Development of Immature Stages and Comparative Demography of Two Cucurbit-Attacking Fruit Flies in Reunion Island: *Bactrocera cucurbitae* and *Dacus ciliatus* (Diptera Tephritidae)

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ABSTRACT   On Reunion Island, two species of Dacini, *Bactrocera cucurbitae* (Coquillett) and *Dacus ciliatus* Loew, infest 16 host plant species belonging to the family Cucurbitaceae from sea level to 1,600 m. These two species represent two primary pests of this plant family on the island. Melon fly, *Bactrocera cucurbitae*, and Ethiopian fruit fly, *D. ciliatus*, larval development was studied at four different constant temperatures (15, 20, 25, and 30°C) with three host plants (cucumber, pumpkin, and squash). Adult life histories of these two species were studied at 25°C with the three host plants. The results led to the conclusion that *B. cucurbitae* had a faster egg incubation time. Its preimaginal instars developed significantly faster than those of *D. ciliatus* independent of temperature. *B. cucurbitae* and *D. ciliatus* had similar mean preoviposition duration and egg hatching success. Fecundity was significantly higher for the melon fly on cucumber and pumpkin and lower on squash. Two distinctly different life-history patterns were evident: (1) later onset of reproduction, longer oviposition time, longer life span, and higher fecundity (*B. cucurbitae*) and (2) early reproduction, lower oviposition time, shorter life span, and lower fecundity (*D. ciliatus*). These results are useful for improving laboratory-rearing methods and for building simulation models to predict Dacini population dynamics.

KEY WORDS   Dacini, temperature, host–plant effect, preimaginal development, adult life history

On Reunion Island (Mascarenes Island in the Indian Ocean), among nine species of Tephritidae, the Six Dacini species are: *Bactrocera (Bactrocera) zonata* (Saunders), *Bactrocera (Bactrocera) montyana* (Munro), *Bactrocera (Daculus) oleae* (Gmelin). *Dacus (Dacus) demmerezi* (Bezzi), *Bactrocera (Zeugodacus) cucurbitae* (Coquillett), *Dacus (Didacus) ciliatus* Loew. Of these, only the last two species are of major economic significance on cucurbit crops with heavy damages. They are actually serious pests of cucurbit crops in Africa and Asia, and the melon fly can also infest several other families in Sub-Saharan Africa (J.F.V., unpublished data).

The melon fly, *B. cucurbitae*, is a particularly harmful species on cucurbit crops in the Indian Ocean (Mauritius and Reunion). It was found in Mali in 2000 (Vayssières et al. 2004) and has become widespread in West Africa (Benin, Burkina, Guinea, Mali, RCI, Senegal, and Togo) over the last 10 yr (J.F.V., unpublished data). It was formerly seen on fruit crops in the New Guinea area (Indonesia and Papua New Guinea), the Hawaiian Islands, and Oriental Asia (Bangladesh, China, India, Japan, Malaysia, Thailand, and Vietnam) (White and Elson-Harris 1992). This species is native to South Asia.

The Ethiopian fruit fly, *D. ciliatus*, is a pest of cucurbit crops in all Africa (except the Maghreb), Oriental Asia (Bangladesh, India, Pakistan, and Sri Lanka), the Middle East (from Iran to Israel and Libya), the Indian Ocean (Madagascar and Mascarenes Islands), and East Africa (Orian and Moutia 1960, Kapoor 1970, Qureshi et al. 1974, Munro 1984). As its common name suggests, *D. ciliatus* is native to East Africa.

Reunion Island is characterized by a particularly diverse topography and variable distribution of host plants for Dacini fruit fly species. *B. cucurbitae* infested 12 genera of three family plants (Cucurbitaceae, Passifloraceae, Solanaceae), whereas *D. ciliatus* infested 9 genera of one family plant (Cucurbitaceae) (Vayssières 1999). These two species have colonized the main part of Reunion Island from sea level to 1,100 m for the melon fly and to 1,400 m for the Ethiopian fruit fly during summer (Vayssières 1999), with seasonal fluctuations of populations.

In the Mascarenes Islands, the melon fly was first recorded in Mauritius (1960) and then in Reunion (1972), probably arriving from the Indian continent (Etienne 1982). The Ethiopian fruit fly, already

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present in Mauritius at the beginning of the century, was recorded later on Reunion Island (Pointel 1964).

Tephritid distribution and abundance are notably dependent on several abiotic factors (e.g., temperature, relative humidity, and rainfall) and several biotic factors (e.g., host plants and natural enemies). This study focused on the effect of temperature on preimaginal development. As expected from other laboratory and field studies (Vargas et al. 1996, Brévault and Quilici 2000, Duyck and Quilici 2002), temperature strongly influenced survival and developmental rates of the immature stages. The aim of this study was to compare preimaginal development under four different temperatures and the main demographic parameters at constant temperature for these two Dacini species. Although this study was primary focused on the factor temperature, we also tested different host fruit species.

Although larval development and demographic parameters have been well described for *B. cucurbitae* in Hawaii (Carey et al. 1985, Vargas et al. 1996, 1997, 2000, our study is the first to give population parameters for *D. ciliatus;* this species in an important pest for Cucurbit crops on Reunion Island and also in India and Africa.

This study aimed to compare the main demographic parameters of two widespread species currently competing in the same ecological niche. Overall results of this study will give a better comprehension of the present world distribution of both species and will be beneficial for future work on the modeling of Dacini population dynamics.

Materials and Methods

The strains of *B. cucurbitae* and *D. ciliatus* were reared, respectively, from infested fruits (from small crops) of bitter gourd (*Mormodica charantia*) from St. Paul (west coast of La Réunion) and of ivry gourd (*Coccina grandis*) from St. Pierre (south coast of La Réunion). Fruit collections of these wild hosts were repeated five times. Adults were fed simultaneously with enzymatic yeast hydrolysate (ICN Biomedicals, Aurora, OH) and sucrose in different cages in the same chamber for two consecutive generations. Three different populations of each fly species were reared on specific cucurbit species (squash [*Cucurbita pepo*], pumpkin [*C. pepo*], and cucumber [*Cucumis sativus*]) for two generations before the experiments. The two species were reared simultaneously in an environmental chamber maintained at 25 ± 1°C with 75 ± 10% (SD) relative humidity under a 12:12 (L:D)-h photoperiod using natural light supplemented by artificial light.

Newly emerged adults were held in cubical cages (40 cm each dimension) for egg collection. Eggs of both species were collected over a 3- to 6-h period. For each temperature, the duration of the egg stage was established by putting 100 randomly collected eggs with a small camel hair brush on a moist filter paper in a petri dish (9 cm diameter). Eggs were observed hourly after the 20th hour using a binocular microscope to record the time and percentage of hatching for each fly species.

Samples of 100 eggs were counted under a binocular microscope and placed on 150 g of a specific cucurbit species in a screen-covered plastic cup. Equal weight was provided of each cucurbit species. Fruits were collected and displayed to Dacine flies at the prematurity stage. Fresh fruits were added two or three times a day as needed to prevent intraspecific resource competition. These rearing densities were lower than those commonly used in mass production facilities to reduce metabolic heat (Tanaka et al. 1972). The cucurbit species used were squash (*C. pepo*), pumpkin (*C. pepo*), and cucumber (*C. sativus*). Larvae were reared in cups with different cucurbit species to study the life history of the emerged adults. Thus, the two species were reared simultaneously on three host plants each. Observations were made twice a day, with observations on changing larval stage. The time needed for 50% of individuals to achieve development to a particular stage was noted at the following constant temperatures: 15, 20, 25, and 30 ± 1.0°C. Each experiment at 15, 20, 25, and 30°C was duplicated three times for each plant species and for each Dacini species. Four incubators were used (one per temperature). Each repetition for the three hosts was tested simultaneously in each incubator.

To measure developmental times of the different instars, a cohort was collected in the middle of the period between the first and last individual that reached a specified instar. Larval instars were differentiated by their size, body surface sculpturing, and color (White and Elson-Harris 1992). By the end of the third larval instar, mature larvae were allowed to leave the cups to pupate in the sand around the cups. Pupae were collected by sifting the sand, were counted, and were carefully cleaned. They were transferred to a plastic box with covered with fine mesh and containing a small moist sponge. At the end of the pupal stage, the number of newly emerged adults was recorded twice a day.

Adult life history traits were assess using 30 pairs of newly emerged adults of each Tephritid species isolated in 30 individual cages; 10 pairs were isolated in 10 individual cages, 10 for each cucurbit crop, at 25 ± 1°C and 75 ± 10% RH with a 12:12 (L:D)-h photoperiod. Adults were fed with enzymatic yeast hydrolysate (ICN Biomedicals) and sugar in addition to three slices of cucurbit put on the wire mesh at the top of the cage. Females could also lay eggs within these three slices. Each morning the eggs previously laid by the females between two slices were easily seen and collected. New fresh slices were provided each morning (even if the old slices were still in good shape). These slices of different cucurbit species were always of the prematurity stage. Eggs were collected and counted daily (each morning) from the cucurbit slices with a small camel hair brush; they were put on moist filter paper and held in petri dishes to follow hatching. Daily mortality and daily fecundity were noted.

Although the temperature development rate curve obtained with constant temperatures is sigmoid rather

Table 1. Total development (d) of *B. cucurbitae* and *D. ciliatus* with three hosts plants at four temperatures

Temperature (°C)	Tephritid species	Host plants		
		Cucumber	Pumpkin	Squash
30	*B. cucurbitae*	13.2 ± 0.96a	14.4 ± 0.26a	13.6 ± 0.37a
	D. ciliatus	16.4 ± 1.73b	17.1 ± 0.74b	15.9 ± 1.79b
25	*B. cucurbitae*	17.2 ± 1.17a	18.4 ± 1.32a	17.0 ± 0.19a
	D. ciliatus	20.6 ± 0.67b	22.7 ± 1.15b	21.1 ± 0.76b
20	*B. cucurbitae*	25.1 ± 1.45a	25.1 ± 1.94a	25.9 ± 1.90a
	D. ciliatus	35.1 ± 1.26b	34.8 ± 0.77b	33.5 ± 0.89b
15	*B. cucurbitae*	44.2 ± 2.52a	—	—
	D. ciliatus	86.3 ± 12.00b	—	—

No larval development was recorded on squash and cucumber at 15°C.

than linear (Wagner et al. 1984), the temperature summation model has proven to be reasonably accurate for predicting developmental times of different fruit flies species in the field (Fletcher 1989). While this approach is only valid over intermediate temperatures (Wagner et al. 1984), the linear relationship requires a smaller dataset and allow interesting comparisons among species. Above a precise lower threshold for development, the temperature–development rate relationship is linear (Arnold 1959). Consequently, a constant number of heat units (or degree days) above this threshold is necessary to complete development. The development time of individual life stages (time necessary for 50% of individuals to complete a given stage) was determined at a series of four constant temperatures. Development rate (100/developmental time) was plotted against temperature. The lower development threshold (t; the temperature at which there is no development) was determined by extrapolation of the regression line back to the x-axis. The thermal constant (K) was defined as the number of degrees days above the lower threshold required to complete development and was calculated from the regression equation using the relationship $y = K/(x − t)$ (Fletcher 1989).

Statistical analyses were performed using the life test procedure (SAS Institute 1997) for life span and analysis of variance (ANOVA), followed by the Student–Newmann–Keuls test for the other parameters. The life test procedure gives the point estimate (in days) of the survival distribution of each quantile (e.g., 50% of surviving flies) for each Dacini species with the 95% confidence interval (lower, upper) for each host species. ANOVA was used to analyze developmental time of the two species; means were compared by Newman–Keuls multiple range tests ($P = 0.05$).

Standard life table parameters and population age structures were calculated from daily records of mortality of immature stages, fecundity, and fertility of pairs of adults. Parameter symbols, formulae, and definitions follow Carey (1993). To compare life table parameters among the different species and treatments, confidence intervals were estimated as the 2.5 and 97.5 percentiles of a bootstrap distribution resampled 1,000 times (Efron and Tibshirani 1993, Caswell 2001). This was done using R software (R Development Core Team 2004).

Results

Egg Incubation Period at Four Temperatures. The melon fly had a significantly shorter incubation period than the Ethiopian fruit fly for all temperatures tested: 30 ($F = 118.5$; df = 1,16; $P < 0.001$), 25 ($F = 139.4$; df = 1,16; $P < 0.001$), 20 ($F = 92.5$; df = 1,16; $P < 0.001$), and 15°C ($F = 128.1$; df = 1,5; $P < 0.001$; Table 1, Appendix 1). At 30°C, *B. cucurbitae* had a 22% shorter incubation period than *D. ciliatus* on the same host plant. At 25°C, *B. cucurbitae* had a 26% mean shorter incubation period than *D. ciliatus.* At 20°C, *B. cucurbitae* had a 32% mean shorter incubation period than *D. ciliatus.* At 15°C, *B. cucurbitae* had a 20% shorter incubation period than *D. ciliatus.*

Relationship Between Developmental Time and Temperature. For all temperatures, preimaginal instars of melon fly developed significantly faster than those of the Ethiopian fruit fly (Table 1). At 30°C, the preimaginal development of *B. cucurbitae* was on average 16% shorter than *D. ciliatus*, whereas at 25°C, the difference between the two species was 19%, at 20°C, the difference was 26%, and at 15°C, the difference was 49%. No differences between host species were detected.

For *B. cucurbitae* and *D. ciliatus*, there was a strong linear regression model between temperature and development rate (Table 2). Temperature thresholds and thermal constants of the different stages are shown in Table 2.

Preoviposition and Oviposition Durations. The mean preovipositional duration was 10.9 d for *B. cu-*

Table 2. Temperature thresholds (t, °C) and thermal constants (K, degree days) of the different immature stages of *B. cucurbitae* and *D. ciliatus* on pumpkin

Stage	Species	t (°C)	K (degree days)	R^2	df	P
Egg	*B. cucurbitae*	10.05	20	0.99	1,10	<0.001
	D. ciliatus	10.56	26	0.98	1,10	<0.001
Larvae	*B. cucurbitae*	7.32	92	0.91	1,10	<0.001
	D. ciliatus	10.23	90	0.85	1,10	<0.001
Pupae	*B. cucurbitae*	7.37	210	0.98	1,10	<0.001
	D. ciliatus	11.20	207	0.98	1,10	<0.001
Total development	*B. cucurbitae*	7.62	322	0.99	1,10	<0.001
	D. ciliatus	11.04	323	0.99	1,10	<0.001

Table 3.   Life history parameters of *B. cucurbitae* and *D. ciliatus* at 25°C with three host plants

Parameter	Species	Host plants		
		Cucumber	Pumpkin	Squash
Immature survivorship (from egg to adult) (%)	*B. cucurbitae*	82 ± 3abA	84 ± 2aA	77 ± 2bA
	D. ciliatus	77 ± 2aA	81 ± 1bA	76 ± 2aA
Preoviposition period	*B. cucurbitae*	10.0 ± 0.48aA	12.0 ± 0.71aA	10.6 ± 0.32aA
	D. ciliatus	9.8 ± 0.69aA	12.5 ± 1.03aA	11.2 ± 0.85aA
Daily eggs	*B. cucurbitae*	7.01 ± 1.08aA	2.2 ± 0.19bA	4.5 ± 0.42cA
	D. ciliatus	3.9 ± 0.16bB	3.4 ± 0.37bA	5.7 ± 0.55cA
Female longevity	*B. cucurbitae*	182 ± 32aA	237 ± 21bA	217 ± 46cA
	D. ciliatus	162 ± 13aA	163 ± 32aB	158 ± 24aB
Male longevity	*B. cucurbitae*	178 ± 11aA	219 ± 19bA	147 ± 21cA
	D. ciliatus	123 ± 15aB	125 ± 17aB	146 ± 12aA

Means in same row followed by the same lowercase letter are not significantly different (intraspecifically). Means in the same column followed by the same uppercase letter are nor significantly different (interspecifically). All significant differences identified by ANOVA and Newmann-Keuls ($P < 0.05$).

curbitae and 11.2 for *D. ciliatus* at 25°C (Table 3). No significant differences were observed for the preoviposition period (in days) between the two fruit fly species and the three host plants ($P > 0.05$).

For the melon fly, gross fecundity was significantly highest on cucumber ($F = 34.67$; df = 2,27; $P < 0.001$), whereas for the Ethiopian fruit fly, gross fecundity was significantly higher on squash ($F = 56.23$; df = 2,27; $P < 0.001$).

Longevity. For *B. cucurbitae*, 50% of the females were still alive after 5 mo on cucumber and 60% after 6 mo on pumpkin at 25°C (Table 3). Rearing with pumpkin resulted in higher longevity. Female longevity of the melon fly was significantly higher than the female longevity for the Ethiopian fruit fly on pumpkin and squash ($F = 3.94$; df = 2,37; $P < 0.05$).

For *D. ciliatus*, 50% of the females were still alive after 4 mo on pumpkin and 50% after 105 d on squash at 25°C (Table 3). Male longevity of the melon fly was significantly higher than male longevity of the Ethiopian fruit fly on cucumber and pumpkin ($F = 10.86$; df = 2,37; $P < 0.001$).

Population Parameters. *Bactrocera cucurbitae* exhibited the highest intrinsic rates of increase at 25°C on cucumber and pumpkin, but *D. ciliatus* had the highest rates on squash and cucumber (Table 4). Net reproductive rates followed the same trend. For *B. cucurbitae*, mean generation time was higher on cucumber and pumpkin than on squash, whereas for *D. ciliatus*, it was higher on squash.

Discussion

Under laboratory conditions, life histories of *B. cucurbitae* and *D. ciliatus* are similar in some aspects, but differ in the duration of larval instars development, mean oviposition period, life span, and fecundity. More generally, this study provided new information on immature stage development and demographic parameters of *D. ciliatus*, which has never been studied, despite its economic significance.

The melon fly had a shorter egg incubation period and a shorter duration of immature stages irrespective of temperature or host plant. This is a crucial com-

Table 4.   Population parameters for *B. cucurbitae* and *D. ciliatus* at 25°C with three host plants

Parameters	Tephritid species	Host plants		
		Cucumber	Pumpkin	Squash
Net reproductive rate ($R0$)	*B. cucurbitae*	456 (433, 479)	219 (192, 246)	132 (123, 140)
	D. ciliatus	145 (135, 154)	171 (162, 182)	217 (198, 239)
Intrinsic rate of increase (r)	*B. cucurbitae*	0.130 (0.125, 0.135)	0.105 (0.101, 0.109)	0.113 (0.105, 0.118)
	D. ciliatus	0.101 (0.098, 0.104)	0.095 (0.092, 0.098)	0.106 (0.105, 0.107)
Gross Reproductive rate (GRR)	*B. cucurbitae*	588 (556, 621)	289 (259, 318)	218 (196, 233)
	D. ciliatus	190 (178, 201)	219 (208, 232)	310 (274, 334)
Finite rate of increase (λ)	*B. cucurbitae*	1.139 (1.134, 1.144)	1.111 (1.106, 1.15)	1.119 (1.111, 1.125)
	D. ciliatus	1.106 (1.103, 1.109)	1.100 (1.096, 1.103)	1.112 (1.110, 1.113)
Intrinsic birth rate (b)	*B. cucurbitae*	0.149 (0.143, 0.154)	0.119 (0.115, 0.124)	0.131 (0.123, 0.137)
	D. ciliatus	0.117 (0.114, 0.120)	0.109 (0.105, 0.112)	0.123 (0.121, 0.125)
Intrinsic death rate (d)	*B. cucurbitae*	−0.019 (−0.019, −0.018)	−0.015 (−0.015, −0.014)	−0.018 (−0.019, −0.017)
	D. ciliatus	−0.016 (−0.016, −0.016)	−0.013 (−0.014, −0.013)	−0.017 (−0.017, −0.017)
Doubling time (DT)	*B. cucurbitae*	5.3 (5.2, 5.5)	6.6 (6.4, 6.9)	6.2 (5.9, 6.6)
	D. ciliatus	6.9 (6.7, 7.1)	7.3 (7.1, 7.6)	6.5 (6.5, 6.6)
Mean generation time (T)	*B. cucurbitae*	46.9 (45.6, 48.7)	51.4 (48.8, 54.0)	43.4 (41.0, 46.8)
	D. ciliatus	49.2 (18.3, 50.3)	54.0 (52.3, 56.2)	50.8 (50.0, 51.6)
Average age in stable population (ā)	*B. cucurbitae*	7.7 (7.5, 8.0)	9.5 (9.2, 9.9)	8.7 (8.3, 9.2)
	D. ciliatus	9.7 (9.4, 9.9)	10.3 (10.1, 10.7)	9.2 (9.1, 9.3)
Expectation of life at birth (e_0)	*B. cucurbitae*	149 (128, 165)	173 (141, 203)	103 (78, 135)
	D. ciliatus	122 (108, 137)	127 (109, 142)	121 (108, 135)

parative advantage when adults of both species are exploiting the same host in the same locality.

Reproductive parameters were defined for both species and can be compared with other studies. For *B. cucurbitae*, available data about the preoviposition period of flies reared on cucumber showed an interval of 7.5 (Vargas et al. 1997) to 11.2 d (Miyatake 1996). For *D. ciliatus*, the only available data about the preoviposition period showed an interval of 6 (Maher 1957) to 10–14 d during summer (El Nahal et al. 1970). No data were available for oviposition period or for fecundity of *D. ciliatus.* In Reunion, this species seems to have a shorter oviposition period than *B. cucurbitae.* For a wild strain of *B. cucurbitae* from Hawaii on cucumber, Carey et al. (1985) obtained a lower longevity, with 50% of females still alive after 3.5 mo. For the same species on cucumber, Vargas et al. (1997) also obtained a lower longevity, with 50% of females still alive after 2.5 mo a laboratory strain from Hawaii. For *D. ciliatus* on squash, Daiber (1966) obtained, in South Africa, about the same longevity as our study, with 50% of females still alive after 100 d. Male longevity was also greater than that of females for this species in our study. According to Miyatake (1996), a longer development period was not necessarily associated with greater fecundity. For instance, we obtained the highest female longevity of the melon fly on pumpkin (237 d), but it was not on this host that we obtained the highest fecundity (521 eggs).

Temperature is known to be a very important abiotic factor affecting immature development of insects (Wagner et al. 1984). Knowledge of the relationship between developmental time and temperature is essential for mass production facilities, for building predictive models, and for predicting population fluctuations in the field. The linearity of the relationship between temperature and developmental time between 15 and 30°C for the melon fly was consistent with previous studies (Messenger and Flitters 1958, Vargas et al. 1996). If lower developmental thresholds were estimated in this study, more data are needed to calculate upper developmental thresholds. We found that rearing at 35°C did not succeed, and although there was some egg hatching for both species, no complete development could be finally obtained. Therefore, we think that the upper developmental threshold is just above 35°C. According to Shibata (1935), larvae of *B. c0ucurbitae* can tolerate temperatures well below zero for ecologically significant periods. Values for the lower temperature threshold and thermal constant are not so different from previous work on the melon fly. In Hawaii, Messenger and Flitters (1958) tested 24 constant temperatures from 11 to 37°C and found a lower developmental threshold of 11.4°C and an upper developmental threshold of 36.4°C. This difference could result from rearing conditions such as different larval density, rearing diets, or air humidity. In Okinawa, Nakamori et al. (1978) obtained developmental thresholds of 34 and 9.1°C. These last results, calculated on a melon fly strain that originated from a closely related agro-climatic area to Reunion Island, are more similar to ours. Future studies on larval development could emphasize a wider range of temperatures to estimate optimum maximum and lethal temperatures.

A few broad ecological characteristics are evident from our data in Reunion Island: (1) all immature stages of both species survived at different temperatures from 15 to 30°C; (2) with its lower development threshold, *B. cucurbitae* showed an eurythermal response to a large spectrum of ecological niches even if it prefers warmer conditions; (3) a higher intrinsic rate for *B. cucurbitae* also gives it an important advantage for interspecific competition; (4) some preference for certain hosts (squash) allows *D. ciliatus* to enhance its biotic potentialities and to maintain its population at low levels in case of competition with the melon fly, especially at low altitudes (from 600 m to sea level); and (5) if other hosts are introduced (except squash) at higher elevations than currently grown, *B. cucurbitae* would be capable to exploit other cucurbit crops as cucumber or pumpkin. In other parts of the world, *D. ciliatus* could colonize areas with lower temperatures it is the case since a few years in Mediterranean areas (Egypt, Israel, Lebanon).

Local adaptation has not been tested in La Réunion for these species, and different strains could give different results regarding important differences in climatic conditions. It would be interesting to compare the thermal thresholds and life history parameters of different strains in further studies. Other abiotic factors such as rainfall may shape the distribution of fruit flies species (Duyck et al. 2006b). Also, natural enemies may differ among fruits and tephritids species (Sivinski et al. 2001). Although a parasitoid (*Psyttalia fletcheri*) of these two species is present on the island, it has (unfortunately) had very limited impact (J.F.V., unpublished data).

There can be no doubt that demographic strategy is a main component of relative successful competition for different fly species. Exploitative competition and different types of interference competition could be involved (Duyck et al. 2004). According to this study, larval development parameters of the melon fly can give this species an advantage over the Ethiopian fruit fly in case of larval exploitative competition, regardless of temperature. This advantage could be confirmed in the field after the monitoring of infested fruits (cucurbit species) by Dacini flies. When fruits are sampled and monitored, it can be seen how these two species exploit the same cucurbit species: same fruit species, same fruit stages, same altitudes, same male flowers, same vegetative organs (Vayssières 1999). Wild cucurbit species, widespread in lowlands, are infested at >90% by *B. cucurbitae*, with *D. ciliatus* and *D. demmerezzi* accounting for the remaining 10%. Among the 12 cultivated cucurbit species, *B. cucurbitae* dominated *D. ciliatus* in 10 of the species (Vayssières 1999). Concerning interactions between larvae, two kinds of competition closely related could occur, i.e., interference and exploitation (Duyck et al. 2004). Interference between larvae of these species could take the form of one species population reduced by fruit deterioration caused by the other Dacini species. Interference between larvae of these species could also take the form of cannibalism. Whatever the mechanism,

the first larva to hatch in a fruit will have a comparative advantage over subsequent larvae. In the case of simultaneous laying of eggs of two Dacini species, the competitive advantage of the melon fly can be explained by its shorter egg incubation period and its shorter duration of immature stages, regardless of temperature. The importance of competitive preemption has recently been shown among four polyphagous tephritids attacking fruit crops in Reunion (Duyck et al. 2006a).

More generally, many field records show that *Bactrocera* species are best adapted to exploit and to compete with other species in the same ecological niche. Several have presently become established outside of their native range: *B. zonata* in the eastern Mediterranean basin (Taher 1998), and in the Mascarenes Islands (Duyck et al. 2004); *B. carambolae* in Surinam, French Guiana, and northern Brazil (J.F.V., unpublished data); *B. invadens* in Kenya (Lux et al. 2003) and more recently in Benin (Drew et al. 2005, Vayssières et al. 2005); *B. dorsalis* in Polynesia and Hawaii (Keiser et al. 1974); and *B. cucurbitae* in the Mascarenes Islands, Hawaii, East Africa, and more recently in West Africa (Vayssières et al. 2004). The new *Batrocera* species, *B. invadens*, is an invasive species in Sub-Saharan Africa, with a large geographic distribution exploiting a broad array of host plants (>30 species) (J.F.V, unpublished data). This new *Bactrocera* species, discovered in 2003 and described in March 2005, has invaded all Sub-Saharan Africa in only a few years.

Many biological invasions result from human activity. They are mainly considered as one of the consequences of increasing international trade. Once an exotic fruit fly species is established, it cannot, in most cases, be eradicated. Attempts at management are often not particularly effective. Forecasting tephritid invasions is a major current issue for both tropical and temperate countries. In all cases, environmental factors, especially temperature, are likely to affect the invasion process. Also, these results are useful for improving laboratory-rearing methods and for building simulation models to predict Dacini population dynamics.

Acknowledgments

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Appendix 1. Egg incubation period and duration of development of larval instars of *B. cucurbitae* and *D. ciliatus* with three host plants at four temperatures

Temperature (°C)	Host species	Tephritid species	Eggs (h)	L1 (h)	L2 (h)	L3 (h)	Pupae (h)	Total development (d)
30	Cucumber	*B. cucurbitae*	23.7 ± 0.58a	8.0 ± 1.00a	12.3 ± 0.58a	65.0 ± 7.00a	208.1 ± 13.92a	13.2 ± 0.96a
		D. ciliatus	30.7 ± 1.15b	15.7 ± 0.58b	14.7 ± 8.14a	92.0 ± 17.78b	240.0 ± 13.92b	16.4 ± 1.73b
	Pumpkin	*B. cucurbitae*	24.3 ± 0.58a	7.7 ± 1.15a	14.0 ± 1.00a	84.0 ± 3.46a	216.0 ± 0.00a	14.4 ± 0.26a
		D. ciliatus	31.7 ± 0.58b	15.0 ± 1.73b	14.3 ± 1.53a	86.0 ± 14.00a	264.0 ± 0.00b	17.1 ± 0.74b
	Squash	*B. cucurbitae*	23.7 ± 0.58a	10.0 ± 0.00a	12.3 ± 1.15a	65.0 ± 7.21a	216.0 ± 0.00a	13.6 ± 0.37a
		D. ciliatus	29.7 ± 0.58b	15.7 ± 2.08b	14.3 ± 8.50a	81.3 ± 7.77b	240.0 ± 1.00b	15.9 ± 1.79b
25	Cucumber	*B. cucurbitae*	30.0 ± 1.00a	23.3 ± 0.58a	24.0 ± 0.00	64.7 ± 12.70a	271.9 ± 0.58a	17.2 ± 1.17a
		D. ciliatus	40.3 ± 0.58b	23.3 ± 0.58a	24.0 ± 0.00	71.3 ± 1.15a	336.0 ± 0.58b	20.6 ± 0.67b
	Pumpkin	*B. cucurbitae*	30.7 ± 1.53a	19.0 ± 3.61a	24.0 ± 0.00	64.7 ± 12.70a	304.1 ± 0.58a	18.4 ± 1.32a
		D. ciliatus	41.7 ± 1.53b	23.7 ± 2.08a	24.3 ± 0.58a	79.0 ± 9.64a	376.1 ± 0.58b	22.7 ± 1.15b
	Squash	*B. cucurbitae*	31.0 ± 0.00a	18.3 ± 2.31a	22.7 ± 2.31a	72.0 ± 0.00a	264.0 ± 0.00a	17.0 ± 0.19a
		D. ciliatus	43.0 ± 1.00b	22.7 ± 1.15b	24.7 ± 1.15b	71.3 ± 1.15b	343.9 ± 0.58b	21.1 ± 0.76b
20	Cucumber	*B. cucurbitae*	49.7 ± 3.21a	17.3 ± 2.31a	46.3 ± 0.58a	96.0 ± 1.00a	391.9 ± 1.15a	25.1 ± 1.45a
		D. ciliatus	72.3 ± 1.53b	21.0 ± 2.00b	49.7 ± 1.15b	179.0 ± 11.79b	520.1 ± 0.58b	35.1 ± 1.26b
	Pumpkin	*B. cucurbitae*	49.7 ± 3.21a	17.0 ± 1.73a	46.7 ± 1.53a	110.3 ± 12.42a	391.9 ± 1.15a	25.1 ± 1.94a
		D. ciliatus	75.3 ± 1.15b	24.0 ± 5.29b	46.0 ± 4.00a	185.0 ± 8.19b	504.0 ± 0.00b	34.8 ± 0.77b
	Squash	*B. cucurbitae*	49.3 ± 2.08a	19.3 ± 1.53a	48.0 ± 0.00a	112.3 ± 14.36a	391.9 ± 1.15a	25.9 ± 1.90a
		D. ciliatus	71.7 ± 1.15b	23.0 ± 1.00b	46.3 ± 2.31b	168.3 ± 3.06b	495.9 ± 0.58b	33.5 ± 0.89b
15	Pumpkin	*B. cucurbitae*	96.0 ± 0.00a	48.0 ± 0.00a	72.0 ± 24.00a	205.0 ± 41.57a	640.1 ± 0.58a	44.2 ± 2.52a
		D. ciliatus	120.0 ± 0.00b	96.0 ± 24.00b	120.0 ± 10.00b	224.0 ± 13.86b	1,512.0 ± 1.00b	86.3 ± 12.00b

Means ± SE for each host plant, followed by different letters in the same column are significantly different by ANOVA and Newmann-Keuls ($P < 0.05$).

L1, first larval instar; L2, second larval instar; L3, third larval instar.