

# Life-history strategy in an oligophagous tephritid: the tomato fruit fly, *Neoceratitis cyanescens*

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**Abstract.** 1. In phytophagous insects, life-history traits mainly depend on host plant range. Substantial longevity, high fecundity and larval competition are the major traits of polyphagous Tephritidae while species with a restricted host range generally exhibit a lower longevity and fecundity as well as mechanisms to avoid larval competition. Our aim in this study was to investigate the life history of an oligophagous species, the tomato fruit fly, *Neoceratitis cyanescens* (Bezzi).

2. We determined life tables under laboratory conditions in order to calculate the main demographic parameters of *N. cyanescens* and studied the influence of larval and adult diet on life-history traits.

3. The mean longevity of *N. cyanescens* females was 40 days. There was a strong synchronisation of female maturity. Oviposition showed an early peak at 9–13 days after a short pre-oviposition period (6 days). The absence of proteins in the adult diet both delayed ovarian maturation and decreased female fecundity. In addition, females originating from tomato fruits produced significantly more eggs than females originating from bugweed or black nightshade, showing that even the larval host plant may strongly affect the subsequent fecundity of adult females.

4. The traits of *N. cyanescens* are then discussed in the light of those documented for polyphagous and monophagous tephritids. *Neoceratitis cyanescens* displayed attributes intermediate between those of polyphagous and monophagous tephritids. Its smaller clutch size compared with polyphagous species and its specialisation on the Solanaceae family whose fruits contain toxic compounds may help in reducing intra- and inter-specific competition, respectively.

**Key words.** Demography, fecundity, host range, longevity, *Neoceratitis cyanescens*, Tephritidae.

## Introduction

The demographic strategies of insects are linked to their ecological function in the ecosystem. In phytophagous insects, these biological traits mainly depend on the host plant range (Schowalter, 2000). Their resource foraging process may be classified into two major strategies: one opportunistic, based on a wide host range including different plant families, the other specialist, restricted to one or only a few host plants (Bernays &

Chapman, 1994; Schoonhoven *et al.*, 1998). While a few insect characteristics (e.g. diapause, difference in the structure of mouth parts, body size) have been related to host range (Bernays & Chapman, 1994; Schoonhoven *et al.*, 1998), the relationship between life-history traits of insects and host range width needs to be further explored.

The Tephritidae family contains a large number of polyphagous species. Most of these generalist species are widespread in tropical and sub-tropical regions of the world and are multivoltine (White & Elson-Harris, 1992). One striking example is the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann), which can infest more than 350 fruit species belonging to a range of different plant families (Liquido *et al.*, 1991). While there are some differences in life-history traits among these polyphagous species, for instance their colonisation and competition abilities

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(Duyck *et al.*, 2004, 2006, 2007), they overall show similar patterns such as high fecundity and intrinsic rate of increase, large clutches, as well as high dispersal ability (Zwölfer, 1982). The adults of these species may fly long distances during the host location process as a result of the temporal and spatial unpredictability of resources (Fletcher, 1987). Intra-specific competition, associated with a high larval population in fruits, leads to a compromise between larval survival and adult fitness which may be reduced through a decrease in body size, low survival rates and low fecundity (Krainacker *et al.*, 1987). The Tephritidae family also contains specialist species such as members of the genus *Rhagoletis* (White & Elson-Harris, 1992) which are monophagous or stenophagous and univoltine (Boller & Prokopy, 1976). The main challenge these species have to face is adapting to host characteristics such as the fruiting period. Accordingly, seasonal synchrony with their host and the host selection process are their key life-history traits. They are generally characterised by lower longevity and fecundity, small clutches (often one or two eggs), low adult dispersal ability and diapause events (Fletcher, 1989). In most *Rhagoletis* species, females mark the host fruit with a pheromone immediately after ovipositing, which deters other gravid females (Boller & Prokopy, 1976). This strategy allows for a wider distribution of egg laying and consequently a better exploitation of resources to the progeny. The high intrinsic rate of increase of polyphagous species enables them to rapidly exploit unpredictable resources, while the *Rhagoletis* species are able to better exploit a more stable resource, particularly through the limitation of intra-specific competition.

While life histories of species exhibiting these two contrasting strategies are well documented within the Tephritidae family, few detailed studies have dealt with the life-history strategies of species with an intermediate host range. *Neoceratitis cyanescens* (Bezzi) infests fruits of several cultivated and wild plants belonging to the Solanaceae family. This species is classified in the subfamily Dacinae and the tribe Ceratitidini, which includes other genera such as *Ceratitis* and *Trirhithrum*. The genus *Trirhithromyia* Hendel, which includes five African species, was originally described as a subgenus of *Ceratitis* before being considered as a distinct genus by Hancock (1984). More recently, Hancock and White (1997) transferred this species to the genus *Neoceratitis* (Hendel), whose host plants belong to the Solanaceae family. This major pest of tomato crops is widespread throughout the Indian Ocean region, including Madagascar, Mauritius, Reunion, and Mayotte islands (OEPP/EPPO-CABI, 1997). The females usually lay eggs in green fruits, causing serious damage to vegetable crops, particularly tomato (*Lycopersicon esculentum* Mill.), but also sweet pepper (*Capsicum annuum* L.), egg-plant (*Solanum melongena* L.), and chilli (*C. frutescens* L.). Additional wild species such as black nightshade (*S. americanum* Mill.), bugweed (*S. mauritanum* Scop.), and *S. torvum* Sw. serve as natural reservoirs. *Neoceratitis cyanescens* populations have the potential to build up rapidly in habitats (smallholdings, gardens, and village communities) where fruiting wild and cultivated hosts are present throughout the year. Although some aspects of its biology and behaviour have been studied in recent years (Brévault & Quilici, 1999, 2000a, b), this study is the first to deal with its demography (OEPP/EPPO-CABI, 1997).

In this study, we have established the life tables of *N. cyanescens* in laboratory conditions in order to calculate its main demographic parameters. In addition, as such factors may strongly influence life-history traits, we have also examined the influence of the quality of larval and adult diet on female fecundity. The traits of *N. cyanescens* are then discussed in the light of those documented for polyphagous and monophagous tephritids in order to establish the relationship between the life history and ecology of this oligophagous species.

## Material and methods

### Insects

Life-history traits and the influence of adult diet on fecundity were conducted on F1 laboratory-reared flies (Etienne, 1973) stemming from larvae that were collected from tomatoes in the western part of Reunion Island (LEGTA, Saint-Paul).

### Life table experiments

Upon emergence, 30 pairs of flies were isolated into small Plexiglas cages of approximately 1 litre volume, in a climatic chamber ( $25 \pm 2^\circ\text{C}$ ,  $70 \pm 20\%$  r.h., and a LD 12:12 h photoperiod). The flies were fed *ad libitum* with sugarcane and enzymatic yeast hydrolysate (ICN Biomedicals, Costa Mesa, CA), presented separately. Water was made available using dampened cotton. Two spherical devices of about 3 cm diameter were presented to flies: a small green tomato fruit (susceptible phenological stage) or an agar ball. Agar balls were prepared with 7.5 g of agar mixed with 450 ml of aqueous extract of green tomato (obtained by the filtration of 100 g of crushed green tomatoes mixed with 500 ml of water) and two drops of edible yellow food colorant. After solidification, they were covered with Parafilm® (Pechiney Plastic Packaging, Chicago, IL). This laying substrate aimed at avoiding the variability of natural fruit characteristics. The number of eggs laid was recorded daily while 100 eggs were collected with a camel brush from the tomato fruit, placed on humid filter paper and incubated at  $25^\circ\text{C}$  for 4 days to determine hatching proportion. The pairs of flies were monitored until females died, while males that died before females were immediately replaced by another male of the same age.

### Influence of adult and larval diets on fecundity

The influence on the ovarian development of two diets, a complete diet of granulated sugar (sugar) and enzymatic yeast hydrolysate (proteins) vs a protein-deprivation diet, was investigated. The developmental stage of the ovaries was determined from the observation of the most advanced follicle (Tzanakakis & Koveos, 1986). A total of 20 females were dissected for each treatment at 3, 4, 5, 6, 7, 8, 10 and 12-days old. The genital apparatus was extracted after the incision of the abdomen just above the ovipositor.

In the subsequent experiment, naturally infested fruits of the major host plants tomato (var. *Jackal*), bugweed, and black

nightshade, were collected in the Southern part of Reunion Island (Bassin Martin, Saint-Pierre). Flies emerged separately in  $30 \times 30 \times 30$  cm screen Plexiglas cages. They were held under controlled conditions ( $25 \pm 2^\circ\text{C}$ ,  $70 \pm 20\%$  r.h., and a LD 12:12 h photoperiod) and had *ad libitum* access to granulated sugar, enzymatic yeast hydrolysate, and water. At 8 days old, 40 females were weighted, and then dissected to assess the number of mature eggs in their ovaries.

#### Data analysis

Daily adult survival and fecundity data were combined with previously published data on developmental rates and survival rates for immature stages (egg, larvae, and pupae) reared on tomato (Brévault & Quilici, 2000b) in order to compute demographic parameters. Standard life table parameters were calculated from daily records of mortality of immature stages, fecundity and fertility of pairs of adults. Parameter symbols, formulae and definitions are according to Carey (1982) and Ebert (1999). In order to compare life table parameters among the two treatments, confidence intervals were estimated as the 2.5 and 97.5% of a bootstrap distribution resampled 1000 times (Efron & Tibshirani, 1993; Caswell, 2001). This was done using R software (R Development Core Team, 2004). Age at first oviposition was statistically analysed using Student's *t*-test while additional demographic parameters obtained from daily observations were compared using pairwise Student's *t*-test (*t'*) (XLSTAT 2007.5, Addinsoft).

The number of eggs in the ovaries of mature females of the same age according to food diet was statistically compared using Student's *t*-test, while frequencies of mature females of the same age according to food diet were analysed using  $\chi^2$ -test (XLSTAT 2007.5, Addinsoft). In order to assess the influence of larval host fruit on the weight of females and the number of eggs per female, data were submitted to an analysis of variance (ANOVA) using the SAS GLM procedure followed by Duncan's multiple range test (SAS Institute, 1989).

## Results

#### Life table analysis

Life-history traits did not vary significantly according to the egg laying substrate except for the number of ovipositions per substrate and the number of eggs per oviposition ( $t = 2.9$ , d.f. = 37,  $P = 0.006$  and  $t = 6.9$ , d.f. = 37,  $P < 0.0001$ , Tables 1 and 2). The survival rate progressively decreased from emergence to age 80 regardless of the egg laying substrate (Fig. 1a). Throughout the 38 day period, females exhibited a high egg laying frequency, regardless of the egg laying devices offered (Table 2). The mean daily proportion of females that laid eggs on tomato was higher than 75% between 8 and 17 days post-emergence while a 95% peak was reached by days 10–11 after emergence (Fig. 1b). From day 18 after emergence, the proportion of females that laid eggs fluctuated between 50 and 75%. The mean daily number of eggs laid per female did not vary significantly with the egg laying substrate (Table 2). A peak of fecundity was observed between 9 and 13 days after emergence (Fig. 1c), linked with both the proportion of ovipositing females at this period (Fig. 1b) and the number of eggs per oviposition (Fig. 1d). Egg hatching remained at a high level ( $> 80\%$ ) during the 38 day period (Table 2). The first oviposition was synchronous among females (Fig. 2). Conversely, fecundity varied greatly among females as only 30% of females laid more than 200 eggs in tomatoes or agar balls (Fig. 2). As a result, only 50% of females contributed to 85% of total progeny, regardless of the egg laying substrate (Fig. 3).

#### Influence of adult and larval diets on fecundity

The onset of ovarian maturity was delayed by 1 day when females were deprived of protein ( $\chi^2 = 13.4$ , d.f. = 1,  $P < 0.01$ ) (Fig. 4a). In addition, egg production significantly decreased when females were deprived of protein (Fig. 4b).

**Table 1.** Life table parameters (Mean and confidence interval) established for *Neoceratitis cyanescens* females in laboratory individual cages.

Parameters	Units	Egg laying substrate	
		Tomato	Agar ball
Gross reproductive rate (GRR)	Eggs/female	187.6 [141.6, 224.6]	199.5 [130.4, 217.6]
Net reproductive rate ( $R_0$ )	Eggs/female	40.7 [27.3, 56.4]	32.6 [22.1, 43.6]
Intrinsic rate of increase ( $r$ )		0.086 [0.075, 0.086]	0.074 [0.068, 0.078]
Intrinsic birth rate ( $b$ )		0.117 [0.110, 0.122]	0.109 [0.103, 0.114]
Intrinsic death rate ( $d$ )		-0.036 [-0.136, -0.135]	-0.035 [-0.135, -0.134]
Finite rate of increase $\lambda$		1.087 [1.078, 1.090]	1.077 [1.071, 1.082]
Mean generation time ( $T$ )	Days	44.6 [42.6, 48.2]	46.0 [43.3, 50.1]
Doubling time (DT)	Days	8.3 [8.0, 9.2]	9.1 [8.8, 10.1]
Average age in stable population ( $\bar{a}$ )	Days	9.5 [9.1, 10.0]	10.2 [9.8, 10.7]
Expectation of life at birth ( $e_0$ )	Days	35.6 [32.3, 39.0]	33.6 [30.3, 36.9]

Formulae of the parameters are given in Carey (1982) and Ebert (1999). Confidence intervals of the first 10 life-history parameters were estimated as the 2.5 and 97.5% of a bootstrap distribution re-sampled 1000 times (Efron & Tibshirani, 1993; Caswell, 2001).

For calculation of reproductive parameters, the number of eggs per female at age  $x$  ( $m_x$ ) has been taken as the total number of eggs/2 and thus is the number of females on the assumption of a 1:1 sex ratio (Ebert, 1999).

**Table 2.** Reproductive traits (Mean  $\pm$  SE) established for *Neoceratitis cyanescens* females in laboratory individual cages.

Parameters	Units	Egg laying substrate		
		Tomato	Agar ball	
Adult age at first oviposition	Days	5.9 $\pm$ 1.0	6.3 $\pm$ 1.2	$t = 0.3$
Daily mated females (%)	%	73 $\pm$ 18	73 $\pm$ 19	$t' = 0.2$
Daily ovipositing females (%)	%	61 $\pm$ 25	57 $\pm$ 26	$t' = 1.2$
Daily production per female	Eggs/female	4.1 $\pm$ 2.1	3.8 $\pm$ 2.4	$t' = 0.9$
Daily production per ovipositing female	Eggs/female	6.2 $\pm$ 2.3	5.6 $\pm$ 2.9	$t' = 1.4$
Number of ovipositions per substrate		3.0 $\pm$ 1.3	3.8 $\pm$ 2.1	$t' = 2.9^{**}$
Number of eggs per oviposition		1.9 $\pm$ 0.8	1.4 $\pm$ 0.6	$t' = 6.9^{**}$
Egg hatching	%	89 $\pm$ 5	—	

Parameters were monitored over 38 days to maintain a sufficient sample size (at 38 days post-emergence,  $n = 13$  and  $n = 14$  females for agar ball and tomato fruit, respectively).

Demographic data were analysed using Student's  $t$ -test ( $t$ ) for individual observations or pairwise Student's  $t$ -test ( $t'$ ) ( $^{**}P < 0.01$ ) for populational daily observations.

Eight-day-old females that emerged from naturally infested fruits presented a higher weight and egg load when collected from tomato fruits than from bugweed or black nightshade ( $F = 103.2$ , d.f. = 2,  $P < 0.01$ ;  $F = 33.4$ , d.f. = 2,  $P < 0.01$ ) (Fig. 4c).

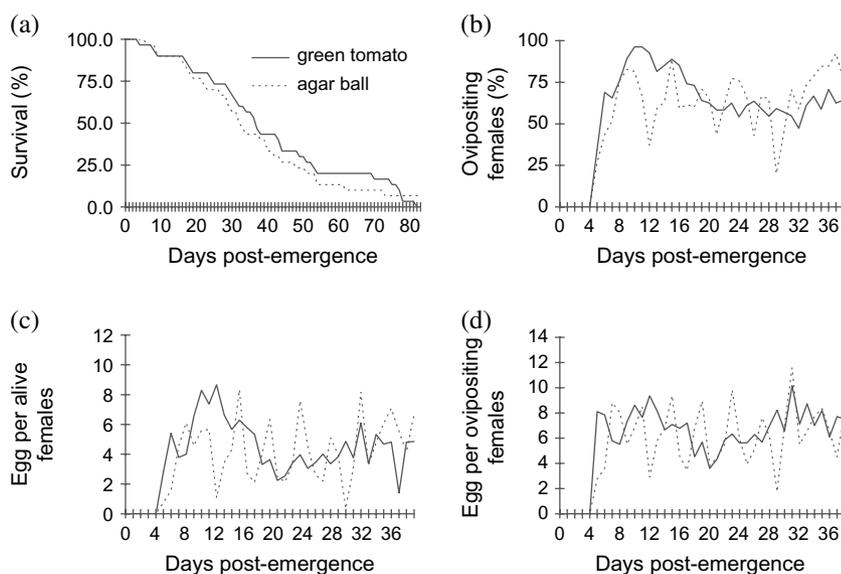
## Discussion

### Life-history strategy

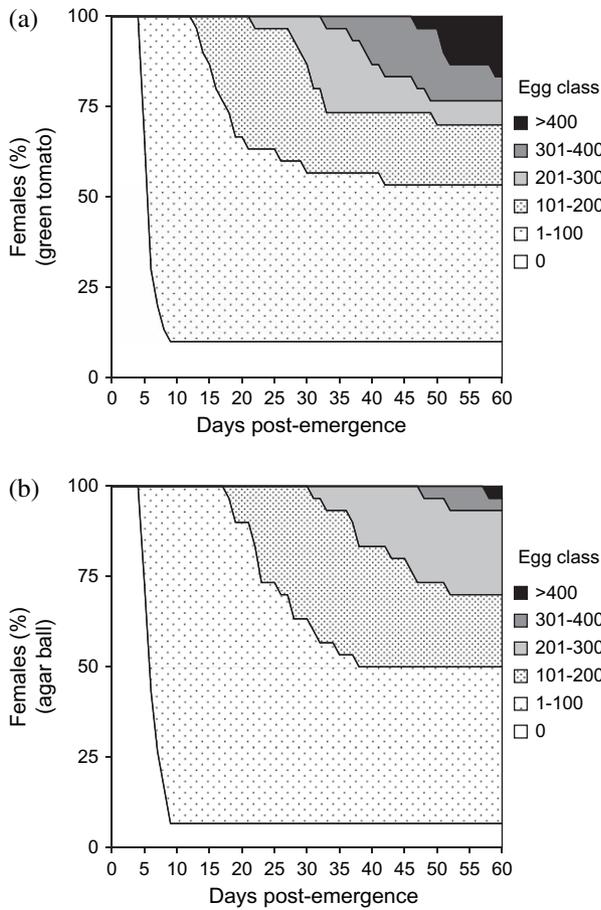
This study is the first to provide demographic parameters for *N. cyanescens*, an important pest of tomato crops in the Indian Ocean. Several studies have drawn attention to the demographic parameters of Tephritidae (Carey, 1982, 1984; Vargas *et al.*, 1984; Carey *et al.*, 1988; Vargas & Carey, 1989; Yang *et al.*, 1994; Vargas *et al.*, 1997). As various factors can affect demographic parameters, comparisons between different species or studies should be done with care. However, such comparisons

are useful to highlight critical elements both in terms of life history and adaptive strategies.

The longevity of *N. cyanescens* females varied consistently between individuals with a mean value of 40 days. The pre-oviposition period (6 days) was short, with a peak of fecundity occurring soon after the start of oviposition period (5–9 days). In *C. capitata*, *Bactrocera cucurbitae* (Coquillett) and *Bactrocera dorsalis* (Hendel), the longevity of laboratory-reared females at 25 °C reached 51, 79 and 108 days, respectively (Vargas *et al.*, 1984). In Hawaii, Carey *et al.* (1988) observed on laboratory strains of *C. capitata*, *B. cucurbitae* and *B. dorsalis*, a pre-oviposition period of 5, 10 and 9 days, respectively. The peak of fecundity was reached between 3 and 5 days after the start of the oviposition period in *C. capitata*, while it required 1–2 weeks in *B. dorsalis* (Carey *et al.*, 1988). Like *C. capitata*, *N. cyanescens* females showed a short longevity and a short pre-oviposition period. The interval between the start of oviposition and the occurrence of a peak of fecundity stands in-between *C. capitata* and the *Bactrocera* species. Carey *et al.* (1988) and Vargas *et al.*

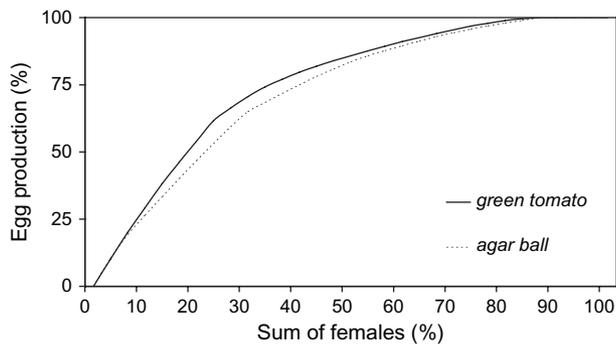


**Fig. 1.** Temporal evolution of the proportion of (a) live and (b) ovipositing females, (c) daily number of eggs per alive female and (d) daily number of eggs per ovipositing female in *Neoceratitis cyanescens*. Green tomato fruit or agar ball were offered as ovipositional substrate.

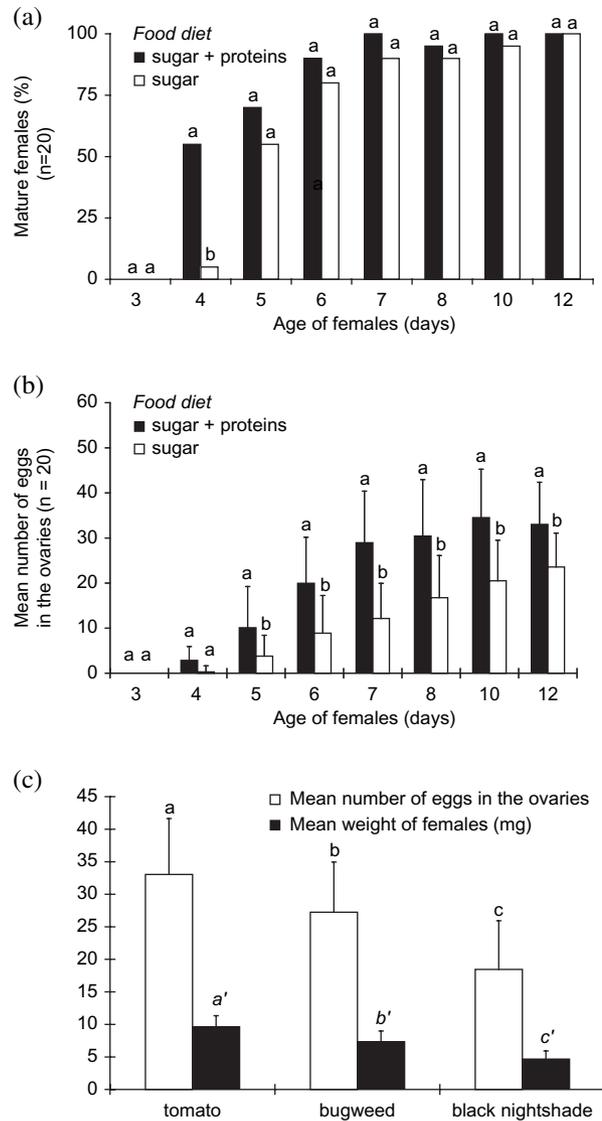


**Fig. 2.** Distribution of *Neoceratitis cyanescens* females based on fecundity classes and age with (a) green tomato fruit or (b) agar ball as ovipositional substrate.

(1984) obtained respectively on *C. capitata*, *B. cucurbitae*, and *B. dorsalis* fecundity values of 641 and 995, 406 and 881, 892 and 1428 eggs per female. Compared with that of *N. cyanescens*, the higher fecundity of polyphagous species such as



**Fig. 3.** Cumulative egg production of *Neoceratitis cyanescens* females within a period of 84 days (study period), according to the ovipositional substrate.



**Fig. 4.** (a) Proportion of mature *Neoceratitis cyanescens* females and (b) mean egg production (+SD) according to the adult food diet. Paired bars followed by different letters are significantly different: (A)  $\chi^2$ -test and (B) Student's *t*-test ( $P < 0.05$ ). (c) Mean weight and egg load (+SD) of 8 day-old *Neoceratitis cyanescens* females according to larval host fruit. Values followed by different letters are significantly different (ANOVA followed by Duncan's multiple range test,  $P < 0.05$ ).

*C. capitata* and *B. dorsalis* may express different reproductive strategies. For a comparable study period, the mean number of eggs laid by a female of *C. capitata* fluctuated between 20 and 30 per day (Carey *et al.*, 1988), as opposed to about five eggs per day for *N. cyanescens*. The polyphagous *A. ludens*, which also shows a relatively low daily fecundity (10.8) nevertheless has a fecundity of 1195 eggs, because of its mean longevity reaching 111 days (Liedo, 1992).

In a recent study, Duyck *et al.* (2007) compared the life history of *C. capitata*, *Ceratitis rosa* Karsch and *Bactrocera zonata*

(Saunders) in Reunion Island. While these authors demonstrated that the life history of these polyphagous species is linked to their ability to compete with each others, all three species showed higher fecundity parameters than *N. cyanescens*.

Regarding host range, *B. cucurbitae* occupies an intermediate position. Indeed, although this species is mostly found on Cucurbitaceae, its host range includes different families of plants (Dhillon *et al.*, 2005). Vayssières (1999) reported for this species a high fecundity and longevity somewhat similar to those of the polyphagous species.

In a similar way to *N. cyanescens*, the Solanaceous fruit fly, *Bactrocera latifrons* (Hendel) also attacks primarily solanaceous fruits, although it may also be found to infest some cucurbitaceous fruits (Liquidó *et al.*, 1994). Its demography was compared to that of *C. capitata*, *B. dorsalis*, and *B. cucurbitae* by Vargas *et al.* (1997) who showed, on lab strains, that this species had a net fecundity lower than that of the other species at various temperatures. It was also characterised by a short longevity (female longevity of 46.3 days at 24 °C) and a short pre-oviposition period (6.3 days at 24 °C) close to that of *C. capitata*. Such demographic characteristics appear similar to those of *N. cyanescens*.

Compared with *N. cyanescens*, monophagous species such as *Rhagoletis* spp. exhibit lower fecundity with a gross fecundity between 100 and 300 eggs per female (Boller & Prokopy, 1976; Fletcher, 1989). For *R. completa* Cresson, Kasana and Aliniaze (1994) determined a mean longevity of 50 and 30 days and a mean preoviposition period of 11 and 10 days at 24 °C and 28 °C, respectively. On the whole, while the longevity of *N. cyanescens* is close to that of *Rhagoletis*, it benefits from a shorter preoviposition period and a higher fecundity. In addition, most of the species in this genus also show a diapause at the pupal stage, a weak mobility and usually deposit only one egg per clutch; all attributes which are not found in *N. cyanescens*.

#### *Influence of adult and larval diets*

The absence of proteins in the adult food diet both delayed the ovarian maturation and decreased the fecundity of females. Similarly, Romanyukha *et al.* (2004) and Nestel *et al.* (2005) reported that the access to protein food sources significantly influences egg production and longevity in the Mediterranean fruit fly, *C. capitata*. Manrakhan and Lux (2006), comparing three natural food sources, showed that fecundity was higher when *Ceratitis fasciventris* (Bezzi) and *C. capitata* females were fed on a protein-rich diet. Mangan (2003) showed that the addition of protein in the adult diet approximately tripled mature egg production of *A. ludens* females. In *Musca domestica* L. (Diptera: Muscidae), females reared on a low protein substrate, did not complete ovarian development (Adams & Nelson, 1990).

Females originating from larvae reared on tomato presented a higher weight and produced more eggs than females originating from bugweed or black nightshade fruits. A linear relationship between pupal weight and fecundity of females was shown for *C. capitata* (Krainacker *et al.*, 1989) as well as other Tephritidae such as *B. dorsalis*, *C. rosa* and *R. pomonella* (Averill & Prokopy,

1987; Krainacker *et al.*, 1989; Duyck *et al.*, 2006). At the susceptible stage, bugweed (10–12 mm diam) and black nightshade (6–7 mm diam) fruits are very small compared with tomato fruits (20–30 mm). The limited resource availability for individual larvae may have induced a subsequent larval competition for food. In addition, if numerous plants allow the complete development of a given tephritid species, host quality may strongly affect larval growth and survival, as well as the subsequent fecundity of adult females (Carey, 1984; Fernandes da Silva & Zucoloto, 1997).

#### *Ecology and life-history strategies*

Substantial longevity, high fecundity and larval competition are the major traits of polyphagous species. Species with a restricted host range such as *Rhagoletis* spp. exhibit a lower longevity and fecundity and developed mechanisms to avoid larval competition with small clutch size and host marking pheromones (Fletcher, 1989). On the whole, the oligophagous *N. cyanescens* showed attributes of fecundity and clutch size that stand in-between polyphagous and monophagous tephritid species. In terms of foraging strategy, monophagous species are strongly linked with predictable resources. Conversely, oligophagous species, although generally less mobile than polyphagous species, are capable of flights over long distances during the host finding process (Zwölfer, 1982; Fletcher, 1989).

Life-history strategy and behavioural traits are important determinants of competition in insects (Huffaker & Gutierrez, 1999). *Neoceratitis cyanescens* may be able to limit inter-specific competition with polyphagous tephritids of Reunion Island by exploiting a particular host plant niche. Indeed, most of its host plants are not shared with other tephritid species (Quilici & Jeuffraut, 2001). Moreover, most species of the family Solanaceae contain toxic compounds (Hawkes *et al.*, 1979): while larvae of *N. cyanescens* can develop in host-fruits belonging to this family, the latter may be toxic for other species. This should be further investigated by infesting Solanaceae fruits in the laboratory with polyphagous tephritid larvae.

The reduction of clutch size in *N. cyanescens* compared with polyphagous species may allow for avoidance of intra-specific competition by decreasing density in fruits. This is of particular importance as this species infests some small fruits such as bugweed. Moreover, the nutritive value (in terms of calories) of most of these fruits may be inferior to that of fruits generally infested by polyphagous tephritids such as mango or guava (Gebhardt & Thomas, 2002). In comparison with monophagous species, together with the absence of an adverse period, the ability of *N. cyanescens* to infest a number of fruit species within the family Solanaceae whose fruiting period covers the whole year may explain the absence of diapause in this species.

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