

# Life History of the Whitefly Predator *Nephaspis oculatus* (Coleoptera: Coccinellidae) at Six Constant Temperatures

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*Nephaspis oculatus* (Blatchley) is a predator of whiteflies including *Bemisia tabaci* (Gennadius) and *B. argentifolii* Bellows and Perring. The usefulness of this and other coccinellid predators of whiteflies could be improved by better information on responses to different temperatures experienced in the field. We reared *N. oculatus* from egg to adult in incubators at six constant temperatures and observed a linear relationship between developmental time and temperature for all preimaginal lifestages through all but the highest temperatures (33°C). Four larval instars were observed, although a significant proportion of third instar larvae molted directly to the pupal stage at 29°C and above. Complete life table data were obtained at all temperatures except 33°C. Survivorship was greatest over all immature stages at 26°C and finite and intrinsic rates of increase were highest at this temperature. Although 26°C appeared to be the optimum temperature for population growth, estimated rates of increase at all temperatures tested above 20°C were within 75% of the maximum, indicating that the beetle can perform well within the temperature range usually found in greenhouses. © 2002 Elsevier Science (USA)

**Key Words:** *Nephaspis oculatus*; *Delphastus catalinae*; *Bemisia argentifolii*; *Bemisia tabaci*; Aleyrodidae; Coccinellidae; biological control; greenhouse; intrinsic rate of increase; lady beetle; life history; predator.

## INTRODUCTION

Ladybeetles of the genera *Nephaspis* and *Delphastus* are whitefly predators with potential as biological control agents of silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring (Hoelmer *et al.*, 1993; Liu *et al.*, 1997; Heinz and Zalom, 1996; Heinz and Parrella, 1994a,b; Heinz *et al.*, 1994). Since its likely introduction to Florida from Central America on imported plant materials, *N. oculatus* (Blatchley) has been recorded preying on several whitefly species, including *Aleurocanthus woglumi* Ashby, *Pealius kelloggi* (Bemis), *Tri-*

*aleurodes floridensis* (Quaintance), *Dialeurodes citri* (Ashmead), and *D. citrifolii* (Morgan) (Muma *et al.*, 1961; Gordon, 1972, 1985; Cherry and Dowell, 1979). Life history parameters and consumption rates for this ladybeetle on *B. argentifolii* under laboratory conditions were estimated by Liu *et al.* (1997) who recognized its suitability for greenhouse conditions. Therefore, it would be useful to understand how populations perform within the range of temperatures found in most growing environments, including greenhouses, where the beetles might be used. Because information on the response of *N. oculatus* or related species to different temperatures is lacking, we evaluated life history traits of *N. oculatus* under different constant temperature regimes using life table analysis.

## MATERIALS AND METHODS

### *Insects and Host Plants*

The colony of *N. oculatus* was maintained in an air-conditioned glass greenhouse set at  $26.5 \pm 1.5^\circ\text{C}$  and  $78 \pm 18\%$  relative humidity (RH) in Immokalee, Florida. The beetles appeared spontaneously in the greenhouse in 1994 and were maintained thereafter on a culture of *B. argentifolii* reared on several host plants, predominantly collard, *Brassica oleracea* L. var. *acephala* 'Georgia LS;' hibiscus, *Hibiscus rosa-sinensis* L., 'pink versicolor;' and sweet potato, *Ipomoea batatas* L., 'Carolina Bunch.' Plants were grown in 1.8-liter plastic pots filled with Metro-Mix 500 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. Whiteflies from this colony were used to supply a smaller caged colony maintained on hibiscus, *H. rosa-sinensis*, in an insectary held at  $25 \pm 2^\circ\text{C}$ ,  $50 \pm 5\%$  RH, and photoperiod 14:10 (L:D) h. Beetles used in the temperature studies were supplied with whitefly eggs obtained from the insectary colony.

TABLE 1

Mean ± SE (*n*) Developmental Periods (Days) of Immature Stages of *N. oculatus* at Six Temperatures

Temp (°C)	Egg	First instar	Second instar	Third instar	Fourth instar (pupating)	Fourth instar	Pupa	Egg to adult
20	8.4 ± 0.9 (86) a	3.7 ± 1.0 (62) a	3.4 ± 1.2 (47) a	3.5 ± 1.1 (39) a		6.7 ± 2.0 (31) a	8.3 ± 0.7 (25) a	34.0 ± 2.0 (25) a
23	6.7 ± 0.7 (96) b	2.8 ± 0.9 (78) b	2.7 ± 1.1 (67) b	3.1 ± 1.1 (63) ab		5.0 ± 1.3 (59) b	5.4 ± 0.5 (59) b	25.2 ± 2.1 (59) b
26	6.0 ± 0.8 (97) c	2.8 ± 0.7 (83) b	2.6 ± 0.9 (74) bc	2.9 ± 1.0 (69) b		3.7 ± 0.8 (69) c	4.5 ± 0.5 (69) c	21.9 ± 1.3 (69) c
29	4.8 ± 0.9 (90) de	2.6 ± 0.6 (75) b	2.4 ± 1.0 (65) bc	2.8 ± 0.9 (30) b	6.1 ± 1.4 (30) a	3.6 ± 1.4 (30) c	3.4 ± 0.8 (60) d	19.6 ± 2.6 (60) d
31	4.6 ± 0.8 (86) e	2.3 ± 0.7 (64) c	2.2 ± 0.9 (53) c	2.7 ± 0.4 (14) b	3.4 ± 1.4 (31) c	2.2 ± 1.1 (14) d	3.1 ± 0.5 (45) e	16.5 ± 1.3 (45) e
33	5.0 ± 1.2 (80) d	2.1 ± 0.5 (57) c	1.6 ± 0.9 (40) d	1.7 ± 0.5 (27) c	4.7 ± 0.5 (10) b	3.3 ± 0.5 (27) c	3.2 ± 0.4 (37) e	16.3 ± 0.7 (37) e

Note. Means in the same columns followed by the same letters do not differ significantly ( $P > 0.05$ , LSD [SAS Institute, 1995]).

*Development and Survivorship of Immatures*

Adult beetles from the greenhouse culture were placed on hibiscus leaves bearing whitefly eggs (0–24 h old) in a clear plastic petri dish (14 cm diameter). A piece of filter paper (9 cm diameter) was placed on the bottom of the dish, to which a few drops of water were added daily for moisture. Petri dishes were placed in six different incubators (Ph Environmental; Harris Manufacturing, North Billerica, MA) one for each of six temperatures: 20, 23, 26, 29, 31, and 33°C. Above each incubator shelf (10 cm) was a bank of two, 30-W fluorescent lights set on a 14:10 (L:D) h cycle. Beetle eggs ( $n = 100$ ) 24 h old or less obtained from these adults were divided into four replicates of 25 eggs each and monitored daily until eclosion, when all neonate larvae were gently removed using a camel’s-hair brush (No. 00). Neonates were placed one each onto a hibiscus leaf disk of about 8 cm diameter bearing immature host stages of mixed ages in a clear petri dish (9 cm diameter). Moisture was provided by a moistened filter paper (7 cm diameter) underneath the leaf disk. Each beetle was reared individually on a single leaf disk and leaf disks were replaced daily except during the pupal stage. All molts into successive instars, adult emer-

gence, and deaths were recorded daily. Sex ratio at each temperature was determined upon emergence of adults.

*Longevity and Fecundity of Adults*

Pairs (one male and one female,  $n = 11$ ) of newly emerged beetle adults (0–24 h old) were placed on hibiscus leaf disks bearing mixed infestations of predominantly whitefly eggs with some nymphs in a clear petri dish (9 cm diameter) lined with a moistened filter paper (7 cm diameter). Dishes were placed in each of five incubators set at 20, 23, 26, 29, and 31°C. Every day leaf disks were replaced, survival and oviposition were recorded, and all beetle eggs were removed. Females surviving  $\leq 7$  days with no egg production were not included in the results.

*Data Analysis*

Values for age-specific survivorship beginning with 1-day-old eggs and age-specific reproduction for adults were used to construct life tables. The intrinsic rate of increase ( $r$ ) was computed using the Euler equation,

$$\sum e^{-r_x} I_x m_x = 1, \quad [1]$$

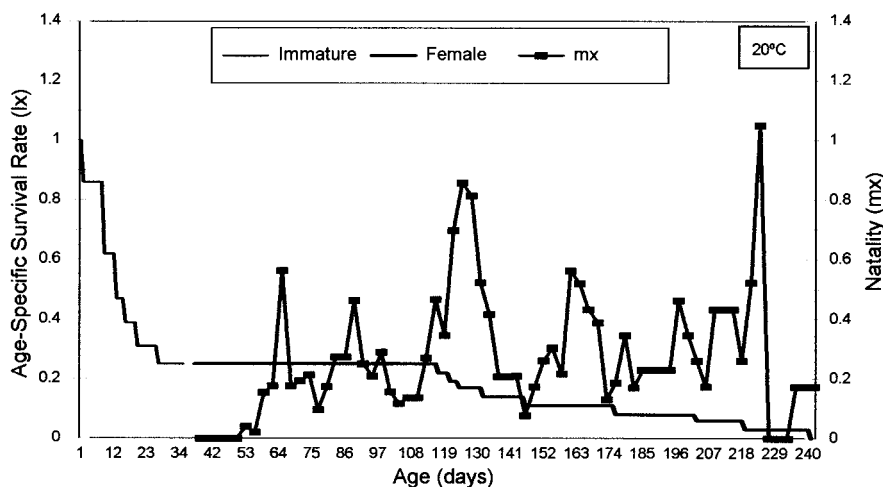


FIG. 1. Age-specific survival rate ( $I_x$ ) and natality ( $m_x$ ) at 20°C.

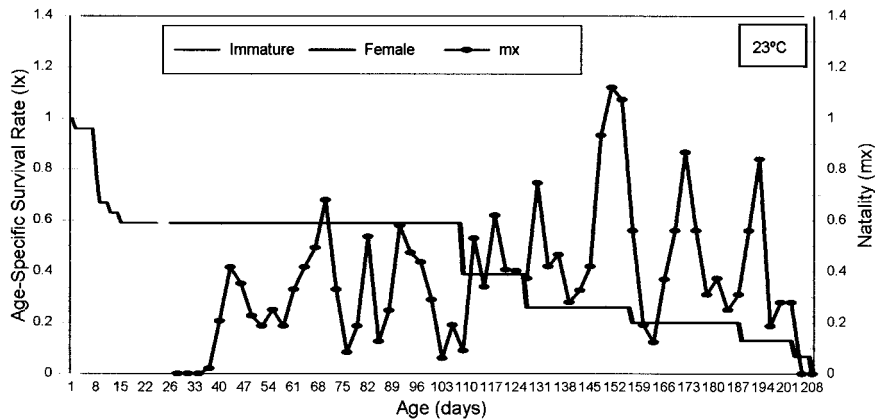


FIG. 2. Age-specific survival rate ( $I_x$ ) and natality ( $m_x$ ) at 23°C.

where  $I_x$  is survivorship of the original cohort over the 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 from the mean number of eggs laid per female per day. Other parameters, including net reproductive rate ( $R_0$ ), generation time ( $T$ ), and finite rate of increase ( $\lambda$ ), were calculated as described by Birch (1948) using a statistical jackknife technique (Maia *et al.*, 2000). Doubling time was calculated from the equation

$$DT = (\ln 2)/r \quad [2]$$

(Mackauer, 1983).

Developmental time, percentage survival, duration of oviposition, and total eggs per female at different temperatures were analyzed using one-way ANOVA followed by Fisher's LSD and linear regression (SAS Institute, 1995). Significance of differences between mean values of life table parameters was determined using Student's  $t$  test (Maia *et al.*, 2000).

## RESULTS

### *Development and Survivorship of Immatures*

Four larval instars were observed for all beetles developing at 20, 23, and 26°C. However, no fourth instar was observed for 50, 69, and 27% of beetles developing at 29, 31, and 33°C, respectively (Table 1). This portion of the population molted directly to the pupal stage from the third instar. For these latter individuals, the third larval stadium was prolonged to almost the length of the combined third and fourth stadia for the remaining beetles (e.g., 6.1 days vs 6.3 days at 29°C, 3.4 days vs 4.9 days at 31°C, and 4.7 days vs 5.0 days at 33°C).

Total developmental time from egg to adult was approximately twice as long at 20°C as at 33°C (Table 1). A significant decrease in developmental time was observed with each successive increment in temperature except above 31°C. Developmental time was reduced at the higher temperature for second and nonpupating third instar larvae but was increased for eggs and

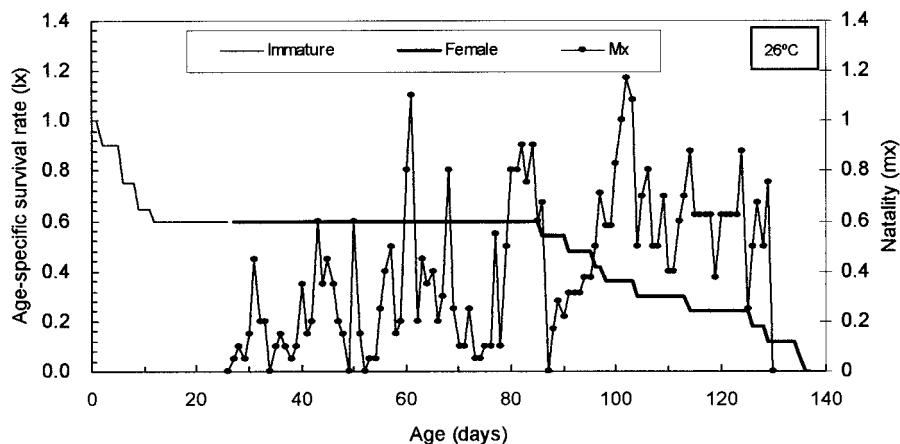


FIG. 3. Age-specific survival rate ( $I_x$ ) and natality ( $m_x$ ) at 26°C.

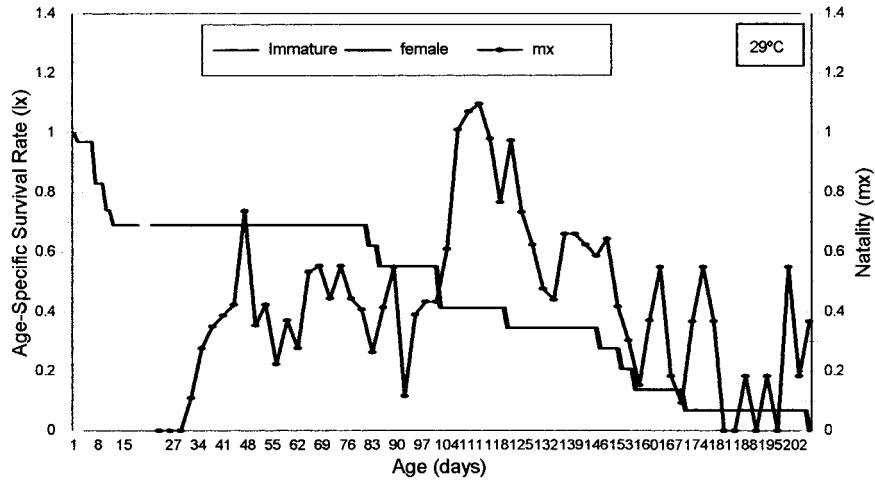


FIG. 4. Age-specific survival rate ( $I_x$ ) and natality ( $m_x$ ) at 29°C.

pupating third instar larvae. The cumulative effect of these contrary trends was no significant difference in total development time between 31 and 33°C. There was little deviation from a linear trend ( $F = 40.3$ ,  $r^2 = 0.93$ ,  $P < 0.008$ ) over the interval 20–31°C described by the regression equation

$$\text{Days} = -1.46 (\text{SE} = 0.23) \text{ temp} + 61 (\text{SE} = 6.0). \quad [3]$$

Age-specific survivorship decreased somewhat at the highest and lowest temperatures tested (20 and 33°C) but varied little over the range of 23–29°C (Figs. 1–5, Table 2). Overall survival rate from egg to adult was lowest at 20°C (25%) and highest at 26°C (69%). Most mortality was observed in the early instars. No mortality was seen in the fourth instar from 26 to 33°C or in the pupal stage between 23 and 33°C.

*Adult Longevity, Preovipositional Period, and Fecundity*

The preovipositional period was longest at 20°C (22.5 days) and decreased from 16.9 to 13.3 days over the interval 23–31°C (Table 3). Although there were no significant differences within this latter interval, regression over the entire range was significant ( $F = 15.6$ ,  $r^2 = 0.84$ ,  $P < 0.029$ ) for the relationship

$$\text{Days} = -0.79 (\text{SE} = 5.2) \text{ temp} + 36.6 (\text{SE} = 0.20). \quad [4]$$

Mean total number of eggs laid per female was highest at 26°C (80.6 eggs) and lowest at 31°C (32.7 eggs), with no significant differences among the remaining temperatures (Table 3, Fig. 1). Most eggs per day (1.0 eggs) were laid at 26 and 29°C, with fewest laid at 20°C

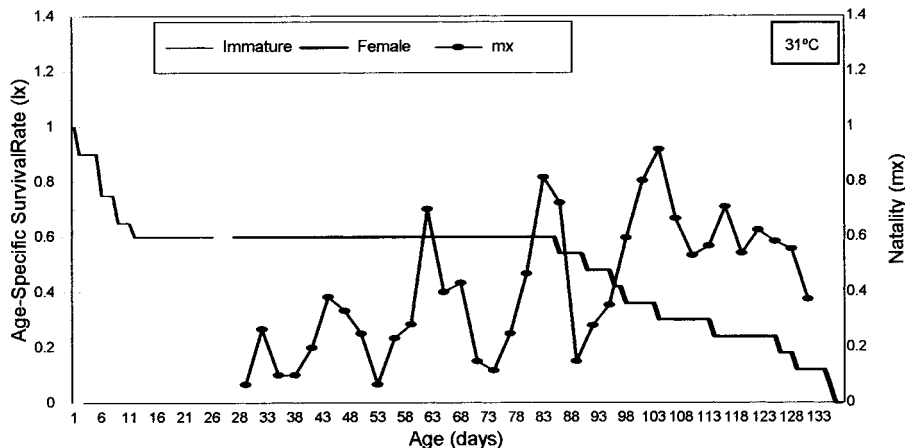


FIG. 5. Age-specific survival rate ( $I_x$ ) and natality ( $m_x$ ) at 31°C.

TABLE 2

Age-Specific Survival Rates for Preimaginal Stages of *N. oculatus* at Six Temperatures

Temp (°C)	Egg	First instar	Second instar	Third instar	Fourth instar		Pupa
					(pupating)	Fourth instar	
20	8.4 ± 0.9 (86) a	3.7 ± 1.0 (62) a	3.4 ± 1.2 (47) a	3.5 ± 1.1 (39) a		6.7 ± 2.0 (31) a	8.3 ± 0.7 (25) a
23	6.7 ± 0.7 (96) b	2.8 ± 0.9 (78) b	2.7 ± 1.1 (67) b	3.1 ± 1.1 (63) ab		5.0 ± 1.3 (59) b	5.4 ± 0.5 (59) b
26	6.0 ± 0.8 (97) c	2.8 ± 0.7 (83) b	2.6 ± 0.9 (74) bc	2.9 ± 1.0 (69) b		3.7 ± 0.8 (69) c	4.5 ± 0.5 (69) c
29	4.8 ± 0.9 (90) de	2.6 ± 0.6 (75) b	2.4 ± 1.0 (65) bc	2.8 ± 0.9 (30) b	6.1 ± 1.4 (30) a	3.6 ± 1.4 (30) c	3.4 ± 0.8 (60) d
31	4.6 ± 0.8 (86) e	2.3 ± 0.7 (64) c	2.2 ± 0.9 (53) c	2.7 ± 0.4 (14) b	3.4 ± 1.4 (31) c	2.2 ± 1.1 (14) d	3.1 ± 0.5 (45) e
33	5.0 ± 1.2 (80) d	2.1 ± 0.5 (57) c	1.6 ± 0.9 (40) d	1.7 ± 0.5 (27) c	4.7 ± 0.5 (10) b	3.3 ± 0.5 (27) c	3.2 ± 0.4 (37) e

Note. Means in the same columns followed by the same letters do not differ significantly ( $P > 0.05$ , LSD [SAS Institute, 1995]).

(0.61 eggs) and 31°C (0.70 eggs). Longevity of both males and females was greatest at 20°C, although not significantly greater than at 23 or 26°C. There was no significant difference in longevity between sexes.

#### Life Table Parameters

Generation time tended to decrease with increasing temperature. The greatest incremental decreases occurred at 20, 23, and 26°C (Table 4). Linear regression over the entire temperature range was highly significant ( $F = 632$ ,  $r^2 = 0.99$ ,  $P < 0.0001$ ) and predicted the relationship

$$\text{Days} = -3.72 (\text{SE} = 0.15) \text{ temp} + 174 (\text{SE} = 3.9).$$

[5]

Net reproductive rate was lowest and nearly equal at the two extreme temperatures and highest (33.7 eggs) at 26°C, giving a significant ( $F = 31.7$ ,  $r^2 = 0.97$ ,  $P < 0.03$ ) quadratic relationship:

$$R_0 = -0.77 (\text{SE} = 0.010) \text{ temp}^2 - 39.3 (\text{SE} = 4.9) \text{ temp} - 473 (\text{SE} = 61.8).$$

[6]

Consequently, doubling time was reduced by half over the increment of 20 to 23°C, but was similar at the remaining temperatures. The result was a nonsignifi-

cant linear regression ( $P < 0.18$ ), but again a significant quadratic model ( $F = 38.1$ ,  $r^2 = 0.97$ ,  $P < 0.025$ ) predicting the relationship

$$\text{Days} = 0.39 (\text{SE} = 0.07) \text{ temp}^2 - 21.3 (\text{SE} = 3.7) \text{ temp} + 306 (\text{SE} = 45.9).$$

[7]

Intrinsic and finite rates of increase reached their maximum values at 26°C, which could therefore be considered the optimum temperature for this beetle. However, estimated values for intrinsic rate of increase at all other temperatures except 20°C were within 75% of this maximum.

#### DISCUSSION

Life table studies of coccinellids are scarce in the literature. In one study, Tanigoshi and McMurtry (1977) compared life histories of the avocado brown mite, *Typhlodromus floridanus* (Hirst) (Acarina: Tetranychidae) and its predators *Stethorus picipes* Casey (Coleoptera: Coccinellidae) and *Typhlodromus floridanus* (Muma) (Acarina: Phytoseiidae). They estimated the intrinsic rate of increase ( $r_m$ ) as 0.22 for the ladybeetle compared to 0.16 for the predaceous mite and 0.12 for the prey mite at 22–26°C. The relatively high  $r_m$  of *S. picipes* compared to *N. oculatus* was partly due to high net reproductive rate ( $R_0 = 43.1$ ) but perhaps

TABLE 3

Mean ± SE (Range) Fecundity and Longevity of *N. oculatus* at Six Temperatures

Temp (°C)	Sex ratio	Preovipositional period (days)	Mean No. eggs per female	Mean No. eggs per female per day	Longevity (days)	
					Female	Male
20	0.52	22.6 ± 6.3 (15–37) a	51.9 ± 34.4 (9–121) ab	0.6 ± 0.9 (0–4) c	118.6 ± 61.1 (33–215) a	120.7 ± 72.6 (36–256) a
23	0.56	16.9 ± 4.9 (13–37) b	64.4 ± 44.4 (10–136) ab	0.8 ± 1.0 (0–5) b	108.8 ± 37.0 (53–183) ab	107.8 ± 55.0 (53–183) ab
26	0.54	14.5 ± 3.3 (11–22) b	80.6 ± 53.7 (13–141) a	1.0 ± 1.1 (0–7) a	104.8 ± 57.9 (21–244) ab	104.6 ± 45.2 (21–183) ab
29	0.50	13.8 ± 5.4 (8–24) b	58.4 ± 33.8 (15–144) ab	1.0 ± 1.2 (0–8) a	80.9 ± 31.5 (20–114) bc	75.5 ± 31.3 (25–109) bc
31	0.51	13.3 ± 4.0 (10–22) b	32.7 ± 29.1 (3–82) b	0.7 ± 1.2 (0–4) bc	66.3 ± 30.6 (10–106) c	61.2 ± 36.1 (10–115) c

Note. Means in the same columns followed by the same letters do not differ significantly ( $P > 0.05$ , LSD [SAS Institute, 1995]).

TABLE 4

Life Table Parameters  $\pm$  95% Confidence Limits for *N. oculatus* in Petri Dishes at Six Temperatures

Temp (°C)	Generation time (T) (days)	Net reproductive rate ( $R_0$ )	Doubling time (DT) (days)	Finite rate of increase ( $\lambda$ )	Intrinsic rate of increase ( $r_m$ )
20	101.0 $\pm$ 17.1	6.7 $\pm$ 3.05	36.1 $\pm$ 7.1	1.019 $\pm$ 0.004	0.019 $\pm$ 0.004
23	87.6 $\pm$ 17.1	23.4 $\pm$ 10.0	19.2 $\pm$ 2.4	1.0367 $\pm$ 0.005	0.036 $\pm$ 0.005
26	79.5 $\pm$ 10.9	33.1 $\pm$ 14.5	15.6 $\pm$ 2.3	1.0452 $\pm$ 0.007	0.055 $\pm$ 0.006
29	66.6 $\pm$ 7.8	20.1 $\pm$ 10.9	15.1 $\pm$ 2.8	1.046 $\pm$ 1.008	0.0436 $\pm$ 0.008
31	59.4 $\pm$ 7.4	9.2 $\pm$ 3.9	17.5 $\pm$ 3.2	1.032 $\pm$ 0.007	0.038 $\pm$ 0.006

more importantly to a female-biased sex ratio ( $\text{♀}:\text{♂}$ ) of 3.1. Although intrinsic rate of increase of *S. picipes* was higher than what we found, it was low compared to a range of 0.60 to 0.73 estimated by Gibson *et al.* (1992) for *Scymnus frontalis* (F) (Coleoptera: Coccinellidae) on a diet of three different aphid species at  $24 \pm 2^\circ\text{C}$ . Additional parameters for *S. frontalis* associated with the highest of these  $r_m$  values included  $R_0 = 156.1$  and mean generation time ( $T$ ) = 48 days compared to our values of 33.1 and 79.5 days, respectively, for *N. oculatus* on a diet of whitefly eggs at  $26^\circ\text{C}$ . Thus, there is diversity in life histories among species of Coccinellidae that could relate to prey types.

Results from this study contrasted somewhat with a previous life history study of *N. oculatus* (Liu *et al.*, 1997) carried out in the laboratory at  $26 \pm 2^\circ\text{C}$ . These authors observed a higher intrinsic rate of increase at  $26^\circ\text{C}$  ( $r_m = 0.078$ ) compared to  $r_m = 0.055$  estimated in this study at the same temperature. The difference was due to higher net reproductive rate (33.1 vs 54.4), shorter generation time (79.5 days vs 51.3 days), and greater survivorship of immatures (0.84 vs 0.69) observed by Liu *et al.* (1997) compared to the present study, respectively.

There were several differences in methods that might explain these different results. Liu *et al.* (1997) used only whitefly eggs as a food source, whereas we used a mixture of eggs and some nymphs for our longevity and fecundity studies. Hoelmer *et al.* (1993) reported greatly reduced oviposition by a similar beetle, *D. catalinae* (identified as *D. pusillus*), on a diet of all *B. argentifolii* (identified as *B. tabaci*) nymphs, indicating that nymphs may be an inferior food. In addition, preferences among glabrous leaf types, such as collard used by Liu *et al.* (1997), versus hibiscus used in this study could exist in addition to the observed preference for glabrous over pubescent types (T. X. Liu and P. A. Stansly, unpublished data). Finally, constant temperatures in this study may have a negative impact on oviposition or survivorship compared to the fluctuating ambient temperatures used in the former study.

Our results revealed  $26^\circ\text{C}$  to be the optimal temperature for population growth of *N. oculatus*. However, intrinsic and finite rates of increase did not vary greatly over the range  $23\text{--}31^\circ\text{C}$ , suggesting that per-

formance may not be seriously compromised at most greenhouse temperatures. Butler *et al.* (1983) reported that maximum fecundity of *Bemisia tabaci* occurred at  $26.7^\circ\text{C}$ , suggesting that predator and prey would seem to share the same optimum temperature. However, *B. tabaci* did almost as well at  $32.2^\circ\text{C}$ , possibly indicating better adaptation to high temperatures than *N. oculatus*.

Nevertheless, our findings indicate that *N. oculatus* exhibits sufficient environmental plasticity to be a useful biological control agent against *B. argentifolii* and other whiteflies on glabrous greenhouse crops under a wide range of temperature conditions.

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