

Life History of *Nephaspis oculatus* (Coleoptera: Coccinellidae), a Predator of *Bemisia argentifolii* (Homoptera: Aleyrodidae)

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ABSTRACT *Nephaspis oculatus* (Blatchley) is a common introduced coccinellid predator in Florida, which feeds on many whitefly species. We evaluated development, consumption rates, survivorship, longevity, and fecundity of a southern Florida (Immokalee) population of this coccinellid on a diet of eggs of *Bemisia argentifolii* Bellows & Perring. Developmental time was 4.6, 3.3, 1.5, 1.5, 3.0, and 5.2 d for eggs, 1st, 2nd, 3rd, 4th instars, and pupae, respectively, with an average of 19.4 d from oviposition to adult emergence for females and 18.3 d for males. Daily consumption of whitefly eggs by male and female larvae was not significantly different (average 79 for males, and 86 for females) with a mean of 16, 68, 128, and 124 eggs consumed per larva per day by 1st, 2nd, 3rd, and 4th instars, respectively, totaling 51, 132, 192, and 373 eggs for each successive larval stage. Male-female pairs of adults consumed a mean of 184.1 eggs per day over a period of 16 wk. Adult females from a 2nd population in central Florida (Apopka) consumed an average of 78.0 *B. argentifolii* eggs per day over a period of 5 wk, and males consumed 123.0 eggs per day. The sex ratio of 1,153 beetles was 1.00:0.89 female to male. Adult longevities averaged 56.1 d for males, and 67.5 d for females. After an average 11.3-d preoviposition period, females laid a mean of 3.03 eggs per day. Net reproductive rate was estimated by life table analysis at 54.27, generation time was 51.27 d, and doubling time was 8.89 d. Intrinsic rate of population increase was estimated at 0.078, or $\lambda = 1.08$ for finite rate of increase. *N. oculatus* showed good potential for biological control of *B. argentifolii*, especially in greenhouses.

KEY WORDS ladybird beetle, sweetpotato whitefly, coccinellid, predator, life table

Bemisia argentifolii Bellows & Perring is a pest of broad leaf field crops, vegetables, and ornamentals in the tropics and subtropics, and of greenhouse crops in temperate regions. Losses and control costs in the United States were estimated at \$500 million in 1992, over 28% of which occurred in Florida (Perring et al. 1993). Because control of *B. argentifolii* with insecticides is often difficult, biological control may make significant contributions to whitefly management.

Since its likely introduction into Florida from Central America on imported plant materials (Gordon 1972, 1985), *Nephaspis oculatus* (Blatchley) has been reported preying on several whitefly species, including *Aleurocanthus woglumi* Ashby, *Pealius kelloggi* (Bemis), *Trialeurodes floridensis* (Quaintance), *Dialeurodes citri* (Ashmead), and *D. citrifolii* (Morgan) (Muma et al. 1961; Gordon 1972, 1985; Cherry and Dowell 1979; Browning and Stimac 1994). Misidentified as *N. gorhami* Casey, it was

introduced from Central America to California to control citrus whitefly, *D. citri* (Rose and DeBach 1981). As *N. amnicola* Wingo (synonymized with *N. oculatus* by Gordon 1985), it was introduced from Honduras, Trinidad, and the West Indies to Hawaii in 1979-1980 where it has become effective in biological control of the spiraling whitefly, *Aleurodicus dispersus* Russell (Kumashiro et al. 1983). *N. oculatus* was also reported as a predator of citrus whitefly in southern Texas (Meyerdirk et al. 1980). Feeding and development of *N. oculatus* in Hawaii on 4th-instar *Aleurodicus dispersus* Russell was studied in the laboratory by Yoshida and Mau (1985), who also observed it feeding in the field on *Aleurothrixus floccosus* (Maskell) and *Orchamoplatus mammaeferus* (Quaintance & Baker). The 1st report of feeding on *B. argentifolii* was made by Hoelmer et al. (1994), who observed the coccinellid on greenhouse ornamentals. However, detailed biology was still lacking in the literature to evaluate the potential of *N. oculatus* as a biological control agent of *B. tabaci* or *B. argentifolii*.

After we noticed this beetle in 1994 devouring our greenhouse colony of *B. argentifolii* in Immokalee, we published studies on morphology (Liu and Stansly 1996a) and susceptibility to some selected biorational insecticides (Liu and Stansly 1996b). Because of its potential to control *B. argentifolii* in the greenhouse, we broadened our studies of *N.*

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oculatus to include developmental time, consumption, oviposition, survival, fecundity, and life table parameters; we used *B. argentifolii* eggs as a food source. Included for comparison are observations made in Apopka during 1992 on egg consumption by adults of a 2nd wild population of *N. oculus*, from central Florida.

Materials and Methods

***Nephaspis oculatus* and *B. argentifolii*.** A beetle colony was maintained in Immokalee on a greenhouse culture of *B. argentifolii* using several host plants: collard, *Brassica oleracea* L. variety *acephala*, 'Georgia LS'; hibiscus, *Hibiscus rosa-sinensis* L., 'Brilliant Red'; tomato, *Lycopersicon esculentum* Miller, 'Lanai'; and sweet potato, *Ipomoea batatas* L., 'Carolina Bunch'. Plants were grown in 15-cm plastic pots filled with Metro-Mix 300 growing medium (Grace Sierra, Milpitas, CA), to which sufficient slow release fertilizer (N:P:K, 12:8:6) (Diamond R Fertilizer, Winter Garden, FL) was added as needed to maintain normal growth. Subject beetles were maintained on eggs of *B. argentifolii* obtained by exposing clean potted collard plants to the whitefly colony for 24–48 h. All experiments in Immokalee were conducted in an air-conditioned insectary at $26.7 \pm 2^\circ\text{C}$, $55 \pm 5\%$ RH, and photoperiod of 14:10 (L:D) h. Voucher specimens of *N. oculatus* and *B. argentifolii* have been deposited in the Insect Collection, Southwest Florida Research and Education Center, University of Florida, Immokalee.

Nephaspis oculatus in Apopka was maintained in a mixed colony of *B. argentifolii* and *Trialeurodes variabilis* (Quaintance) cultured, respectively, on hibiscus, *Hibiscus rosa-sinensis* L., and papaya, *Carica papaya* L., variety 'Sunrise'. The beetles had been originally collected from *T. variabilis* on outdoor papaya and from *B. argentifolii* on outdoor hibiscus (varieties unknown). Laboratory studies in Apopka were conducted in an air-conditioned insectary at $28 \pm 3^\circ\text{C}$ with a photoperiod of 12:12 (L:D) h, and $40\text{--}50 \pm 5\%$ RH, and greenhouse studies at $19\text{--}30^\circ\text{C}$ and $60\text{--}95\%$ RH.

Development of Immatures and Egg Consumption by Larvae. Adult beetles from the greenhouse culture in Immokalee were placed on collard plants bearing whitefly eggs (>20 eggs per square centimeter, and >1,000 eggs per leaf) for oviposition. Individual beetle eggs >12 h old were isolated on circular leaf disks (4.5 cm diameter) placed individually in a clear plastic petri dish (5 cm diameter). A piece of filter paper (5 cm in diameter) was placed on the bottom of the dish, and a few drops of water were added daily for moisture. Beetle eggs ($n = 46$) were monitored daily until eclosion when 46 neonate larvae were gently removed using a camel's-hair brush (No. 00) onto a piece of collard leaf of $9\text{--}15\text{ cm}^2$ upon which were a known number of whitefly eggs. Every day consumption was monitored daily by counting remaining whitefly eggs, after which fresh eggs were provided. Molts were

also noted at this time. Sex of each individual was determined at adult eclosion (Liu and Stansly 1996a).

Emergence Periodicity and Sex Ratio of Adults. Pupae of *N. oculatus* of Immokalee population on leaf disks (8–9 cm in diameter) were placed on moistened filter paper in glass petri dishes (9 cm diameter) and monitored hourly from 0800 to 1700 hours for emergence. Sex ratio was determined for newly emerged adults from this and other tests as well as from randomly collected pupae for the greenhouse colony ($n = 1,153$) in Immokalee.

Egg Consumption, Longevity, Fecundity, and Survivorship of Adults. For studies in Immokalee, each of 45 newly emerged male–female pairs (<12 h old) was provided with a known number of whitefly eggs (between 282 and 1,620) on a leaf disk of 5–8 cm diameter placed on moistened filter paper in a plastic petri dish (9 cm diameter). The number of whitefly eggs partially or totally consumed was determined by counting intact eggs 24 h later. Beetle eggs laid during the 24-h interval were also noted at this time, and a new batch of counted whitefly eggs on a fresh leaf disk was provided. The process continued until all beetles died. For preliminary observations of beetle feeding in Apopka, 7 females and 6 males feeding on *T. variabilis* on papaya in the field were placed in the laboratory. Three females and all 6 males were immediately given *B. argentifolii* eggs on hibiscus leaf disks, and the remaining 4 females given *T. variabilis* eggs on papaya leaf disks. They were allowed to feed ad libitum on 350+ eggs per day to provide a preliminary estimate of whitefly egg consumption. All other field-collected beetles collected from hibiscus and papaya were placed into culture. Their progenies were collected as pupae from the insectary and placed into petri dishes for feeding studies when they emerged. Individual beetles were placed into ventilated 3-cm plastic petri dishes containing a layer of 5% agar gel with methyl parabenzoate (methyl P-hydroxy-benzoate) added as preservative. *B. argentifolii* eggs (>300) were provided on leaf disks placed on the agar, exposed for 24 h to each beetle for feeding, and recounted to record consumption. Females were paired with males for 24 h, and mating behavior observed on days 8, 9, 10, or 11 after eclosion. Because of malfunctioning environmental control in the insectary, beetles of both sexes in this experiment were moved to a greenhouse ($19\text{--}30^\circ\text{C}$, $60\text{--}90\%$ RH) 20–23 d after eclosion. Oviposition was also recorded; any eggs seen were removed to prevent their consumption because beetles consumed their own eggs if other food became scarce. Females surviving <7 d were not included in the results.

Life Table Analysis. Age-specific survivorship beginning with 1-d-old eggs, and age-specific reproduction for 22 females from the Immokalee culture were used to construct a life table. Intrinsic rate of increase (r) was computed using the Euler equation:

Table 1. Developmental duration (days) of immature stages of ♂ and ♀ *N. oculatus* on a diet of *B. argentifolii* eggs

Stage	Overall		Male		Female	
	n	Days ± SE	n	Days ± SE	n	Days ± SE
Eggs	46	4.6 ± 0.1	24	4.6 ± 0.2	22	4.5 ± 0.1
Larvae						
First instars	46	3.3 ± 0.1	24	3.1 ± 0.1	22	3.4 ± 0.2
Second instars	46	1.5 ± 0.1	24	1.3 ± 0.2	22	1.6 ± 0.1
Third instars	46	1.5 ± 0.1	24	1.4 ± 0.2	22	1.5 ± 0.2
Fourth instars	43	3.0 ± 0.2	22	2.7 ± 0.2	21	3.2 ± 0.3
Pupae	39	5.2 ± 0.1	20	5.2 ± 0.2	19	5.2 ± 0.2
Total	39	18.9 ± 0.3	20	18.3 ± 0.3	19	19.4 ± 0.5

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

where l_x is survivorship of the original cohort over age interval from day $x-1$ to day x , and m_x is the mean number of female offspring produced per surviving female during the age interval x (Birch 1948). Values of m_x for the population were calculated by multiplying the mean number of eggs laid per female per day by 0.53, the ratio of females to males. Other parameters, including net reproductive rate (R_0), generation time (T), and finite rate of increase (λ), were calculated as described by Birch (1948). Doubling time was calculated from $DT = (\ln 2)/r$ (Mackauer 1983).

Data Analysis. 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 1988). A BASIC computer program written by Abou-Setta et al. (1986) was used to calculate life table parameters.

Results

Development of Immatures. *N. oculatus* completed development from egg to adult eclosion in 18.9 d (18.3 d for males, and 19.4 d for females), with no significant difference between the sexes ($F = 0.67$; $df = 1, 38$; $P = 0.41$) (Table 1). Eggs hatched after a 4- to 6-d incubation period followed by a larval period consisting of 4 stadia. Stadia 1 and 4 were longest and approximately of equal length (≈ 3 d); stadia 2 and 3 each lasted 1.5 d.

Consumption of Whitefly Eggs. An average of 748 eggs was consumed by a larva during its development from egg hatch until pupation. Male larvae consumed a mean of 730 ± 37.8 (mean \pm SE) eggs, and females consumed a mean of 765 ± 11.4 eggs

with no significant differences between the sexes ($F = 0.02$; $df = 1, 42$; $P = 0.84$) (Table 2). Daily consumption of eggs by 3rd and 4th instars was approximately equal. However, 4th instars consumed twice as many whitefly eggs as 3rd instars, almost half the total of all larval consumption, because of the greater duration of the 4th stadium.

Mean consumption of whitefly eggs by adult beetles from the population in Immokalee was 184.1 ± 12.1 eggs per male and female pair per day over a period of a 16-wk lifespan (Fig. 1). Day-to-day consumption of whitefly eggs varied considerably from a minimum of zero to a maximum of 265 per beetle, although mean daily consumption remained relatively constant with age. The longest lived male and female pair consumed 34,354 whitefly eggs over a period of 189 d.

In the earlier studies with adults conducted in Apopka, field-collected beetles moved to the laboratory ceased feeding after several days. The 4 females offered *T. variabilis* eggs, the host on which they had been collected, consumed an average of 269.5 ± 25.5 eggs during the 1st d in the laboratory. Average consumption declined to 47.3 ± 11.5 eggs on day 2; and to <1.0 egg on days 3 and 4, after which observations were discontinued. Average consumption for the 3 females given *B. argentifolii* was 160.7 ± 14.2 eggs on the 1st d, 175.3 ± 35.7 eggs on the 2nd d, and zero eggs on days 3 and 4. Daily consumption of *B. argentifolii* eggs by males declined after the 1st d but not as dramatically as with the females, averaging 212.5 ± 25.6 , 46.3 ± 5.4 , 116.2 ± 13.1 , 52.5 ± 11.8 , and 67.5 ± 11.9 on days 1-5, respectively.

Beetles reared in Apopka from pupae and fed after eclosion in the laboratory had a more uniform pattern of feeding than did the field-collected individuals brought into the laboratory. Of 6 females

Table 2. *B. argentifolii* egg consumption (mean \pm SE) by all larval stages of *N. oculatus* on collard leaves in the laboratory (sex was determined after adult emergence)

Stage	Overall			Male		Female	
	n	Total	Per day	n	Total	n	Total
Second instars	46	101.6 ± 11.0	67.7	24	101.8 ± 10.8	22	101.3 ± 11.2
Third instars	46	192.4 ± 23.3	128.3	24	189.3 ± 35.4	22	195.5 ± 11.3
Fourth instars	43	372.9 ± 29.1	124.3	22	369.9 ± 40.8	21	375.9 ± 17.4
All larval stages	43	717.9 ± 19.5	77.2	22	710.2 ± 37.8	21	725.4 ± 11.4

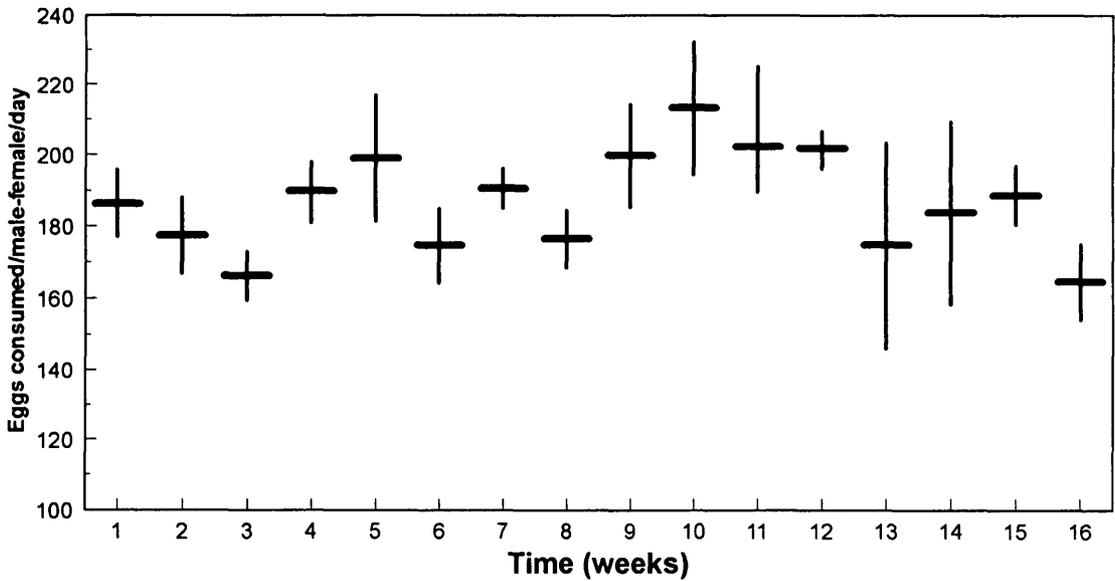


Fig. 1. Mean number \pm SE of *B. argentifolii* eggs on collard leaf disks in petri dishes consumed by 45 δ - φ pairs of *N. oculatus*, Immokalee population, per day during each week over a 16-wk period.

surviving >1 wk, 1 died after 9 d, 2 escaped on days 25 and 33, and 3 were still alive after 37 d when the observations were ended. Daily consumption by individuals varied widely from 0 to 266. Mean consumption of *B. argentifolii* eggs by these 6 females was 78.0 ± 20.8 eggs per day; with consumption per individual ranging from 71.3 to 93.9. The 12 males observed from 1 to 4 d consumed 123.0 ± 13.0 ; range 23–208 eggs per day, which when summed with daily consumption by females would give 201.0 per pair per day, similar to the 184.1 from Immokalee. Daily

consumption varied considerably from day to day, highest initially and then diminishing over the 5-wk period (Fig. 2), in contrast to the Immokalee beetles. Greater variability in the Apopka population may be the result of the smaller sample size or changes in the whitefly prey, or both.

Emergence Periodicity and Sex Ratio of Adults. Emergence of adults at night (1700–0800 hours) was 52%, or 3.5%/h compared with 48%, or 5.3%/h of total adults emerged during the day (0900–1700 hours) ($n = 433$). Hourly observations revealed no

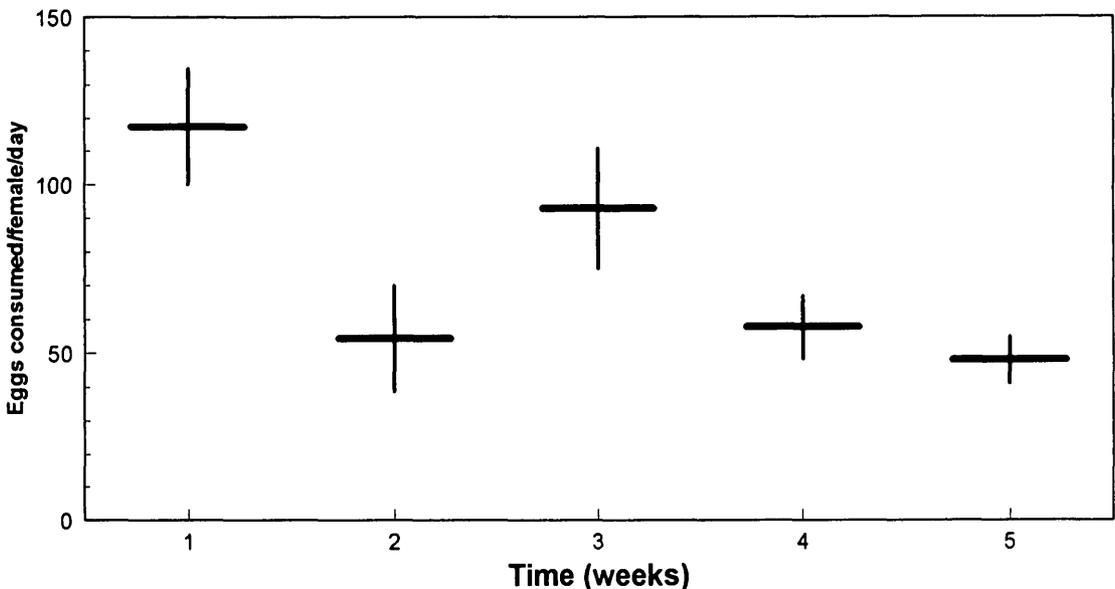


Fig. 2. Mean number \pm SE of *B. argentifolii* eggs on hibiscus leaf disks in petri dishes consumed by 6 φ *N. oculatus*, Apopka population, per d during each week over a 5-wk period.

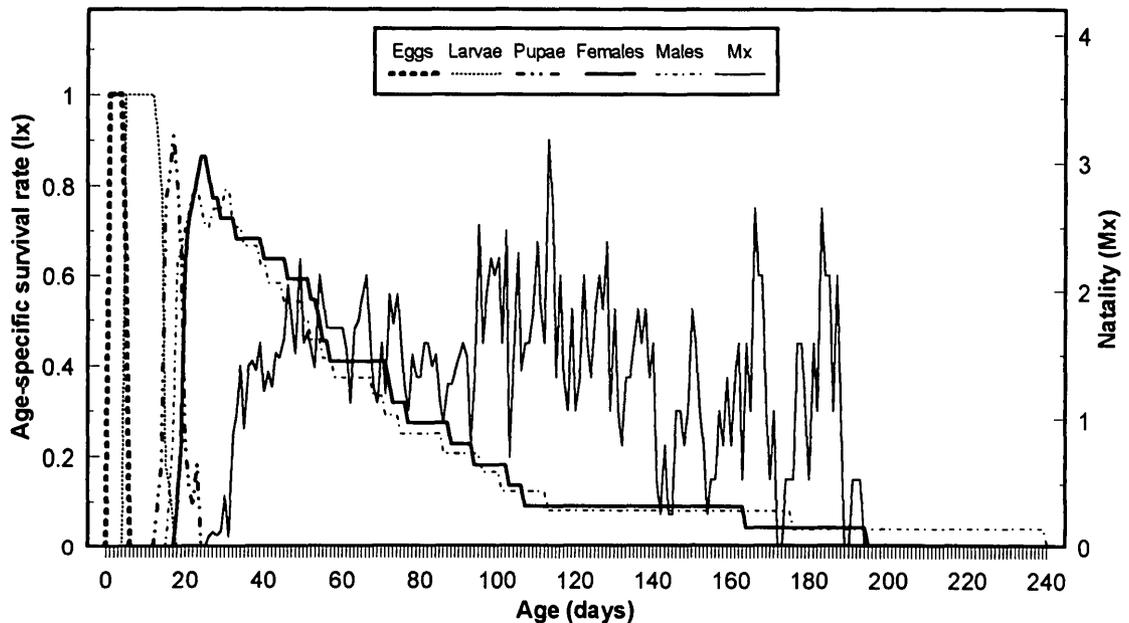


Fig. 3. Age-specific survival rate (l_x) and natality (m_x) of *N. oculatus* ($n = 44$ at day 0) feeding on *B. argentifolii* eggs on collard leaf disks in petri dishes under laboratory condition.

trends during the period from 0800 to 1700 hours, and both male and female showed a similar emergence pattern. The sex ratio was 1.00:0.89 female: male, or 53% females and 47% males ($n = 1,153$).

Adult Longevity, Preoviposition Period, and Fecundity. Adult longevity of beetles from the Immokalee population varied from 12 to 243 d, with an average of 60.5 d ($n = 36$) over both sexes. Males ($n = 22$) lived 6–243 d with a mean longevity of 56.1 ± 9.4 d, and females ($n = 14$) lived from 7 to 189 d with a mean longevity of 67.5 ± 11.3 d, and the longevity of male and female did not differ significantly ($F = 0.26$; $df = 1, 34$; $P = 0.61$). The longest lived male and female pair lived 189 d. Preoviposition period was 11.27 ± 2.27 (range, 7–16) d after emergence of the adult females ($n = 14$). Females oviposited a mean of 3.03 ± 0.58 (range, 0–9) eggs per day. The longest lived female oviposited 536 eggs over a period of 178 d. Daily egg production was fairly consistent over the entire productive lifespan (Fig. 3).

The 6 females observed in Apopka appeared to engage in mating behavior but only 2 laid eggs. Their mean daily oviposition rate was 2.33 eggs per day over a 5-d period and 2.88 eggs per day over a 14-d period. These values are similar to the range in oviposition noted in the Immokalee population. Oviposition began on 11 and 13 d after mating, which was also similar to the preoviposition period seen in Immokalee.

Life Table. Egg hatch was 100% ($n = 44$); 83.3% of male larvae and 86.4% of female larvae pupated; and 77.3% of female pupae and 75.5% male pupae successfully emerged as adults (Fig. 3). Mortality of adults was low during the first 2 wk, reached 50% by

4 wk, and >80 by 10 wk. Parameters calculated from life table analysis and related data were listed in Table 3.

Discussion

The 2 populations of *N. oculatus* observed, separated by >250 km, were alike with respect to feeding and fecundity in laboratory studies. Field-collected beetles brought into the laboratory, however, responded unexpectedly by ceasing or reducing their feeding on whitefly eggs within days of collection. No explanation was apparent for this behavior, but we suggest that the beetles may have been responding to environmental changes or to differences in the ready availability

Table 3. Life table parameters and related statistics for *N. oculatus* fed on *B. argentifolii* eggs on collard leaf disks in petri dishes

Parameter	Value
No. ♀♀ in cohort	22
No. ♂♂ in cohort	21
Avg longevity of ♀♀, d	67.5
Avg longevity of ♂♂, d	56.1
Avg longevity of adults, d	60.5
Preoviposition period, d	11.3
Mean no. progeny per ♀/d	
Fraction of ♀♀ ($\sigma : \delta = 1.00 : 0.89$)	0.53
Mean generation time (T), d	51.27
Gross reproductive rate (Σm_x)	229.12
Net reproductive rate (R_0)	54.27
Intrinsic rate of increase (r)	0.078
Doubling time ($\ln 2/r$), d	8.89
Finite rate of increase (γ)	1.08

of food between the field and the ideal conditions of the laboratory. *Delphastus pusillus* (LeConte), another predacious coccinellid of *B. argentifolii* and other whiteflies, commonly exhibited greatly reduced feeding for several days after consumption of exceptionally large amounts of prey (Hoelmer et al. 1993).

Nephaspis oculus shared many common biological and behavioral characteristics with *D. pusillus* (e.g., a preference for whitefly eggs over nymphs; and aggregation of pupae on lower leaf surface of older leaves) (Hoelmer et al. 1993; T.-X.L., unpublished data). *N. oculus* consumed fewer whitefly eggs (mean of 977 versus 718) during larval development than did *D. pusillus*, and daily egg consumption was lower (90.5 versus 77.2 eggs per larva per day). Developmental time of *N. oculus* was ≈ 2 d less than that of *D. pusillus* (Hoelmer et al. 1993). In this study, *N. oculus* feeding on *B. argentifolii* developed notably faster (18.9 d versus 26.0 d) than reported by Yoshida and Mau (1985) when reared at slightly lower temperatures on *A. dispersus*. *N. oculus* laid approximately the same numbers of eggs per day as *D. pusillus* (Hoelmer et al. 1993).

Life history parameters of *N. oculus* in this study were obtained under favorable experimental conditions, including high density of prey (whitefly eggs), suitable temperature and relative humidity for activity, and small arenas. These parameters will probably be much different under most field and greenhouse conditions. Nevertheless, the intrinsic rate of natural increase (r) calculated for *N. oculus* of 0.078 appears rather low, although we were not able to find r -values for other coccinellids in the literature for comparison. The low r -value is caused by the prolongation of reproduction over an extended lifespan. Van Giessen et al. (1995) recently reported the r 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, in the absence of extrinsic sources of mortality, the whitefly has a much greater potential for population increase on most hosts than the beetle. However, it should be possible to reduce whitefly population growth at or below that of the beetle by imposing sufficient egg mortality in the form of predation.

A more complete evaluation of the potential of *N. oculus* as a biological control agent and its interaction with *B. argentifolii* requires additional information on feeding and searching behavior, including functional responses to different densities of prey.

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