Life History Parameters of *Diachasmimorpha longicaudata* on *Ceratitis capitata* Under Laboratory Conditions: Implications for Mass Rearing and Biological Control

Ahlem Harbi, Institut Supérieure Agronomique de Chott-Mariem (ISA-ChM), Université de Sousse, 4042 Chott-Mariem, Tunisia; Unidad Asociada de Entomología UJI-IVIA-CIB CSIC, Centro de Protección Vegetal y Biotecnología, Instituto Valenciano de Investigaciones Agrarias (IVIA), 46113 Montcada, València, Spain, **Khaled Abbes and Brahim Chermiti,** ISA-ChM, Université de Sousse, 4042 Chott-Mariem, Tunisia, **David Martins,** Unidad Asociada de Entomología UJI-IVIA-CIB CSIC, Centro de Protección Vegetal y Biotecnología, Instituto Valenciano de Investigaciones Agrarias (IVIA), 46113 Montcada, València, Spain; Department of Entomology, Instituto Capixaba de Pesquisa, Assistencia Tecnica e ExtensaoRural (INCAPER), Rua Afonso Sarlo 160, CEP 29052-010, Vitoria-ES, Brazil, **Abir Hafsi,** ISA-ChM, Université de Sousse, 4042 Chott-Mériem, Tunisia; CIRAD-University of La Réunion, UMR-PVBMT CIRAD, France, **Beatriz Sabater-Muñoz,** Unidad Asociada de Entomología UJI-IVIA-CIB CSIC, Centro de Protección Vegetal y Biotecnología, Instituto Valenciano de Investigaciones Agrarias (IVIA), 46113 Montcada, València, Spain; Smurfit Institute of Genetics, Trinity College of Dublin, Dublín, Ireland, **and Francisco Beitia,** Unidad Asociada de Entomología UJI-IVIA-CIB CSIC, Centro de Protección Vegetal y Biotecnología, Instituto Valenciano de Investigaciones Agrarias (IVIA), 46113 Montcada, València, Spain

ABSTRACT

Harbi, A., Abbes, K., Chermiti, B., Martins, D., Hafsi, A., Sabater-Muñoz, B., and Beitia, F. 2016. Life history parameters of *Diachasmimorpha longicaudata* on *Ceratitis capitata* under laboratory conditions: Implications for mass rearing and biological control. Tunisian Journal of Plant Protection 11: 207-217.

The Mediterranean fruit fly, *Ceratitis capitata*, is considered one of the most destructive pests worldwide. The braconid *Diachasmimorpha longicaudata* is the most widely used parasitoid in biological control programs of tephritids. It has been mass-reared and used in augmentative releases against major fruit fly species in tropical and subtropical countries, and recently in the Mediterranean Basin. After its introduction into Spain and then Tunisia, reproductive and demographic parameters have been studied on *C. capitata* under laboratory conditions. These parameters were compared to those published elsewhere. The role of artificial diet for rearing the host is discussed. Our findings showed the good fitness of the parasitoids produced on *C. capitata* in laboratory with a generation time of 28.1 days, a reproductive rate of 39.2, an intrinsic rate of increase of 0.125, a doubling time of 5.2 days and the finite rate of increase (per day) was 1. Involvements on the biological control of the Mediterranean fruit fly in Tunisia are discussed.

Keywords: Biocontrol, *Ceratitis capitata*, *Diachasmimorpha longicaudata*, parasitoids, rearing conditions

Corresponding author: Brahim Chermiti Email: chermiti54@yahoo.fr Accepted for publication 12 July 2016

The Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Diptera: Tephritidae), is one of the most polyphagous and important pests of fruits worldwide (14, 29, 30). It is native from sub-Saharan Africa, where it is found in relatively small populations that do not cause major damage (2, 17, 35). However, in its other distribution zones, this species has a great ability to disperse, to explore alternative hosts and to exhibit a high ecological plasticity which allows it to overwinter and survive throughout the year in many countries causing economically important losses (30).

The use of conventional suppression techniques to control or eradicate the Medfly from an area where it is well established has been demonstrated to be insufficient in many cases, and consequently, the efficient control schemes have developed integrated management strategies through the use of multiple and compatible control techniques, including insecticide sprays, toxic baits, mass trapping systems, sterile insect technique (SIT) and classic biological control mainly based on the release of parasitoids (21, 33).

The opiine wasp *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) is considered among the successful parasitoid species currently used in biological control programs (inundative releases). It is a koinobiont, synovigenic, larval-pupal endoparasitoid of several genera of fruit fly species (Diptera: Tephritidae) (22, 27). Native from the Indo-Pacific region, it was widely disseminated into America (23). This wasp is increasingly used as part of integrated pest management schemes through augmentative releases to control many fruit fly pests and is regarded as one of the most important parasitoid species against fruits flies of the genera *Bactrocera, Anastrepha* and *Ceratitis* worldwide (5, 22, 24).

D. longicaudata has a high capacity to adapt to the different environmental conditions where it has been introduced (1, 7, 15), and can achieve higher levels of parasitism, up to 50% in field conditions, than other known parasitoids of fruit flies (8, 11, 20, 28). Consequently, efficient mass-rearing methods and augmentative release procedures of this parasitic wasp have been extensively developed (10, 27).

In Spain, *D. longicaudata* was introduced from Mexico in 2009, where it has been reared on *Anastrepha ludens*, and subsequently imported in Tunisia from Spain in 2013 in the framework of a cooperation project between the *Institut Supérieur Agronomique de Chott-Mariem* (ISA-CM), University of Sousse, Tunisia, and the *Intituto Valenciano de Investigaciones Agrarias* (IVIA), Valencia, Spain (AECID projects A/01877/08 and A/024220/09). Approximately 6000 wasps were imported as parasitized pupae of *C. capitata*. The aim of these introductions was to include this parasitoid in an integrated control program of the Medfly in citrus orchards in the two countries (18).

In insect mass production, the quality of reared parasitoids is assessed throughout the study of biological parameters which depends, among others, on the host used as well as on the general conditions of the laboratory rearing including climatic parameters (4). Recently, many research works studying the basic biological parameters of *D. longicaudata* reared on *C. capitata* and using similar experimental conditions as our rearings installed in Spain and Tunisia have been published. These studies showed many differences regarding reproductive fitness and life

history parameters which were explained by several factors including, differences of host flies, used parasitoid strains and climatic conditions of rearings. According to several authors, there are differences in reproductive fitness and life history parameters among strains of the wasp (19, 32, 34).

The aim of this research work is to evaluate the fitness of *D. longicaudata* strain imported from Mexico, reared first on *A. ludens* and later on *C. capitata*, in order to provide data to improve its laboratory rearing. Thus, we evaluated: (i) developmental and reproductive parameters of the wasp (adult life span, oviposition, pre-oviposition, post-oviposition, fertility, immature development time and daily and total sex ratio), and (ii) demographic parameters (net reproductive rate (R_0), intrinsic rate of natural increase (r_m), finite rate of increase (k), doubling time (Dt) and mean generation time (T)).

The incidence of laboratory rearing conditions on the expected performance of the parasitoid, as a biological control agent of the Medfly in Mediterranean countries including Tunisia, was explored.

MATERIALS AND METHODS

Insects.

Fruit flies and parasitoids were obtained from laboratory rearings maintained in the facilities of IVIA, Valencia, Spain, where all experiments were performed.

D. longicaudata rearing was initiated with individuals obtained from parasitized pupae of *A. ludens* provided by the *Centro Internacional de Capacitación en Moscas de la Fruta* (*CICMF*), *Plantas de Cría y Esterilización de Moscas del Mediterráneo y Mosca Mexicana de la Fruta*, Metapa de Domínguez, Chiapas, Mexico, in 2009. The laboratory rearing of the parasitoids was maintained since then in the IVIA on larvae of *C. capitata* as host for more than 6 years and refreshed yearly with adults collected in the field to avoid high levels of endogamy (18, 26). Both insects, *D. longicaudata* and *C. capitata*, are reared under constant conditions in environmental chambers (25 ± 2ºC, 65 ± 10% RH and 16:8 (L:D) photoperiod).

The fruit fly culture on artificial diet is maintained in plastic cages (40 × 30 × 30 cm) with one mesh framed lateral side to allow the oviposition of females according to the rearing method described by Harbi *et al*. (11). Briefly described, the artificial diet on which the Medfly was reared is a mixture of wheat bran, distilled water, yeast, sugar, benzoic acid, nipagin, and nipazol. Eggs of the fly were daily collected from the rearing cages and put on the diet before being incubated in climatic chambers (25 ± 2ºC, 65 ± 10% RH and 16:8 (L:D) photoperiod). *D. longicaudata* is reared on third instar larvae of Medfly, in plastic cages (40 × 40 × 40 cm) using various adult densities (4,000-5,000 female wasps per cage). Adults were provided ad libitum with water, honey and sugar. Medfly larvae mixed with the artificial diet were daily exposed to the parasitic action of *D. longicaudata*. Parasitized larvae were collected and allowed to pupate in separate cages until the emergence of the new parasitoid generation 14-16 days later.

Experimental procedure.

A total of 20 newly emerged parasitoid couples of the same age (one day-old), were put separately in experimental units consisting of 15 ×15 × 10 cm transparent plastic boxes with side aeration windows of 16 cm² and provided ad libitum with water, sugar and honey as

adult complementary food. The upper part of each box was provided with a mesh-framed rectangular opening allowing the exposition of fruit fly larvae to the parasitoids. Twenty larvae of the third instar were offered daily and for 24 hours to each of the parasitoid couples until the death of all females (maximum 55 days, see results section). After exposure, the supposed parasitized larvae/pupae were removed daily and kept in darkness to reproduce natural pupation conditions which occur in the soil until the emergence of adult fruit flies or parasitoids. The experiment was conducted in controlled climatic chambers at 23 ± 2ºC, 65 ± 10% RH and 16:8 (L:D) photoperiod.

Developmental and reproductive parameters.

Longevity of adults (male and female) and periods of pre-oviposition (the number of days between female emergence and the day of the first oviposition), post-oviposition (the number of days the female stays alive after the last oviposition) and oviposition, as well as performed fertility (the total progeny of females) were assessed. Longevity was assessed by checking the parasitoid couples daily whereas pre-oviposition, oviposition, post-oviposition periods as well as performed fertility were estimated by counting the emerged progeny of each couple.

Total developmental time of immature stages, from egg to adult emergence, was calculated based on daily observations of parasitized Medfly individuals (third instar larvae and then pupae) and counting the number of days between the exposition of the larvae to parasitism and the days of emergence of the adult parasitoid. The daily sex ratio was estimated as the proportion of female offspring in the total number of progeny (males + females) produced per day. The total sex ratio was assessed as the proportion of female offspring in the total number of progeny (males + females) produced during the life span of the female.

Demographic parameters.

This study was based on several population parameters which are detailed in Table 1.

Data analysis.

Life tables were constructed using the daily survival values and the number of progeny produced by the females. Demographic parameters were calculated according to Birch (3) and Mackauer (16). Kaplan Meyer survival curves of males and females were compared using Log-rank test with the statistical software IBM-SPSS statistics version 20.0.

Table 1. Assessed population parameters of *Diachasmimorpha longicaudata* on third instar larvae of *Ceratitis capitata* under laboratory conditions (25 ± 2ºC, 65 ± 10% RH and 16:8 L:D) (6)

Parameter	Designation	Definition	Formula
Net reproductive rate	(R_0)	Number of females produced by one female during its life	$\sum_{x=x}^{ß} lxmx$
Intrinsic rate of natural increase	r_m	Rate at which the population increases in size	$1=\sum_{x=x}^{ß} e^{-rx}\, lxmx$
Finite rate of increase	k	Factor by which a population increases in size from time *t* to time *t*+1	e^r
Doubling time	Dt	Time span necessary for doubling the initial population	$(\log_e 2)/r$
Mean generation time	T	Mean time span between the birth of an individual and the birth of its offspring	$(\log_e \mathrm{R0})/r$

x: Age in days; lx: Cohort survival; mx: Number of female eggs laid by average female at age x; Ex: expectation of life.

RESULTS

Developmental and reproductive parameters.

The mean developmental period of immature stages, from egg to adult emergence, was 21.3 ± 0.1 days for males and 22.9 ± 0.1 days for females. Our results show that the pre-oviposition period was very short or absent, with an average time of 0.3 ± 0.1 day and a maximum of 2 days. The mean oviposition period was 16.4 ± 0.8 days and the average post-oviposition period was of 5.4 ± 0.8 days.

The performed fertility was 71.2 ± 6.4 individuals/female, remained low the first day after emergence then increased to reach its maximum, 7-9 individuals/female/day, between the second and the sixth day after emergence. During this period, 75% of the total progeny of the females were produced. Beyond this period, the performed fertility decreased gradually until the end of the oviposition period (Fig. 1).

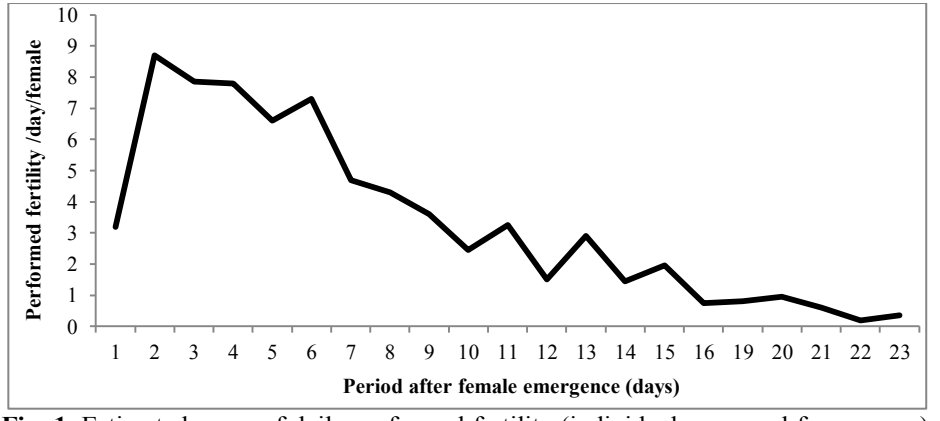

Fig. 1. Estimated mean of daily performed fertility (individuals emerged from pupae) of *Dichasmimorpha longicaudata* females reared on third instar larvae of *Ceratitis capitata*.

Males were able to live significantly longer than females according to the survival analysis (P = 0.013). The maximum life span was 55 days for females and 57 days for males (Fig. 2). The average longevity of females was 33.7 ± 1.8 days while that of males was 40.1 ± 2.8 days.

The sex ratio of the wasps was female biased, 0.8:1 (male: female). During the first three days of the oviposition period, the produced progeny was mainly males while in the rest of the period a predominance of females was observed. Thus, the wasp reproduction was marked by a protandry since males emerge earlier than females (Fig. 3).

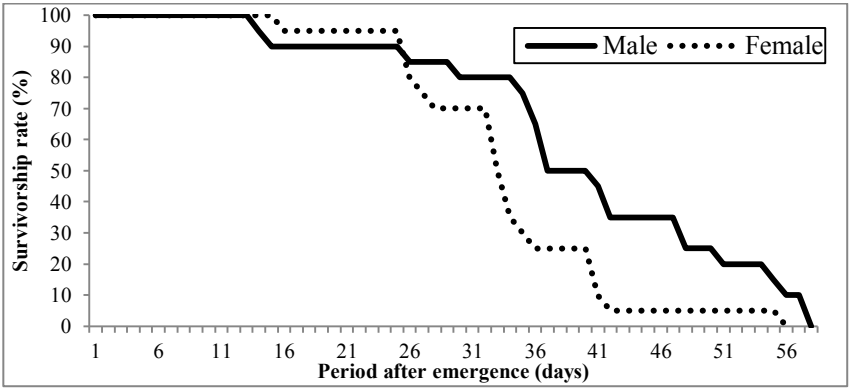

Fig. 2. Survivorship (*lx*) curves of males (n = 20) and females (n = 20) of *Dichasmimorpha longicaudata* reared on third instar larvae of *Ceratitis capitata.*

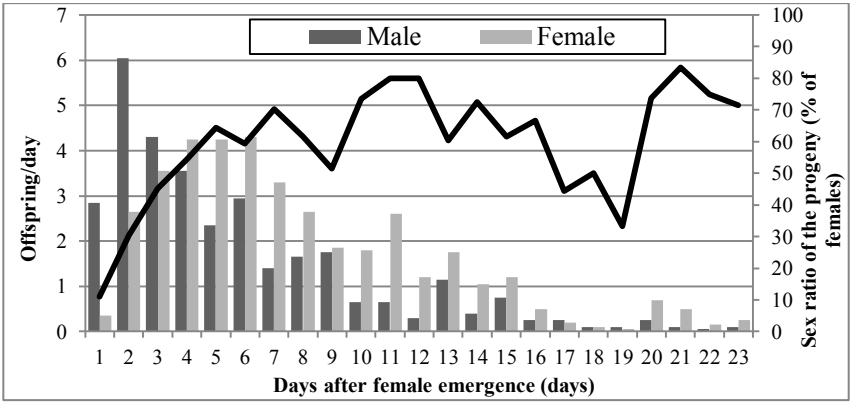

Fig. 3. Daily sex ratio of the progeny of *Dichasmimorpha longicaudata* reared on third instar larvae of *Ceratitis capitata*.

Demographic parameters.

In our experiment the generation time of *D. longicaudata* was 28.1 days, the reproductive rate was 39.2, the intrinsic rate of increase was 0.125, the doubling time was 5.2 days and the finite rate of increase (per day) was 1.

DISCUSSION

Biological parameters.

This experiment was conducted to assess life history parameters of our laboratory strain of *D. longicaudata* and compare the results with available data of other strains. Life history parameters of several laboratory strains of this parasitoid maintained on different hosts of fruits flies are shown in Table 2. Although reared on the same host species, performed fertility of *C. capitata* differed among our study and those of other research works. Ovruski *et al*. (25) found that the fertility of *D. longicaudata* (established in Argentina in 1999 with individuals imported from Mexico (24), and reared on *A. ludens* (22)) is 32.1±1.5 emerged adults, which is lower than that of the strain tested in the current study

(71.2 ± 6.4 individuals/female). Conversely, Meirelles *et al*. (19) reported a higher fertility than of our strain with 104.6 ± 4.12 individuals/female on *C. capitata* (the strain was obtained from *Embrapa Mandioca e Fruticultura Tropical*, Cruz das Almas, state of Bahia, Brazil). On the other hand, Meirelles *et al*. (19) reported a fertility of 124.8±1.11 individuals/female on the same host species.

Significantly lower adult longevity than that found in this work was reported by other studies when rearing different strains of *D. longicaudata* on *C. capitata*, *A. fraterculus* and *Bactrocera dorsalis* (19, 32, 34). By contrast, our strain presents a shorter oviposition period than that reported for other strains on all tested host flies species except on *B. dorsalis* (Table 2). Development duration from egg to adult of our strain was similar to those reported by Meirelles *et al*. (19) on *C. capitata* and *A. fraterculus*. Concerning the sex ratio of the progeny, it is female biased for all strains and on all host flies.

Demographic parameters.

Reported demographic parameters from the literature are summarized in Table 3. The generation time calculated for our strain of *D. longicaudata* was similar to that of other strains as reported by Vargas *et al*. (32) and Meirelles *et al*. (19) on *B. dorsalis* and *C. capitata*, respectively, whereas the strain tested by Viscarret *et al*. (34) had longer generation time. Conversely, this parameter was shorter on *A. fraterculus* (19).

The reproductive rate was similar to that found by Viscarret *et al*. (34), lower than that reported by Meirelles *et al*. (19) on *C. capitata* and *A. fraterculus* and higher than that reported by Vargas *et al*. (32) on *B. dorsalis*. The estimates of the intrinsic rate of increase and the finite rate of increase were comparable in all presented studies. However, the doubling time of our strain was shorter than that found by Viscarret *et al*. (34) on two strains of Medfly and longer than that reported by Meirelles *et al*. (19) either on *C. capitata* or *A. fraterculus*.

In summary, our data and those available in the literature suggest that differences in the origin of a parasitoid strain could have important effect on the reproductive and demographic traits of the parasitoid. Likewise, available data suggest also the presence of significant within-strain differences depending on the host fly species used for the rearing of *D. longicaudata*. In particular, the intrinsic rate of increase (r_m), which is of high interest to determine the development capacity of a population in field and thus the potential capacity of a parasitoid in controlling a pest, showed important variations among and within strains and/or hosts. Furthermore, these variations can be more significant since Lawrence *et al*. (13) found differences in immature development of *D. longicaudata* depending the age of the parasitized larvae. Moreover, Kitthawee and Dujardin (12) found differences in three populations of *D. longicaudata* coupled with lack of inter-population reproductive compatibility or the production of rare, sterile female offspring using Forced-contact mating technique, concluding that possible presence of three indistinguishable species rather than one (referred to as "The *Diachasmimorpha longicaudata* complex") based on the geometry of the wing. Further studies are needed, mainly on the genetic level to advance our knowledge on this wasp which can ultimately lead to a better understanding of the differences highlighted in this work and in the literature.

Table 2. Biological parameters of *Diachasmimorpha longicaudata* reported in the literature on different fruit fly species compared to this work

Fruit fly host	Experimental conditions	Adult longevity	Oviposition period	Fertility (individuals/♀)	Egg to adult duration	Sex ratio (female proportion)	References
Bactrocera dorsalis	T: 26 ± 2°C; RH: 60 ± 10%; 10:14 L: D photoperiod	15.67 ± 4.10	9.33 ± 1.64	---	---	0.59 ± 0.05	32
Ceratitis capitata	23 ± 2ºC, 65 ± 10% RH and 16:8 (L:D) photoperiod.	33.7 ± 1.8 (♀) 40.1 ± 2.8 (♂)	16.4 ± 0.8	71.2 ± 6.4	21.3 ± 0.1(♂) 22.9 ± 0.1 (♀)	0.55	This work
	Larvae and pupae: 24.61 ± 0.33°C; HR (65.00 ± 2.75%, continuous light. Adults: 22.90 ± 2.90°C; RH: 47.73 ± 1.66%, and 12L:12D photoperiod	28.33 ± 2.07	22.57 ± 1.87	---	---	0.56 ± 0.05	34
	Larvae and pupae: 24.61 ± 0.33°C Temperature; 65.00 ± 2.75% HR, and continuous light. Adults: 22.90 ± 2.90°C Temperature; 47.73 ± 1.66% RH, and 12L:12D photoperiod	34.08 ± 3.13	28 ± 2.56	---	---	0.55 ± 0.04	34
	25 ± 2°C Temperature; 65 ±10% RH and 14:10 h L:D photoperiod	20.7 ± 2.11 (♀) 14.2 ± 20.3 (♂)	27.4 ± 3.17	104.6 ± 4.12	19.2 ± 0.23 (♀) 18.5 ± 0.13 (♂)	0.55	19
	25 ± 1°C Temperature; 75 ± 5% RH, and 12:12 (L:D) h photoperiod	---	---	32.1 ± 1.5	---	50.7 ± 2.8	25
Anastrepha fraterculus	25 ± 2°C Temperature; 65 ± 10% RH and 14:10 h L:D photoperiod	20.4 ± 3.39 (♀) 15.6 ± 2.09 (♂)	29.6 ± 2.98	124.8 ± 1.11	18.8 ± 0.17 (♀) 17.2 ± 0.13 (♂)	0.59	19
	25 ± 1°C Temperature; 75 ± 5% RH, and 12:12 (L:D) h photoperiod	---	---	36.3 ± 1.8	---	82.4 ± 1.5	25

Table 3. Demographic population parameters of *Dichasmimorpha longicaudata* reported in the literature on different fruit fly species

Host fruit fly	T	R_0	k	r_m	DT	References
Bactrocera dorsalis	27.2	28.2	1.13	0.12	---	32
Ceratitis capitata	28.1	39.2	1	0.125	5.2	This work
Ceratitis capitata	37.93 ± 0.68	32.54 ± 5.65	1.102 ± 0.006	0.098 ± 0.005	7.11 ± 0.38	34
Ceratitis capitata	39.37 ± 0.55	33.84 ± 5.14	1.0990 ± 0.004	0.094 ±0.004	7.36 ± 0.28	34
Ceratitis capitata	26.03 ± 0.451	45.56 ± 5.685	1.15 ± 0.028	0.14 ± 0.019	4.73 ± 0.074	19
Anastrepha. fraterculus	22.57 ± 0.594	53.82 ± 10.001	1.19 ± 0.051	0.17 ± 0.031	3.92 ± 0.082	19

T (mean generation time, days); R_0 (net reproductive rate, female/female); k (finite rate of increase, per day); DT (doubling time, days); r_m (intrinsic rate of increase/day).

From a practical perspective, we can conclude that, in the case of *D. longicaudata*, reared strain for later use in the field should have the highest intrinsic rate of increase and all the conditions of the rearing should be optimal as the wasp showed variations in its demographic traits depending on rearing conditions especially temperature and host fly species. The good choice of these factors can improve the quality of produced natural enemies which is a key factor for a successful biological control of insect pests (9, 31).

RESUME

Harbi A., Abbes K., Chermiti B., Martins D., Hafsi A., Sabater-Muñoz B. et Beitia F. 2016. Paramètres de vie de *Diachasmimorpha longicaudata* en conditions de laboratoire: Implications pour l'élevage en masse et le contrôle biologique de *Ceratitis capitata.* Tunisian Journal of Plant Protection 11: 207-217.

La mouche méditerranéenne des fruits, *Ceratitis capitata*, est considérée comme l'un des ravageurs des fruits les plus dommageables du monde en raison de sa grande capacité d'affecter la production, sa distribution mondiale et sa large gamme d'hôtes. Le braconide *Diachasmimorpha longicaudata* est l'un des parasitoïdes les plus utilisés dans les programmes de lutte biologique contre les *Tephritidae*. Il a été élevé en masse et utilisé dans les lâchers augmentatifs contre diverses espèces de mouches des fruits dans les pays tropicaux et subtropicaux et récemment dans le bassin méditerranéen. Après son introduction en Espagne et puis en Tunisie, l'étude de ses paramètres de reproduction et démographique sur une souche méditerranéenne de *C. capitata* en conditions de laboratoire proches des conditions climatiques méditerranéennes, a été réalisée pour améliorer nos connaissances sur ce parasitoïde et améliorer son utilisation dans les programmes de contrôle biologique. Les résultats de cette étude ont été comparés à d'autres dans différentes conditions d'élevage pour les mêmes espèces et l'influence des conditions de l'élevage sur l'utilisation pratique du parasitoïde a été discutée. Ces résultats ont révélé les bonnes aptitudes des parasitoïdes produits sur *C. capitata* avec un temps de génération de 28,1 jours, un taux de reproduction de 39,2, un taux intrinsèque d'accroissement de 0,125, un temps de dédoublement de 5,2 jours et un taux fini d'accroissement (par jour) égal à 1. Les implications sur la lutte biologique contre la mouche méditerranéenne des fruits en Tunisie ont été discutées.

Mots clés: *Ceratitis capitata*, conditions d'élevage, contrôle biologique, *Diachasmimorpha longicaudata*, parasitoïdes

ملخص

حربي، أحلام وخالد عباس وابراهيم شرميطي ودافيد مرتين وعبير حفصي وبياتريس سابتار- مونوزو وفرانسيسكو بايتيه. 2016. الخصائص الحياتية للحشرة *Diachasmimorpha longicaudata* تحت ظروف المخبر : تداعياتها على التربية المكثفة والمكافحة البيولوجية لحشرة *Ceratitis capitata*.

Tunisian Journal of Plant Protection 11: 207-217.

تعتبر الذبابة المتوسطية للفاكهة *Ceratitis capitata* أحد أخطر الآفات نظرا لقدرتها على إلحاق أضرار كبيرة بالمحاصيل، و لتوزعها الجغرافي الممتد، ولتنوع عوائلها. من أفضل الكائنات المضادة المستعملة في برامج المكافحة البيولوجية لذباب الفاكهة، شبه الطفيل *Diachasmimorpha longicaudata*. تمت تربيته واستعماله بطريقة النثر ضد عدة انواع من الذباب في البلدان الاستوائية والشبه استوائية ومؤخرا في بعض البلدان المتوسطية. بعد أن تم إدخاله إلى إسبانيا ثم إلى تونس، تمت دراسة قدراته الحيوية وخصائصه الديموغرافية على سلالة متوسطية لذبابة الفاكهة في المخبر في ظروف شبيهة بالمناخ المتوسطي لتحسين معارفنا حول هذا الشبه طفيل وتطوير استعمالاته في برامج المكافحة الحيوية. تمت مقارنة نتائج هذه الدراسة بمثيلاتها ومناقشة مدى تأثير سلالة شبه الطفيل وظروف تربيته على نجاعتها البيولوجية. أظهرت نتائجنا الحالة البيولوجية الجيدة لشبه الطفيل المربى على *C. capitata* في المخبر فكان زمن الجيل 28,1 يوما ومعدل التكاثر 39,2 ومعدل الصميم للزيادة 0,125 ومضاعفة الوقت 5,2 يوم وكانت نسبة محدودة من

الزيادة (يوميا) بقيمة 1. وقد تمت مناقشة تداعيات هذه النتائج على المكافحة البيولوجية للذبابة المتوسطية للفاكهة في تونس.

كلمات مفتاحيه: شبه طفيل، ظروف التربية، مكافحة بيولوجية، *Ceratitis capitata*، *Diachasmimorpha longicaudata*

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