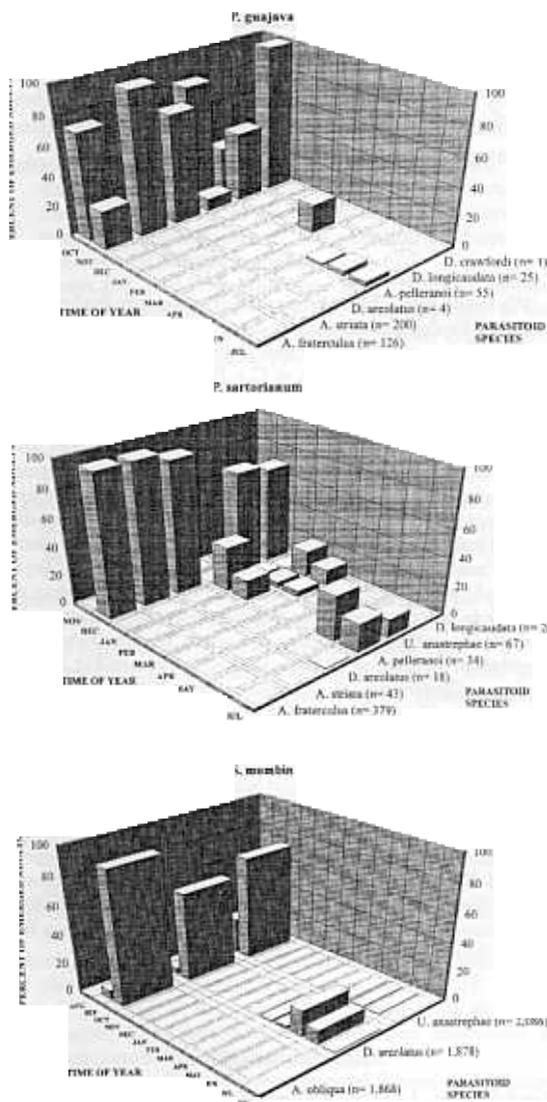


Fig. 12. Diapause history of parasitoids collected from *Psidium guajava*, *P. sartorianum* and *Spondias mombin* fruit during 1995. In contrast to method described in Figs. 10 and 11, in this case we kept fruit fly pupae under field conditions in an enclosure under tree from which they stemmed.

those parasitoids that take advantage of available hosts, rather than "betting" on survival until the next season, may increase in fitness. At some point the risks and benefits of the 2 tactics might balance and both would be preserved in the same population (Waldbauer 1978).

Diapause duration varied between and within species. Presumably, the duration of diapause is sufficient to bridge unfavorable conditions (as already discussed before), and what constitutes an unsuitable environment may vary among parasitoid species. The longest diapause periods (11 mo) appeared in *A. pelleranoi*, *U. anastrephae*, and *D. areolatus*. Both *A. pelleranoi* and *U.*

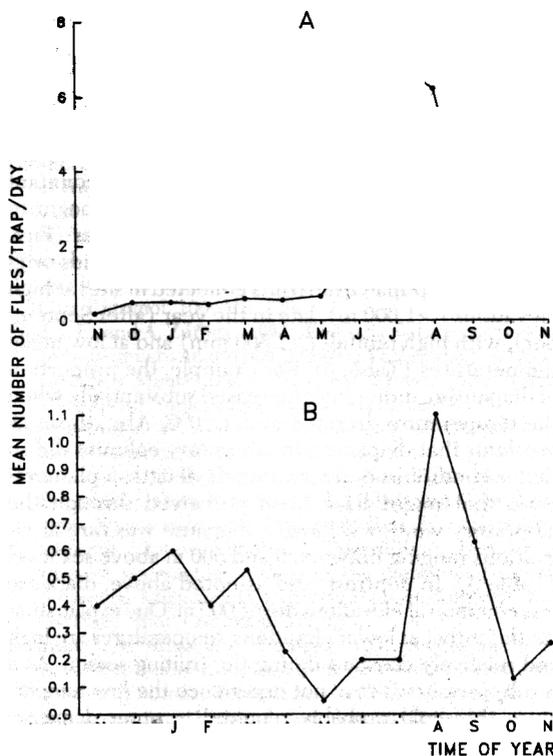


Fig. 13. Adult *Anastrepha* population fluctuations (flies/trap/d) in the Monte Blanco/Tejeria study region (from Piedra and Zuñiga 1993). (A) Data averaged over total number of species captured in McPhail traps (*alveata*, *bicolor* (Stone), *canalis* Stone, *chiclayae* Greene, *distincta* Greene, *fraterculus*, *hamata* (Loew), *leptozonea* Hendel, *limae* Stone, *obliqua*, *ludens*, *serpentina*, *spatulata* Stone, and *striata*). (B) *A. ludens* only.

*anastrephae* have narrow host ranges. They are found parasitizing fruit fly larvae developing on guava and a few native species that bear small fruits (see Sivinski et al. 1997 for further details). A specialist may have to wait an entire year for the reappearance of its particular host. However, *D. areolatus* has the broadest range of any of the fruit fly parasitoids in Veracruz. Long diapauses by particular individuals could be the result of the same reasons suggested above for the presence of diapause in particular individuals (e.g., individuals that are small and thus probably less able to disperse, might benefit from a longer diapause than larger ones). Certain diapause periods in *D. areolatus* are extremely short as well (4 mo). The parasitoid with the 2nd broadest host range, *D. longicaudata*, had consistently short periods of diapause (2-7 mo with a mode of 4 mo).

With respect to the factors regulating diapause induction, maintenance and termination we only have circumstantial evidence gathered under field and laboratory conditions. All of the fruit fly parasitoids discussed here have been reared for multiple generations at the Instituto de Ecología, Xalapa, Veracruz. Only 2 of these, *U. anastrephae* and *D. areolatus*, exhibited

diapause in the laboratory. Presumably, cues important to the induction of diapause in the other species are absent under artificial rearing conditions. Among the factors kept relatively constant when compared with conditions in the field, were temperature, relative humidity and photoperiod.

Temperature, precipitation (and the concomitant effect on soil humidity), and daylength all begin to drop during the period of September–October (Figs. 2–4). Diapause was most common in parasitoids originating in fly pupae from fruits collected in sites at high elevations (>1,000 m), late in the year (after September), with high rainfall (>1,500 mm) and at low mean temperatures (Table 3). For example, the proportion of diapausing individuals increased substantially when the temperature dropped under 20°C. Also, those *D. areolatus* that diapaused in laboratory colonies did so under conditions of decreasing daylength, a phenomenon that might have been perceived through the laboratory windows. Finally, diapause was rare at elevations ranging between 0 and 500 m above sea level (Table 3). In contrast, and as noted above, diapause was common at elevations over 1,000 m. One explanation for this is that at lower elevations, temperatures are high and relatively constant during the fruiting season. As a result, parasitoids may not experience the low temperature threshold probably required to enter diapause. Diapause itself may be less adaptive at low altitudes.

Pemberton and Willard (1918a, b), Darby and Knapp (1934) and Ashley et al. (1976) argued that diapause in *Diachasmimorpha* (= *Diachasma*, *Bios-teres*) *tryoni* (Cameron), *D. fullawayi*, *D. longicauda*, and *Doryctobracon crawfordi* was triggered and maintained by soil moisture and low temperatures. For example, Ashley et al. (1976), tested 3 soil moisture contents (25, 50, and 75%) and 6 temperatures (22–32°C in 2°C increments). They found that incidence of diapause was consistently higher at 25% moisture content and increased significantly for the cooler temperatures at 50 and 75% moisture contents. This coincides with our findings indicating that a higher proportion of individuals entered diapause in regions of high rainfall and at times of the year during which mean temperatures drop below 20°C (Table 3).

There are practical, agricultural implications of widespread diapause in tropical fruit fly parasitoids. Diapause schedules should be considered in parasitoid mass rearing and release programs (e.g., Wong et al. 1991, Aluja 1996, Sivinski et al. 1996). If the Mexican parasitoids examined here are to be used, it might be necessary to select for nondiapausing lines or to avoid exposing parasitoids to stimuli eliciting onset of diapause (e.g., adequate control of temperature and daylength drop in late summer and autumn). Artificial selection for nondiapausing lines can significantly reduce or increase incidence of diapause (Denlinger 1979). For example, in *Diatraea grandiosella* Dyar, incidence of diapause could be increased from 43 to 94% in only 4 generations (Kikukawa and Chippendale 1983). Selection for the opposite has also been carried out. In *Poecilometopa spilogaster* (Wiede-

mann), incidence of diapause dropped from 80 to 20% in 5 generations (Denlinger 1979). However, artificial selection may not be able to eliminate diapause completely (Aeschlimann 1974). This could complicate handling procedures and raise costs of mass rearing certain parasitoid species.

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### References Cited

- Aeschlimann, J. 1974. Hibernation chez trois espèces de Metopiines: Hymenoptera: Ichneumonidae. *Entomol. Exp. Appl.* 17: 487–492.
- AliNiazee, M. T. 1968. Diapause modalities in some *Rhagoletis* species, pp. 13–25. In M. T. Alimiazee [ed.], *Ecology and Management of Economically Important Fruit Flies*. Agricultural Experiment Station Special Report 830. Oregon State University, Corvallis.
1985. Opiine parasitoids (Hymenoptera: Braconidae) of *Rhagoletis pomonella* and *R. zephyria* (Diptera: Tephritidae) in the Willamette Valley, Oregon. *Can. Entomol.* 117: 163–166.
- Aluja, M. 1996. Future trends in fruit fly management, pp. 309–320. In B. A. McPherson and G. J. Steck [eds.], *Fruit Fly Pests. A World Assessment of their Biology and Management*. St. Lucie, Delray Beach, FL.
- Aluja, M., J. Guillén, P. Liedo, M. Cabrera, E. Rios, G. de la Rosa, and H. Celedonio. 1990. Fruit infesting tephritids (Dipt.: Tephritidae) and associated parasitoids in Chiapas, Mexico. *Entomophaga* 35: 39–48.
- Aluja, M., H. Celedonio-Hurtado, P. Liedo, M. Cabrera, F. Castillo, J. Guillén, and E. Rios. 1996. Seasonal population fluctuations and ecological implications for management of *Anastrepha* fruit flies (Diptera: Tephritidae) in

- commercial mango orchards in Southern Mexico. *J. Econ. Entomol.* 89: 654-667.
- Ando, Y. 1983. Diapause and geographic variation in a leaf beetle, pp. 127-141. *In* V. K. Brown and I. Hodek [eds.], *Diapause and adult life cycle strategies in insects*. W. Junk, The Hague.
- Ashley, T. R., P. D. Greany, and D. L. Chambers. 1976. Adult emergence in *Biosteres (Opus) longicaudatus* and *Anastrepha suspensa* in relation to the temperature and moisture concentration of the pupation medium. *Fla. Entomol.* 59: 391-395.
- Cameron, P. J., and P. O. Morrison. 1974. *Psilus* sp. (Hymenoptera: Diapriidae), a parasite of the pupal stage of the apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae) in Southwestern Quebec. *Phytoprotection* 55: 13-16.
- Carl, K. P. 1968. Collection of and observations on the natural enemies of *Rhagoletis cerasi*. Commonwealth Institute of Biological Control Internal Report 8. Commonwealth Institute of Biological Control, Delemont, Switzerland.
- Celedonio-Hurtado, C., M. Aluja, and P. Liedo. 1995. Adult population fluctuations of *Anastrepha* species (Diptera: Tephritidae) in tropical orchard habitats of Chiapas, Mexico. *Environ. Entomol.* 24: 861-869.
- Christenson, L. D. 1953. Investigations of fruit flies in Hawaii. Policy Committee Meeting Proceedings (October). U.S. Department of Agriculture, Honolulu, HI.
- Clausen, C. P., D. W. Clancy, and Q. C. Chock. 1965. Biological control of the oriental fruit fly (*Dacus dorsalis* Hendel) and other fruit flies in Hawaii. *U.S. Dep. Agric. Tech. Bull.* 1322: 102.
- Darby, H. H., and E. M. Knapp. 1934. Studies on the Mexican fruit fly, *Anastrepha ludens* (Loew). *U.S. Dep. Agric. Tech. Bull.* 444: 1-20.
- Denlinger, D. L. 1979. Pupal diapause in tropical flesh flies: Environmental and endocrine regulation, metabolic rate and genetic selection. *Biol. Bull.* 156: 31-46.
1986. Dormancy in tropical insects. *Annu. Rev. Entomol.* 31: 239-264.
- García, E. 1981. Modificaciones al sistema de clasificación climática de Köppen. Offset Larios, Mexico D.F.
- Gut, L. J., and J. F. Brunner. 1994. Parasitism of the apple maggot, *Rhagoletis pomonella*, infesting hawthorns in Washington. *Entomophaga* 39: 41-49.
- Hodek, I. 1983. Role of environmental factors and endogenous mechanisms in the seasonality of reproduction in insects diapausing as adults, pp. 9-33. *In* V. K. Brown and I. Hodek [eds.], *Diapause and adult life cycle strategies in insects*. W. Junk, The Hague.
- Hoffmeister, T. 1990. Zur Struktur und dynamik des parasitoidenkomplexes der Kirschenfliege *Rhagoletis cerasi* L. (Diptera: Tephritidae) auf Kirschen und Heckenkirschen. *Mitt. Deutschen Ges. Allg. Angew. Entomol.* 7: 546-551.
- Hoffmeister, T. 1992. Factors determining the structure and diversity of parasitoid complexes in tephritid fruit flies. *Oecologia (Berl.)* 89: 288-297.
- Kikukawa, S., and G. M. Chippendale. 1983. Seasonal adaptations of populations of the southwestern corn borer, *Diatraea grandiosella*, from tropical and temperate regions. *J. Insect Physiol.* 29: 561-667.
- Lopez, M., M. Aluja, and J. Sivinski. 1999. Hymenopterous larval-pupal and pupal parasitoids of *Anastrepha* species (Diptera: Tephritidae) in Mexican tropical deciduous and subtropical forests and agroecosystems. *Biol. Control* (in press).
- Maier, C. T. 1981. Parasitoids emerging from puparia of *Rhagoletis pomonella* (Diptera: Tephritidae) infesting Hawthorn and apple in Connecticut. *Can. Entomol.* 113: 867-870.
- Marucci, P. E. 1952. Notes on parasites of fruit flies. *Proc. Hawaii. Entomol. Soc.* 14: 371.
- Masaki, S. 1980. Summer diapause. *Annu. Rev. Entomol.* 25: 1-25.
- Pemberton, C. E., and H. F. Willard. 1918a. Interrelations of fruit-fly parasites in Hawaii. *J. Agric. Res.* 12: 285-303.
- 1918b. A contribution to the biology of fruit fly parasites in Hawaii. *J. Agric. Res.* 15: 419-465.
- Prokopy, R. J. 1968. Influence of photoperiod, temperature, and food on initiation of diapause in the apple maggot. *Can. Entomol.* 100: 318-329.
- Piedra, E., and A. Zúñiga. 1993. Ecología de las moscas de la fruta del género *Anastrepha* (Diptera: Tephritidae) en Llano Grande y Monte Blanco, Veracruz, Mexico. B.Sc. thesis, Universidad Veracruzana, Xalapa, Veracruz, Mexico.
- Schwerdtfeger, W. [ed.]. 1976. *Climates of Central and South America*. Elsevier, New York.
- Sivinski, J. M., C. O. Calkins, R. Baranowski, D. Harris, J. Brambila, J. Díaz, R. E. Burns, T. Holler, and G. Dodson. 1996. Suppression of a Caribbean fruit fly (*Anastrepha suspensa* (Loew) Diptera: Tephritidae) population through augmented releases of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biol. Control* 6: 177-185.
- Sivinski, J., M. Aluja, and M. López. 1997. Spatial and temporal distributions of parasitoids of Mexican *Anastrepha* species (Diptera: Tephritidae) within the canopies of fruit trees. *Ann. Entomol. Soc. Am.* 90: 604-618.
- Sivinski, J., K. Vulinec, E. Menezes, and M. Aluja. 1998. The bionomics of *Coptera haywardi* (Ogloblin) (Hymenoptera: Diapriidae) and other pupal parasitoids of tephritid fruit flies (Diptera). *Biol. Control* 11: 193-202.
- Tauber, M. J., and C. A. Tauber. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. *Annu. Rev. Entomol.* 21: 81-107.
- Tauber, C. A., and M. J. Tauber. 1981. Insect seasonal cycles: Genetics and evolution. *Annu. Rev. Ecol. Syst.* 12: 281-308.
- Tauber, C. J., C. A. Tauber, J. R. Nechols, and J. J. Obyrcki. 1983. Seasonal activity of parasitoids: Control by external, internal and genetic factors, pp. 87-108. *In* V. K. Brown and I. Hodek [eds.], *Diapause and life cycle strategies in insects*. W. Junk, The Hague.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. *Seasonal Adaptations of Insects*. Oxford University Press, New York.
- Taylor, F., and J. B. Spalding. 1986. Geographical patterns in the photoperiodic induction of hibernation diapause, pp. 66-85. *In* F. Taylor and R. Karban [eds.], *The evolution of insect life cycles*. Springer, New York.
- Vinogradova, E. B. 1986. Geographical variation and ecological control of diapause in flies, pp. 35-47. *In* F. Taylor and R. Karban [eds.], *The evolution of insect life cycles*. Springer, New York.
- Waldbauer, G. P. 1978. Phenological adaptation and the polymodal emergence patterns of insects, pp. 127-144. *In* H. Dingle [ed.], *Evolution of insect migration and diapause*. Springer, New York.
- Wong, T., M. M. Ramadan, D. O. McInnis, N. Mochigulu, J. L. Nishimoto, and J. C. Herr. 1991. Augmentative releases of *Diachasmimorpha tryoni* (Hymenoptera: Braconidae) to suppress a Mediterranean fruit fly (Diptera: Tephritidae) population in Kula, Maui, Hawaii. *Biol. Control* 1: 2-7.
- Young, A. M. 1982. *Population biology of tropical insects*. Plenum, New York.