

# Life history and life table analysis of the whitefly predator *Delphastus catalinae* (Coleoptera: Coccinellidae) on collards

TONG-XIAN LIU

Vegetable IPM Laboratory, Department of Entomology, Texas Agricultural Experiment Station, Texas A&M University, Weslaco, Texas, USA

**Abstract** The ladybeetle, *Delphastus catalinae* (Horn), is one of the most commonly used predacious natural enemies being commercially reared for controlling whiteflies, including *Bemisia tabaci* (Gennadius) biotype B (= *B. argentifolii* Bellows & Perring), on various ornamental and vegetable crops under greenhouse conditions. The development, survivorship, and fecundity of *D. catalinae* feeding on *B. tabaci* biotype B on collard plants were determined in the laboratory, and the age-specific life table parameters were analyzed based on the life history data. Developmental time was 4.0, 1.9, 1.1, 1.4, 5.2, and 5.3 days for eggs, first, second, third, fourth instars, and pupae, respectively, with an average of 18.9 days from oviposition to adult emergence for both sexes, 19.0 days for females, and 18.8 days for males. Adult longevities averaged 146.6 days for both sexes, 122.6 days for females, and 170.5 days for males. After an average 4.9 days preoviposition period, females laid a mean of 5.6 eggs per day over a 97.0-day period. Net reproductive rate ( $R_0$ ) and gross reproductive rate ( $\sum m_x$ ) were estimated by life table analysis at 276.8 and 325.1, respectively. Generation time (T) and doubling time (DT) were 35.6 and 4.8 days respectively, and the intrinsic rate of natural population increase ( $r_m$ ) was estimated at 0.158, or  $l = 1.171$  for the finite rate of increase. The  $r_m$  value of *D. catalinae* is similar to or higher than those of the whitefly feeding on most vegetable and ornamental crops, indicating that the ladybeetle is capable of regulating populations of *B. tabaci* biotype B and other whiteflies under greenhouse conditions.

**Key words** coccinellids, whiteflies, biological control, greenhouse, life table, predation  
DOI 10.1111/j.1744-7917.2005.00015.x

## Introduction

The ladybeetles in the genus *Delphastus* Casey (Coleoptera: Coccinellidae) are important predators of whiteflies, including three native North American species, *D. catalinae* (Horn), *D. pallidus* (LeConte) and *D. pusillus* (LeConte) (Muma *et al.*, 1961; Meyerdirk *et al.*, 1980; Gordon, 1985, 1994; Hoelmer & Pickett, 2003). Because of the outbreaks of *Bemisia tabaci* (Gennadius) biotype B (= *B. argentifolii* Bellows & Perring) (Homoptera: Aleyrodidae) on vegetables, ornamental plants, and field crops in the 1980s (Hamon & Salguero, 1987; Bellows *et al.*, 1994) and

insecticide resistance thereafter (Prabhaker *et al.*, 1997), considerable attention has been directed toward biological control of the whiteflies using natural enemies. Of numerous predacious natural enemies, *D. catalinae* (reported previously as *D. pusillus*) has been one of the most studied ladybeetle predators (Hoelmer *et al.*, 1994b), and has gradually become one of the most commonly used commercially reared predacious natural enemies used for controlling whiteflies on various ornamental and vegetable crops under greenhouse conditions (Hunter, 1998). Hoelmer and Pickett (2003) recently pointed out that many recent studies on the life history, biology, and behavior of *D. pusillus* actually refer to *D. catalinae*, including those studies by Hoelmer *et al.* (1993), Heinz and Parrella (1994), Heinz *et al.* (1994), Hoelmer *et al.* (1994a), Heinz and Nelson (1996), and Heinz and Zalom (1996).

In a study to determine the lethal and sublethal effects of

Correspondence: Dr. Tong-Xian Liu, Texas A&M University AES, 2415 E. Highway 83, Weslaco, TX 78596, USA. Tel: +956 968 5585; fax: +956 968 0641; e-mail: tx-liu@tamu.edu

two insect growth regulators, pyriproxyfen and buprofezin, on adult *D. catalinae*, Liu and Stansly (2004) also examined the effects of insect growth regulators on the life history parameters including development times of immatures, and longevities of both female and male adults. They found higher fecundities of *D. catalinae* on collards than those reported in the literature (Hoelmer *et al.*, 1993; Heinz *et al.*, 1994; Heinz & Zalom, 1996). To confirm their findings, a comprehensive life history study of *D. catalinae* was conducted to compare the results with those reported in the literature, although the published results were obtained from a variety of different host plants. This paper reports all life table parameters, including the intrinsic rate of natural increase ( $r_m$ ), gross reproductive rate ( $\sum m_x$ ), net reproductive rate ( $R_0$ ), generation time (T), finite rate of increase ( $\lambda$ ), and doubling time (DT), which are essential for utilization and predicting the outcome once *D. catalinae* is introduced for management of whiteflies under greenhouse conditions.

## Materials and methods

### *Delphastus catalinae* and prey

*Delphastus catalinae* were originally supplied by the Arizona Biological Control Inc. (Tucson, Arizona, USA) in 1998, and were maintained in a greenhouse at the Vegetable IPM Laboratory, Texas A&M University Agricultural Research and Extension Center at Weslaco, Texas, USA. Collard (*Brassica oleracea* L. var. *acephala*, 'Georgia LS') was used as the host plant for the prey, *B. tabaci* biotype B. The collard plants were grown in 15-cm plastic pots filled with Metro-Mix 300 growing medium (Grace Sierra, Horticultural Products Company, Milpitas, California, USA), to which sufficient slow release fertilizer (N-P-K: 12-8-6) was added as needed to maintain normal growth.

All experiments were conducted in an air conditioned insectary at  $26.0 \pm 2^\circ\text{C}$ ,  $55 \pm 5\%$  RH, and a photoperiod of 14: 10 (L: D) hours. Voucher specimens of *D. catalinae* were deposited in the Insect Collection of the Texas Agricultural Experiment Station, Texas A&M University at Weslaco, Texas, USA.

### Life table data

Adult *D. catalinae* from the greenhouse culture were placed on collard plants bearing whitefly eggs (>30 eggs per square centimeter, and  $\approx 1\ 000$  eggs per leaf) for oviposition. All life table data of *D. catalinae* were obtained beginning with newly deposited *D. catalinae*

eggs ( $\leq 12$  h), and ending when all adults died. Initially, 50 newly deposited eggs were collected and individually isolated on circular leaf disks (4.5 cm diameter) that were individually placed in clear plastic Petri dishes (9 cm diameter  $\times$  1.5 cm in depth). A piece of filter paper (8 cm in diameter) was placed on the bottom of the dish, and a few drops of water were added daily for moisture. These eggs were monitored daily until larval hatching. Neonate larvae were individually removed using a camel-hair brush (No. 00) onto a piece of collard leaf with >500 whitefly eggs in a Petri dish. Development, molts and pupation of these larvae were recorded daily until adult emergence.

A few hours after adults emerged, they were sexed, and males were paired with females. Each pair was placed in a Petri dish (9 cm diameter  $\times$  1.5 cm in depth) containing a 7–8 cm collard leaf disk bearing >1 000 whitefly eggs. Leaf disks bearing whitefly eggs were replaced daily. The beetles in each Petri dish were monitored daily. If the male of the pair died within 20 days, another male of approximately the same age that had been maintained in several extra Petri dishes for this purpose was added. Data from 16 pairs of *D. catalinae* adults were used in the analysis. Numbers of eggs deposited by each adult female on the leaf disks were counted and examined after new leaf disks were replaced. The leaf disks bearing *D. catalinae* eggs were then individually incubated in separate Petri dishes until either the eggs died or larvae hatched.

The following parameters were obtained: development of eggs, development of each instar and pupae, sex ratio of emerged adults, preoviposition period, adult longevity, fecundity, oviposition period, eggs that were oviposited per day per female, and eggs that eventually hatched. Developmental time, percentage of survival, duration of oviposition, and total eggs per female were analyzed using analysis of variance (ANOVA), and means were separated using least significant difference test (SAS Institute, 2003).

### Life table analysis

The age-specific life table method (Birch, 1948) was used to analyze life table parameters. Age-specific survivorship beginning with pivotal age of 0.5-day-old adults and age-specific reproduction were used to construct a life table. Intrinsic rate of increase ( $r_m$ ) was computed using the Euler equation:

$$\sum e^{-rx} l_x m_x = 1,$$

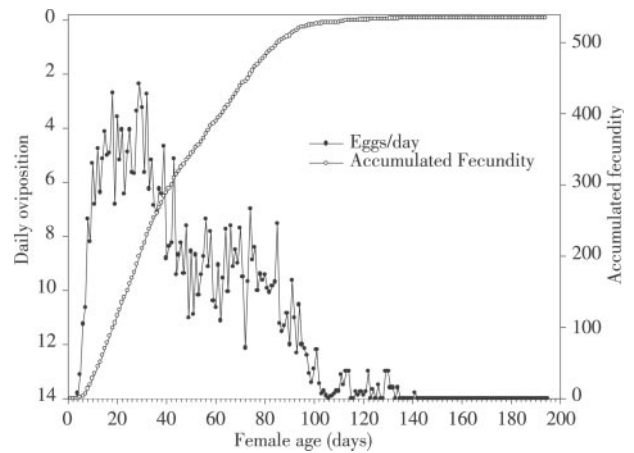
where  $l_x$  is survivorship of the original cohort over age interval from day  $x-1$  to day  $x$  (pivotal age), and  $m_x$  is the mean number of female offspring produced per surviving female during the age interval  $x$  (Birch, 1948). Other parameters, including gross reproductive rate ( $\sum m_x$ ), net reproductive rate ( $R_0$ ), generation time (T), and finite rate

of increase ( $\lambda$ ), were calculated as described by Birch (1948). Doubling time was calculated from:  $DT = (\ln 2)/r$  (Mackauer, 1983). All life table parameters were computed using an SAS program written by Maia *et al.* (2000).

**Results**

*Development of immature stages*

All eggs of *D. catalinae* successfully eclosed in 4 days (Table 1). Of the four instars, the development time for each of the first three instars (unsexed) was 1–2 days, whereas that for the 4th instars was much longer, 5.2 days. The development time for pupae was 5.3 days, and that from egg to adult emergence was 18.9 days. There were no significant differences in development times between each corresponding stage that developed to either female or



**Fig. 1** Fecundities of *Delphastus catalinae* feeding on *Bemisia tabaci* biotype B on collards.

**Table 1** Development and mortality of *Delphastus catalinae* immature stages feeding on eggs of *Bemisia tabaci* biotype B on collards.

Stage	Development, Days $\pm$ SE				Survival(%)
	Overall	Female	Male	Hoelmer <i>et al.</i> (1993) <sup>†</sup>	
Egg	4.0 $\pm$ 0.0	4.0 $\pm$ 0.0	4.0 $\pm$ 0.0	4.1 $\pm$ 0.2	100.0
1st instar	1.9 $\pm$ 0.1	2.0 $\pm$ 0.1	1.9 $\pm$ 0.1	1.8 $\pm$ 0.2	100.0
2nd instar	1.1 $\pm$ 0.1	1.1 $\pm$ 0.1	1.1 $\pm$ 0.1	1.4 $\pm$ 0.1	95.9
3rd instar	1.4 $\pm$ 0.1	1.4 $\pm$ 0.1	1.5 $\pm$ 0.1	1.8 $\pm$ 0.3	91.8
4th instar	5.2 $\pm$ 0.1	5.1 $\pm$ 0.1	5.0 $\pm$ 0.2	6.6 <sup>‡</sup>	91.8
Larval stage	9.6 $\pm$ 0.2	9.6 $\pm$ 0.2	9.5 $\pm$ 0.2	11.6	88.4
Pupa	5.3 $\pm$ 0.1	5.4 $\pm$ 0.1	5.3 $\pm$ 0.1	6.1 $\pm$ 0.2	100.0
Egg to pupa	18.9 $\pm$ 0.1	19.0 $\pm$ 0.2	18.8 $\pm$ 0.1	21.8 <sup>‡</sup>	88.4

<sup>†</sup> On hibiscus (see discussion in the text). <sup>‡</sup> Combined the days of 4th, 4th (pupating) and 5th instars.

male adults ( $F_{1,36} = 0.01-1.02$ ;  $P = 0.3198-0.9184$ ). Of the emerged adults, 22 were females, and 16 were males, giving a sex ratio of 1.00: 0.73 of female: male ( $n = 38$ ), or 57.9% females and 42.1% males.

*Age-specific fecundity*

Newly emerged adult females began laying eggs on day 5, and deposited one or more eggs on each of an average of 83.8 days during an average oviposition period of 97.0 days (Table 2). Over 50% of total eggs were deposited in the first 37 days, 80% in the first 68 days, 90% in the first 80 days, and 100% on day 142 (Fig. 1). Each female deposited an average of 6.5 (range 1–22) eggs on each of its oviposition day, with an average of 544.0 eggs (range 186–728) per female during its lifespan, and a daily average of 5.6 eggs (range 0–22) during the entire ovipo-

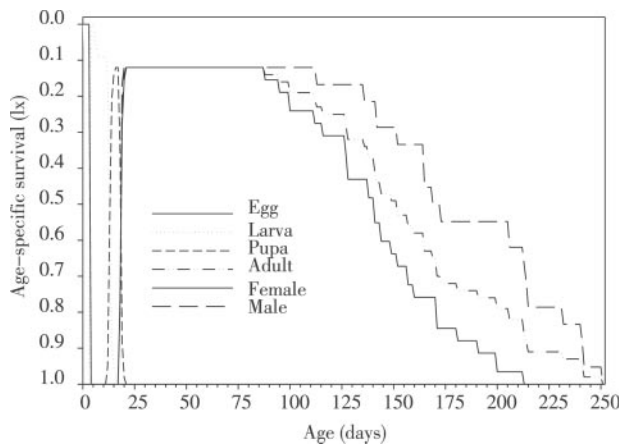
sition period.

*Adult longevity*

Adult longevity varied from 70 to 233 days, with an average of 146.6 days over both sexes. Females lived 70–194 days with an average longevity of 122.6 days ( $n = 16$ ), and males lived 95 to 233 days with an average longevity of 170.5 days ( $n = 16$ ). Male adults lived significantly longer than females ( $F_{1,36} = 12.67$ ;  $P = 0.0011$ ).

*Age-specific survivorship and life table parameters*

All eggs successfully developed to larvae (100%,  $n = 43$ ), 88.4% larvae ( $n = 39$ ) successfully pupated, and all pupae ( $n = 38$ ) developed to adults (Table 1, Fig. 2). Only five immature individuals died before maturity. Survival



**Fig. 2** Age-specific survival rate ( $l_x$ ) of *Delphastus catalinae* feeding on *Bemisia tabaci* biotype B on collards.

**Table 2** Life history parameters and related statistics of *Delphastus catalinae* fed on eggs of *Bemisia tabaci* biotype B on collard leaf disks in Petri dishes.

Parameter	Value
No. ♀♀ in cohort	16
No. ♂♂ in cohort	16
Longevity of adults, d	146.6 ± 8.2
Longevity of ♀♀, d	122.6 ± 9.5
Longevity of ♂♂, d	170.5 ± 10.7
Fraction of ♀♀ (♀ : ♂ = 1.0000 : 0.7272)	0.5789
Survivorship from egg to adult	0.8837
Preoviposition period, d	4.9 ± 0.4
Oviposition period, d	97.0 ± 7.6
Days ≥ 1 eggs were deposited	83.8 ± 6.8
Fecundity per ♀	544.0 ± 26.9
No. eggs per ♀ /oviposition d	6.5 ± 0.1
No. eggs per ♀ /d during entire oviposition period	5.6 ± 0.1
Egg survival rate %	95.9 ± 0.7

**Table 3** Life table parameters of *Delphastus catalinae* ( $n = 16$ ) fed on eggs of *Bemisia tabaci* biotype B on collard leaf disks in Petri dishes.

Parameter	True calculation	Jackknife estimate (95% CL)
Gross reproduction ( $\sum m_x$ )	325.12	—
Intrinsic rate of increase ( $r_m$ )	0.158	0.158 (0.146–0.169) <sup>†</sup>
Net reproductive rate ( $R_0$ ), d	276.80	276.80 (238.29–315.31)
Mean generation time ( $T$ ), d	35.56	35.61 (32.64–38.57)
Doubling time ( $DT$ ), d	4.38	4.39 (4.07–4.71)
Finite rate of increase ( $\lambda$ )	1.17	1.17 (1.16–1.18)

<sup>†</sup> $r_m = 0.12908$  by using the approximate method (Maia *et al.*, 2000).

rates of adults were high, and the first adult died on day 70 (one female) (Fig. 2). Over the lifespan of the adults for both sexes, 50% survived to day 139 and 20% survived up to 187 days. Males generally lived longer than females. Approximately 50% of males lived up to 187 days, and 20% up to 214 days, compared with 123 and 153 for the same survival rates for females. Of the 8 704 eggs deposited by the 16 females, 95.9% developed to larvae.

Based on all life history parameters above, the intrinsic rate of increase ( $r_m$ ) of *D. catalinae* was 0.158, the net reproductive rate ( $R_0$ ) was 276.8 offspring, the finite rate of increase ( $\lambda$ ) was 1.171, the generation time ( $T$ ) was 35.6 days, the doubling time ( $DT$ ) was 4.4 days, and the gross reproductive rate ( $\sum m_x$ ) was 325.1 offspring (Table 3).

## Discussion

Many of the life history and life table parameters, including development of immature stages, longevity of both adult females and males, and fecundity of the adult females, obtained from this study are higher than those reported in previous studies for *D. catalinae* (originally reported as *D. pusillus*) (Hoelmer *et al.*, 1993; Heinz *et al.*, 1994; Heinz & Zalom, 1996). Recently, Hoelmer & Pickett (2003) summarized the historical reasons for the misidentification of the two species, and considered that all recent studies of *D. pusillus* by Hoelmer *et al.* (1993, 1994a, b), Heinz & Parrella (1994), Heinz & Nelson (1996) should be *D. catalinae*. Nevertheless, all major life history parameters of *D. catalinae* were remarkably different from those reported in the previous studies, which different host plants were used, and host plant characteristics are known to influence natural enemy activity and life history parameters.

Hoelmer *et al.* (1993) observed that approximately half of the fourth instars of *D. pusillus* molted to a fifth instar that lasted 2.0 days before pupation. In this study, all fourth instars pupated, and no fifth instars were observed. They

also observed a somewhat longer developmental time of *D. pusillus* from egg to adult emergence (21.8 days), compared with  $18.9 \pm 0.1$  days in this study and approximately 18 days at  $27.5^\circ\text{C}$  on cotton (Heinz *et al.*, 1994) for *D. catalinae*.

The longevities of *D. catalinae* found in this study were significantly different from those reported. Hoelmer *et al.* (1993) found that the longevities of the *D. pusillus* adult females and males were  $60.5 \pm 6.3$  days and  $44.8 \pm 2.6$  days, respectively. Heinz *et al.* (1994) reported that the longevities of *D. catalinae* adult females and males were 64 days and 36 days on poinsettia, respectively, and 21.2 days and 20 days on two tomato cultivars, respectively. In contrast, results in this study show that the *D. catalinae* adult females lived an average of  $122.6 \pm 9.5$  days, and the adult males  $170.5 \pm 10.7$  days, up to twofold longer in female longevities and fivefold in male longevities than *D. pusillus* on hibiscus (Hoelmer *et al.*, 1993) and *D. catalinae* on poinsettia (Heinz *et al.*, 1994), and sixfold longer in adult female longevities and eightfold longer in adult male longevities than *D. catalinae* in tomato (Heinz *et al.*, 1994).

The fecundity of *D. catalinae* found in this study were also approximately twofold more than those reported in the literature, probably due to the greater longevity of the females. Results in this study show that each female deposited an average of 7.0 eggs per day during a 90.8-day oviposition period, and in 77.7 days of this period the female deposited one or more eggs. Hoelmer *et al.* (1993) found that females of *D. pusillus* deposited an average of 3.0 eggs per day under laboratory conditions with a total fecundity of 183 eggs per female (maximum 385) during its lifespan, and a twofold increase under greenhouse conditions. In either case, these numbers are significantly fewer than *D. catalinae* in this study (557 eggs per female).

Whereas it is obvious that the life history parameters of *D. catalinae* using collards as a host plant were distinctly different from those of *D. catalinae* (reported as *D. pusillus*) on hibiscus (Hoelmer *et al.*, 1993), various biotic and abiotic factors and methodologies might contribute to the differences of the life history parameters of *D. catalinae* found between the fecundity results in this study and those by Heinz *et al.* (1994) and Heinz and Zalom (1996) who found that trichome density of plant leaves may adversely affect the oviposition rate by reducing the number of prey the beetle can consume. In another study to compare various life history traits of *D. catalinae* (as *D. pusillus*) on two tomato cultivars with different trichome densities, Heinz and Zalom (1996) found that the beetles on the glabrous tomato cultivar 'VF145B7879' had almost fivefold greater lifetime fecundity ( $34.5 \pm 3.7$  days) than beetles on the pubescent tomato cultivar 'Alta' ( $7.9 \pm 1.2$  days). However, they did not find significant differences

between the adult longevities on the two tomato cultivars. Thus, different host plants on which the predator and prey lived are able to cause significant differences in performance and life history traits of *D. catalinae*. In a study on a similar coccinellid, *Nephaspis oculatus* (Blatchley), Liu and Stansly (2002) also found that the beetles significantly preferred collards to sweetpotato, soybean, eggplants, and hibiscus for oviposition. Probably many unrecognized factors influence host plant preferences and life history characteristics.

Although data obtained from this life table study in the laboratory may not be directly applied to greenhouse populations, they clearly show the potential of the upper limits of *D. catalinae* under ideal conditions in the absence of natural enemies and competition, and without problems of finding a mate or prey. Life tables of *N. oculatus* that also prey on whiteflies (*B. argentifolii*) have been studied by Liu *et al.* (1997) and Ren *et al.* (2002) under different temperatures and host plants. These authors found much lower intrinsic rates of increase at  $26^\circ\text{C}$  for *N. oculatus*,  $r_m = 0.078$  and  $0.055$ , respectively, compared with  $r_m = 0.158$  for *D. catalinae*, a 2–3-fold difference between the two species. These differences were partly due to higher net reproductive rates (5.3–8.6-fold), shorter generation times (1.4–2.2-fold), shorter doubling times (2.0–3.5-fold), and higher finite rate of increase (1.1-fold) in *D. catalinae* than *N. oculatus* as reported in Liu *et al.* (1997) and Ren *et al.* (2002), respectively. Therefore, the life table parameters in coccinellids could be specific or related to prey types, or are affected by various biotic factors, such as host plants, or abiotic factors, such as temperature.

Based upon the data from their laboratory studies, Hoelmer *et al.* (1993) estimated that individual beetles are able to consume as many as 10 000 whitefly eggs or 700 fourth instar nymphs during their life span under laboratory conditions, and significantly more under greenhouse conditions. Assuming the egg consumption is the same as that reported in the literature (167 whitefly eggs or 11.6 early fourth instar whitefly nymphs per day under laboratory conditions, and 252 under greenhouse conditions) and using the longevity data from this study (147 days for both sexes), an individual adult beetle could prey on as many as 24 500 whitefly eggs or 1 700 early fourth instars under laboratory conditions, and 37 000 whitefly eggs under greenhouse conditions during its lifespan.

Intrinsic rate of increase, net reproductive rate, finite rate of increase, and gross reproduction of *D. catalinae* were relatively high compared with those in other similar coccinellids (Table 3). Theoretically, a predator should efficiently regulate the population of its prey if its  $r_m$  value is equal to or greater than that of its prey's (Sabelis, 1992). In biological control, the  $r_m$  values of the natural enemies

have been used for the selection of promising biological control agents and to predict the outcome once a natural enemy is used (Jervis & Copland, 1996). Tsai and Wang (1996) reported that the  $r_m$  values of *B. argentifolii* were 0.192, 0.153, 0.138, 0.131 and 0.120 when the whitefly fed on eggplants, tomato, sweetpotato, cucumber, and garden bean, respectively. Van Giessen *et al.* (1995) reported the  $r_m$  values for *B. tabaci* biotype "B" (= *B. argentifolii*) were 0.12, 0.13, 0.14, and -0.05, respectively, on tomato, collard, eggplant, and pepper. Thus, it would appear that the potential population increase of *D. catalinae* is higher than or similar to those of the whiteflies on most vegetable crops under greenhouse conditions. In addition, *D. catalinae* is compatible with parasitoids of whiteflies, including *Encarsia sophia* (Girault & Dodd) [= *Encarsia transvena* (Timberlake)], *Encarsia luteola* Howard, *Encarsia formosa* Gahan and *Eretmocerus* spp. (Hymenoptera: Aphelinidae) because the beetle's larvae and adults avoid feeding on the whitefly nymphs or pupae with late stage developing parasitoids (Hoelmer *et al.*, 1994a; Heinz *et al.*, 1994). The compatibility with whitefly parasitoids enables growers to use both parasitoids and *D. catalinae* for biological control of whiteflies of vegetables and ornamental crops under protected environments, such as greenhouses, where high-value crops are grown (Pickett *et al.*, 1999).

## Acknowledgements

The author thanks K. A. Hoelmer (USDA-ARS, European Biological Control Laboratory, Montpellier, France) and C. H. Pickett (California Department of Food and Agriculture, Biological Control Program, Sacramento, California, USA) for reviewing an early version of this manuscript, and Y. M. Zhang for technical assistance. This study was partially funded by Texas A&M University Agricultural Experiment Station. This manuscript has been approved for publication by the Director of Texas A&M University Agricultural Research and Extension Center at Weslaco, and the Head of the Department of Entomology, Texas A&M University, College Station, Texas, USA.

## References

- Bellows, T.S., Perring, T.M., Gill, R.J. and Headrick, D.H. (1994) Description of a new species of *Bemisia* (Homoptera: Aleyrodidae). *Annals of Entomological Society of America*, 87, 195–206.
- Birch, L.C. (1948) The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology*, 17, 15–26.
- Gordon, R.D. (1994) South American Coccinellidae (Coleoptera) Part III: Taxonomic revision of the Western Hemisphere genus *Delphastus* Casey. *Frustrula Entomologica*, n.s. 17, 71–133.
- Gordon, R.D. (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of New York Entomological Society*, 93, 1–912.
- Hamon, A.B. and Salguero, V. (1987) *Bemisia tabaci*, sweetpotato whitefly, in Florida (Homoptera: Aleyrodidae: Aleyrodinae). *Florida Department of Agriculture Consumer Service Entomology Circular*, 292, 1–2.
- Heinz, K.M. and Nelson, J.M. (1996) Interspecific interactions among natural enemies of *Bemisia* in an inundative biological control program. *Biological Control*, 6, 384–393.
- Heinz, K.M. and Parrella, M.P. (1994) Biological control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) infesting *Euphorbia pulcherrima*: Evaluations of releases of *Encarsia luteola* (Hymenoptera: Aphelinidae) and *Delphastus pusillus* (Coleoptera: Coccinellidae). *Environmental Entomology*, 23, 1346–1353.
- Heinz, K.M. and Zalom, F.G. (1996) Performance of the predator *Delphastus pusillus* on *Bemisia* resistant and susceptible tomato lines. *Entomologia Experimentalis et Applicata*, 81, 345–352.
- Heinz, K.M., Brazzle, J.R., Pickett, C.H., Natwick, E.T., Nelson, J.M. and Parrella, M.P. (1994) *Delphastus pusillus* as a potential biological control agent for sweetpotato (silverleaf) whitefly. *California Agriculture*, 48, 35–40.
- Hoelmer, K.A. and Pickett, C.H. (2003) Geographic origin and taxonomic history of *Delphastus* spp. (Coleoptera: Coccinellidae) in commercial culture. *Biocontrol Science and Technology*, 13, 529–535.
- Hoelmer, K.A., Osborne, L.S. and Yokomi, R.K. (1993) Reproduction and feeding behavior of *Delphastus pusillus* (Coleoptera: Coccinellidae), a predator of *Bemisia tabaci* (Homoptera: Aleyrodidae). *Journal of Economic Entomology*, 86, 322–329.
- Hoelmer, K.A., Osborne, L.S. and Yokomi, R.K. (1994a) Interaction of the whitefly predator *Delphastus pusillus* (Coleoptera: Coccinellidae), with parasitized sweetpotato whitefly (Homoptera: Aleyrodidae). *Environmental Entomology*, 23, 136–139.
- Hoelmer, K.A., Osborne, L.S. and Yokomi, R.K. (1994b) Biological control of sweetpotato whitefly in Florida. *Pest Management in the Subtropics: Biological Control—a Florida Perspective* (eds. D. Rosen, F.D. Bennett & J.L. Capinera), pp. 103–113. Intercept, Andover, U.K.
- Hunter, C.D. (1998) *Suppliers of Beneficial Organisms in North America*. California Environmental Protection Agency, Division of Pesticide Regulation, Sacramento, CA, USA.
- Jervis, M.A. and Copland, M.J.W. (1996) The life cycle. *Insect Natural Enemies, Practical Approaches to Their Study and Evaluation* (eds. M.A. Jervis & B. Kidd), pp. 63–161. Chapman and Hall, London, UK.
- Liu, T.-X. and Stansly, P.A. (1999) Feeding and searching behavior of *Nephaspis oculatus* and *Delphastus catalinae* (Coleop-

- tera: Coccinellidae), predators of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Environmental Entomology*, 28, 901–906.
- Liu, T.-X. and Stansly, P.A. (2002) Functional response and plant preference of *Nephaspis oculatus* (Coleoptera: Coccinellidae), preying on *Bemisia argentifolii* (Homoptera: Aleyrodidae) in the laboratory. *Entomologia Sinica*, 9, 1–9.
- Liu, T.-X., Stansly, P.A., Hoelmer, K.A. and Osborne, L.S. (1997) Life history of *Nephaspis oculatus* (Coleoptera: Coccinellidae), predator of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Annals of Entomological Society of America*, 90, 776–782.
- Mackauer, M. (1983) Quantitative assessment of *Aphidius smithi* (Hymenoptera: Aphidiidae): fecundity, intrinsic rate of increase, and functional response. *Canadian Entomologist*, 115, 399–415.
- Maia, A. de H.N., Luiz, A.J.B. and Campanhola, C. (2000) Statistical influence on associate fertility life table parameters using Jackknife technique: Computational aspects. *Journal of Economic Entomology*, 93, 511–518.
- Meyerdirk, D.E., Kreasky, J.B. and Hart, G.W. (1980) Whiteflies (Aleyrodidae) attacking citrus in southern Texas with notes on natural enemies. *Canadian Entomologist*, 112, 1253–1258.
- Muma, M.H., Selhime, A.G. and Denmark, H.A. (1961) An annotated list of predators and parasites associated with insects and mites on Florida citrus. *Florida Agricultural Experiment Station Technical Bulletin*, 634, 1–39.
- Pickett, C.H., Casanave, K.A., Schoenig, S.E. and Heinz, K.M. (1999) Rearing *Delphastus catalinae* (Coleoptera: Coccinellidae): practical experience and a modeling analysis. *Canadian Entomologist*, 131, 115–129.
- Prabhaker, N., Toscano, N.C., Castle, S.J. and Henneberry, T.J. (1997) Selection of imidacloprid resistance in silverleaf whitefly from the Imperial Valley and development of a hydroponic bioassay for resistance monitoring. *Pesticide Science*, 51, 419–428.
- Ren, S.X., Stansly, P.A. and Liu, T.-X. (2002) Life history parameters for the whitefly predator *Nephaspis oculatus* (Coleoptera: Coccinellidae) at constant temperatures. *Biological Control*, 23, 262–268.
- Sabelis, M.W. (1992) Predatory arthropods. *Natural Enemies, the Population Biology of Predators, Parasites and Diseases* (ed. M.J. Crawley), pp. 225–264. Blackwell, Oxford, UK.
- SAS Institute (2003) *SAS/STAT User's Guide*. SAS Institute, Cary, NC, USA.
- Tsai, J.H. and Wang, K.H. (1996) Development and reproduction of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on five host plants. *Environmental Entomology*, 25, 810–813.
- Van Giessen, W.A., Mollema, C. and Elsey, K.D. (1995) Design and use of a simulation model to evaluate germplasm for antibiotic resistance to the greenhouse whitefly (*Trialeurodes vaporariorum*) and the sweetpotato whitefly (*Bemisia tabaci*). *Entomologia Experimentalis et Applicata*, 76, 271–286.

Accepted August 12, 2004