Life table parameters of the pseudococcid predators *Nephus includens* and *Nephus bisignatus* (Coleoptera: Coccinelidae)

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Abstract. The fecundity of the pseudococcid predators *Nephus includens* (Boheman) and *N. bisignatus* (Kirsch) (Coleoptera: Coccinellidae), fed on *Planococcus citri* Risso (Hemiptera: Pseudococcidae), was studied at several constant temperatures (15, 20, 25, 30, 32.5 and 35°C). With additional data for the development of the immature stages, life-fecundity tables were constructed and some population parameters calculated. The average total fecundities of *N. includens* at the above temperatures were 49.2, 97.8, 162.8, 108.5, 87.4 and 31.1 eggs/female, and average longevities 99.5, 84.7, 69.5, 61.1, 49.6 and 30.1 days, respectively. The net reproductive rates (R_o) were 8.0, 32.2, 60.7, 32.6, 20.7 and 2.6 females/female, and the intrinsic rates of increase (r_m) 0.014, 0.041, 0.083, 0.086, 0.077 and 0.024 females/female/day, respectively. The average total fecundities of *N. bisignatus* at 15, 20, 25, 30 and 32.5 ^{c}C were 54.7, 72.1, 96.9, 56.0 and 22.8 eggs/female, and average longevities 116.1, 108.7, 71.8, 68.8 and 43.7 days, respectively. The net reproductive rates (R_o) were 13.9, 26.4, 31.3, 15.2 and 3.6 females/female and the intrinsic rates of increase (r_m) were 0.017, 0.035, 0.060, 0.051 and 0.024 females/female/day, respectively. The survival of females at each temperature was fitted using a Weibull distribution $[S_{(t)} = e^{-\left(\frac{t}{b}\right)^c}]$. Furthermore two mathematical models [Enkegaard equation: $F = (a + b + x) \cdot e^{(c+d \cdot x)}$, Analytis equation: $F = a \cdot (x - x_{\min})^n \cdot (x_{\min} - x)^m$] were fitted to the fecundity data.

INTRODUCTION

Nephus bisignatus (Boheman) and *N. includens* (Kirsch) (Coleoptera: Coccinellidae) are important indigenous predators of mealybugs (Homoptera: Pseudococcidae) in Greece (Argyriou et al., 1976; Kontodimas, 1997). *Nephus bisignatus* is found in Northern Europe (South Norway, Finland, Sweden, Denmark, Netherlands and Germany) (Pope, 1973), but is also reported from Morocco, Southern France, Italy and Portugal (Pope, 1973; Francardi & Covassi, 1992; Magro & Hemptinne, 1999; Magro et al., 1999). It was recently reported in Greece on *Thuja orientalis* L. (Cupressaceae) and *Pistacia lentiscus* L. (Anacardiaceae) infested with *Planococcus citri* (Homoptera: Pseudococcidae) (Kontodimas, 1997). *Nephus includens* is reported from Greece, Turkey, Italy, Spain and Portugal (Bodenheimer, 1951; Viggiani, 1974; Argyriou et al., 1976; Longo & Benfatto, 1987; Suzer et al., 1992; Katsoyannos, 1996; Magro & Hemptinne, 1999; Magro et al., 1999). Although there are rare data on the fecundity of *N. bisignatus* or *N. includens*, Tranfaglia & Viggiani (1972) report that females lay 150.6 eggs and live for 74 days at 25–27°C when fed on *P. citri*. The developmental zeros (lower temperature threshold) are estimated to be 10.9 and 9.4°C and thermal constants to be 490.5 and 614.30 degree-days

for *N. includens* and *N. bisignatus*, respectively, using a linear model. The upper temperature thresholds are estimated to be 36.1 and 34.7°C, respectively, using the Lactin non-linear model (Kontodimas et al., 2004). Life table parameters are often used by biological control workers (Messenger, 1964) when choosing the most effective biocontrol agents. In the absence of other criteria, the species with the greatest r_m is usually selected.

In the present study the fecundities of the two predators were examined under laboratory conditions and used to obtain the following life table parameters: age specific survival and fecundity, reproductive value, expected remaining life time, net reproductive value, intrinsic rate of increase, mean generation time, finite rate of increase and doubling time. The above parameters can be used to estimate the rate of increase of a natural or released population (El Hag & Zaitoon, 1996) and to determine when to release laboratory-reared coccinellid. In addition, two mathematical models were fitted to the fecundity data and the survival of adult females were described using the Weibull distribution. The current study compares the life table parameters of *N. bisignatus* and *N. includens* feeding on *P. citri* and provides useful information on their future use as biocontrol agents of mealybug pests.

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TABLE 1. Fecundity of *Nephus includens* and *Nephus bisignatus* at constant temperatures (15, 20, 25, 30, 32.5 and 35°C) (relative humidity: 65%, photoperiod: 16L : 8D, prey: *Planococcus citri*).

Temperature (°C)	Females (percentage)	Average total fecundity (eggs)	Survival of instars (%)			Duration of (egg-pupa) development (days)	Pre-ovipositional period (days)	Longevity (days)		
			Egg	Larva	Pupa			Maximum	Average	Median
N. includens										
15	67.5	49.2	75.0	50.0	92.6	94	20	174	99.5	93
20	62.0	97.8	86.8	84.8	92.6	46	9	128	84.7	85
25	55.5	162.8	94.3	78.8	96.2	30	6	94	69.5	73
30	58.5	108.5	90.0	77.8	89.3	21	4	91	61.1	68
32.5	59.5	87.4	87.0	67.5	92.6	19	4	77	49.6	53
35	63.5	31.1	69.4	36.5	78.9	21	4	52	30.1	29
N. bisignatus										
15	64.0	54.68	77.8	48.1	96.2	91	22	193	116.1	107
20	60.0	72.12	82.9	79.4	92.6	48	10	159	108.7	113
25	53.0	96.88	90.2	73.0	92.6	32	7	110	71.8	76
30	57.5	56.00	83.0	65.9	86.2	25	5	98	68.8	73
32.5	60.5	22.80	73.7	42.9	83.3	28	6	74	43.7	46

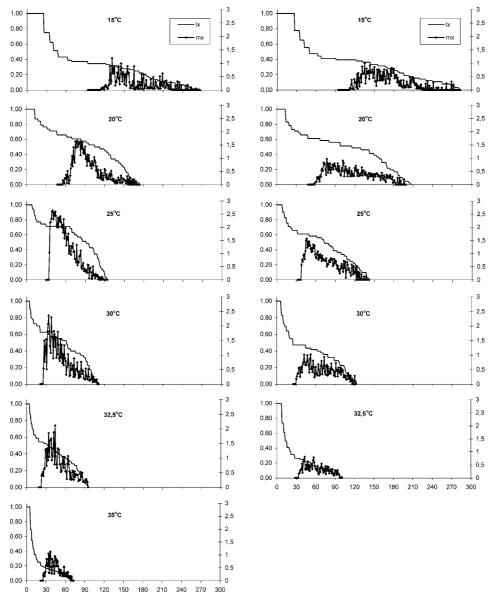Fig. 1. Age specific survival (l_x) and age specific fecundity (m_x) of *Nephus includens* and *Nephus bisignatus* at different constant temperatures.
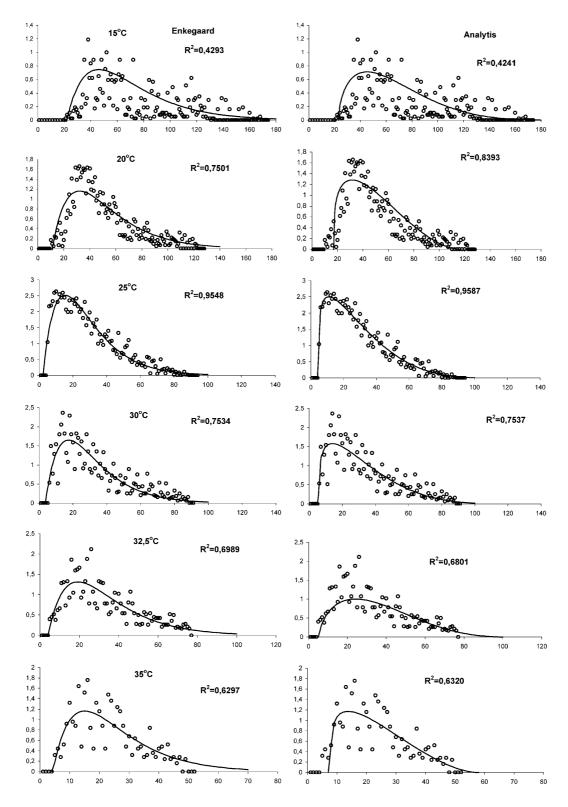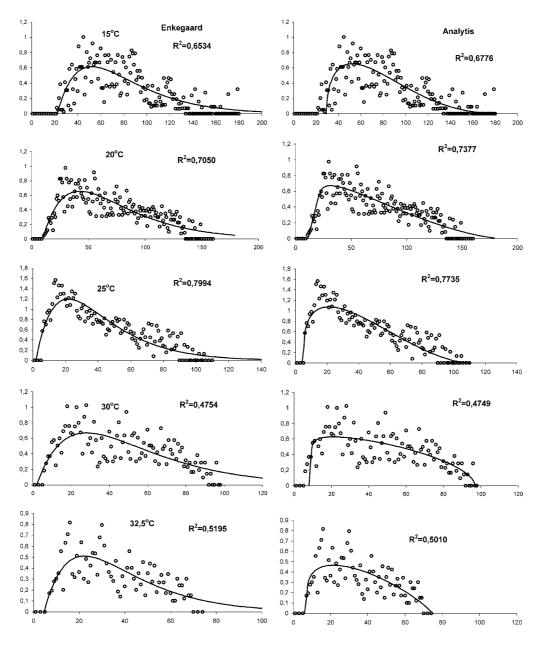
Fig. 2. The age specific fecundity (m_x) of *Nephus includens* at different constant temperatures fitted using Enkegaard and Analytis models.

MATERIAL AND METHODS

Rearing methods and experimental conditions

Nephus bisignatus and *N. includens* were originally collected in 1997 from *Thuja orientalis* L. (Cupressaceae) in Attiki County (Central Greece) and *Citrus* sp. (Rutaceae) in Preveza County (Northwestern Greece), respectively, both infested with *P. citri*. The same mealybug was used as prey for rearing these predators in the laboratory. Citrus mealybug was reared on potato sprouts (*Solanum tuberosum*) and pumpkins (*Cucurbita pepo* and *C. maxima*) at 25 ± 1°C, 16L : 8D photoperiod and 65 ± 2% RH, in large plastic boxes (30 × 40 × 15 cm) tightly covered with mesh (holes: 0.3 × 0.4 cm). Both predators were reared in large cylindrical Plexiglas cages (50 cm height × 30

Fig. 3. The age specific fecundity (m_x) of *Nephus bisignatus* at different constant temperatures fitted using Enkegaard and Analytis models.

cm diameter) containing an abundance of prey under the following controlled conditions: 15, 20, 25, 30, 32.5, or 35 ± 1°C; 65 ± 2% RH; 16L : 8D.

The fecundity of the two predators was determined using 25 newly emerged pairs of adults of each species, which were kept in plastic cages under constant conditions (temperature: 15 ± 1, 20 ± 1, 25 ± 1, 30 ± 1, 32,5 ± 1, 35 ± 1°C, relative humidity: 65 ± 2% and an abundant supply of *Planococcus citri* as food). The same conditions were used to study the survival of the immature stages and the sex ratio of the progeny. These experiments were done in the spring of 2001.

The longevity and fecundity of the 25 females were recorded daily and the following table parameters calculated (Birch, 1948; Southwood, 1966; Izhevsky & Orlinsky, 1988; Carey, 1993; Liu et al., 1997; Lysyk, 2001):

Age specific survival (l_x) of 25 females.

Age specific fecundity (m_x) (= females born/female) by multiplying the mean number of eggs by the ratio ($♀/♀+♂$) (Liu et al, 1997).

Net reproductive value: $R_0 = \Sigma(l_x.m_x)$, the average number of offspring a female in a population will produce in her lifetime.

Intrinsic rate of increase (r_m) from the solution of the Euler equation, $\Sigma(e^{r_m \cdot x} \cdot l_x \cdot m_x) = 1$.

Mean generation time using two different formulas: $T_c = \frac{\Sigma(x \cdot l_x \cdot m_x)}{R_0}$ and $T = \frac{\ln R_0}{r_m}$.

Finite rate of increase: $\lambda = e^{r_m}$, the number of times the population increases per unit time.

Doubling time: $DT = \frac{\ln 2}{r_m}$, the time it takes a population to double in size.

Reproductive value of the females: $V_x = \frac{\sum_{y=x}(e^{r_m \cdot y} \cdot l_y \cdot m_y)}{l_x \cdot e^{r_m \cdot x}}$.

Expected remaining life time of the females: $E_x = \frac{\sum_{y=x} \frac{l_y + l_{y+1}}{2}}{l_x}$.

The fecundity was calculated as females/female.

TABLE 2. Values of the parameters of the Analytis and Enkegaard models fitted to the data for *Nephus includens* and *Nephus bisignatus*.

	Parameter	15°C	20°C	25°C	30°C	32.5°C	35°C
		Nephus includens					
Enkegaard equation $F=(a+b+x)\cdot e^{(c+d\cdot x)}$	a	−1.4494	−0.8606	−0.4189	−0.1422	−0.0490	−0.0544
	b	0.0665	0.0771	0.1846	0.0387	0.0118	0.0125
	c	−1.1245	−1.2111	−1.2156	−2.3972	−3.2682	−3.5749
	d	0.0411	0.0480	0.0764	0.0726	0.0661	0.0938
	R^2	0.4293	0.7501	0.9548	0.7534	0.6989	0.6297
	RSS	5.7820	7.2077	5.2818	7.6727	4.9999	3.9593
Analytis equation $F=a\cdot(x-x_{min})^n\cdot(x_{min}-x)^m$	p	0.1943×10^{-10}	0.1564×10^{-3}	0.4203×10^{-6}	0.1662×10^{-7}	0.9668×10^{-6}	0.1427×10^{-2}
	x_{min}	23.0013	17.0021	4.9757	5.9522	5.3796	7.9372
	x_{max}	213.0101	117.1020	113.5814	129.3580	104.7326	57.2146
	m	0.5802	0.3101	0.1923	0.2604	0.6388	0.2246
	n	4.3973	1.8400	3.2941	3.7543	2.7292	1.6743
	R^2	0.4241	0.8393	0.9587	0.7536	0.6809	0.6320
	RSS	5.6799	3.2129	2.8179	7.4036	5.1083	3.6718
		Nephus bisignatus					
Enkegaard equation $F=(a+b+x)\cdot e^{(c+d\cdot x)}$	a	−3.9781	−0.4657	−0.0653	−0.1173	−0.0683	
	b	0.1780	0.0475	0.0355	0.0578	0.0147	
	c	0.4192	−0.4376	−1.6212	−0.2671	−1.9440	
	d	0.0333	0.0306	0.0504	0.0383	0.0568	
	R^2	0.6534	0.7050	0.79939	0.4754	0.5195	
	RSS	4.3339	2.5592	3.6085	2.8634	1.2330	
Analytis equation $F=a\cdot(x-x_{min})^n\cdot(x_{min}-x)^m$	p	1.8740×10^{-7}	1.3201×10^{-4}	2.0744×10^{-4}	0.0448	0.0089	
	x_{min}	29.4975	21.0000	4.9452	8.9900	6.9457	
	x_{max}	193.9480	189.2699	110.0528	97.0369	74.5461	
	m	0.4456	0.1079	0.3126	0.0875	0.2311	
	n	2.7602	1.6363	1.7119	0.5595	0.8399	
	R^2	0.6776	0.7377	0.7735	0.4749	0.5010	
	RSS	3.8887	2.0879	4.8254	2.4862	1.1778	

Two mathematical models were used to fit the data on fecundity:

1. The Enkegaard equation: $F=(a+b\cdot x)\cdot e^{-(c+d\cdot x)}$ (Enkegaard, 1993),

2. The Analytis equation: $F=q\cdot(x-x_{min})^n\cdot(x_{min}-x)^m$ (Analytis, 1974, 1977, 1980; Kontodimas et al., 2004), where F is the fecundity, x are the days after emergence, $a, b, c, d, q, x_{min}, x_{max}, n, m$: parameters and $e = 2.178$.

The Weibull frequency distribution was used to describe the age specific survival of female adults. The probability that an individual lives at least to time t was calculated following Deevey (1947), Pinder et al. (1978), Tingle & Copland (1989) and Wang et al. (2000): $S_{(t)}=e^{\left(\frac{t}{b}\right)^c}$, for $t > 0$ where b is a scale parameter that is inversely related to the mortality rate (ie, larger b value indicates slower decline of the population) and c is a shape parameter that allows the model to produce survival distributions of different forms, from exponential to an extreme inverted S shape. Values of the shape parameter $c > 1$, $c = 1$ or $c < 1$ correspond to Deevey's (1947) type I, II or III survivorship curves, respectively (Pinder et al., 1978).

Estimates of the models' parameters and coefficients of non-linear regression (R^2) were obtained with statistical packages JMP v.4.0.2 (SAS, 1989) and SPSS v.9.0.0 (SPSS, 1999).

RESULTS AND DISCUSSION

Both species were most fecund at 25°C (162.8 eggs/female in *N. includens*, 96.9 eggs/female in *N. bisignatus*). *N. includens* had a consistently higher fecundity than *N. bisignatus* at each experimental temperature, except 15°C (Table 1). However for both species, the highest fecundity was smaller than that reported for *C. montrouzieri* (Babu & Azam, 1988) and *N. reunioni* (Izhevsky & Orlinsky, 1988) but higher than that reported by Persad & Khan (2002) for *C. montrouzieri* and *Scymnus coccivora*. Longevity of each species was different at each experimental temperature. Average longevity of *N. includens* was shorter than that of *N. bisignatus* at each temperature, except 32.5°C. It seems that although *N. bisignatus* had a longer lifespan, its reproductive activity was shorter than that of *N. includens*. However both species oviposited 60% of their eggs within the first 40% of their adult lifetime. The age specific survival (l_x) and age specific fecundity (m_x) of the two predators are presented in Fig. 1. The description of the age specific fecundity (m_x) by Enkegaard and Analytis models is presented in Figs 2 and 3 and the values of
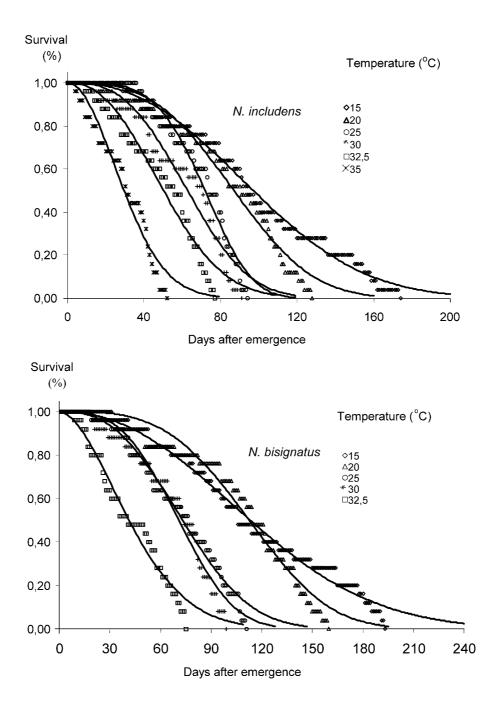
Fig. 4 . Survival of *Nephus includens* and *Nephus bisignatus* at different constant temperatures fitted using the Weibull function.

TABLE 3. Values of the Weibull parameters $S_{(t)} = e^{-\left(\frac{t}{b}\right)^c}$.

	Parameter	15°C	20°C	25°C	30°C	32.5°C	35°C
N. includens	b	112.9614	98.0543	78.4127	71.2303	58.7081	35.5751
	c	2.4175	3.0638	4.1966	2.8617	2.3469	1.9733
	R²	0.9929	0.9772	0.9771	0.9532	0.9628	0.9556
	RSS	0.1382	0.2716	0.1923	0.3820	0.2427	0.2111
N. bisignatus	b	133.5318	125.4435	83.7265	79.5416	50.9824	133.5318
	c	2.2264	3.4027	2.6717	3.1422	1.7921	2.2264
	R²	0.9917	0.9722	0.9890	0.9698	0.9776	0.9917
	RSS	0.1539	0.4003	0.1132	0.2522	0.1445	0.1539

TABLE 4. Summaries of the life tables of *Nephus includens* at different constant temperatures (15, 20, 25, 30, 32.5 and 35 ± 1°C), relative humidity: 65 ± 2% and photoperiod 16L : 8D, when fed on *Planococcus citri*.

Day	Age specific survival (l_x)	Age specific fecundity (sum of days before) (m_x) (females/female)	Reproductive value (V_x) (females/female)	Expected remaining life time (E_x) (days)
		15°C		
12	0.35	0.5	15.0	72.0
15	0.28	14.3	9.4	56.4
18	0.21	9.3	4.4	38.6
21	0.11	5.4	2.6	31.5
24	0.07	32	0.3	12.5
26	0.01	0.6	0.0	1.0
		20°C		
60	0.66	0.8	17.3	70.2
80	0.61	17.5	20.3	55.8
10	0.53	23.0	9.4	42.7
12	0.45	10.6	4.3	28.1
14	0.32	5.0	1.8	16.0
16	0.08	3.2	0.5	9.8
17	0.03	0.7	0.0	1.0
		25°C		
30	0.71	0.0	17.0	61.6
45	0.71	25.3	23.1	46.6
60	0.71	31.1	13.7	31.6
75	0.60	18.2	7.1	20.8
90	0.51	10.1	2.9	20.0
10	0.34	4.5	0.7	10.3
12	0.06	1.1	0.0	2.5
		30°C		
30	0.63	5.6	16.2	50.6
45	0.58	24.0	11.2	40.5
60	0.53	16.0	5.2	27.9
75	0.40	8.0	3.8	21.2
90	0.33	6.0	1.6	9.1
10	0.05	3.5	0.3	4.0
		32.5°C		
26	0.54	1.8	12.1	41.9
39	0.48	15.6	11.6	33.8
52	0.39	15.2	7.0	26.0
65	0.33	9.5	4.1	16.9
78	0.22	5.5	2.1	8.8
91	0.04	3.8	0.7	2.5
		35°C		
30	0.17	1.6	10.9	25.0
40	0.14	7.1	7.5	18.7
50	0.12	2.8	6.3	11.8
60	0.08	2.9	1.1	5.3
70	0.01	1.8	0.2	2.5

TABLE 5. Summaries of the life tables of *Nephus bisignatus* at different constant temperatures (15, 20, 25, 30, 32.5 and 35 ± 1°C), relative humidity: 65 ± 2% and photoperiod 16L : 8D, when fed on *Planococcus citri*.

Day	Age specific survival (l_x)	Age specific fecundity (sum of days before) (m_x) (females/female)	Reproductive value (V_x) (females/female)	Expected remaining life time (E_x) (days)
		15°C		
120	0.40	1.6	18.8	85.6
150	0.33	16.8	15.0	69.0
180	0.27	16.0	7.2	52.8
210	0.17	8.4	2.9	45.0
240	0.11	3.1	0.9	29.2
270	0.06	1.2	0.2	8.0
		20°C		
60	0.61	0.2	12.9	84.4
80	0.59	10.0	14.2	69.1
100	0.51	12.3	12.2	55.6
120	0.49	10.0	9.5	37.6
140	0.46	8.9	5.7	22.0
160	0.34	6.9	3.3	27.6
180	0.20	5.3	0.8	10.8
200	0.05	1.1	0.0	3.8
		25°C		
45	0.61	17.4	7.3	58.34
60	0.59	11.3	18.6	45.6
75	0.49	8.5	12.7	37.9
90	0.39	6.1	10.3	30.2
105	0.32	4.0	7.3	20.3
120	0.22	1.5	5.6	12.2
135	0.10	0.1	1.9	3.8
		30°C		
30	0.47	9.8	0.2	61.1
45	0.43	10.5	8.4	50.2
60	0.42	7.7	9.6	37.1
75	0.36	6.5	7.5	26.8
90	0.28	4.8	7.1	16.7
105	0.19	1.4	6.5	7.4
		32.5°C		
39	0.25	8.9	1.9	32.4
52	0.21	6.6	6.0	26.4
65	0.14	5.1	5.7	23.1
78	0.12	2.8	4.4	12.9
91	0.05	1.0	3.2	7.3

sented in Fig. 4 and the values of the Weibull parameters in Table 3. In both species it is a type I survival curve, as parameter *c* is >1 (Tingle & Copland, 1989; Wang et al., 2000). Using mathematical models to describe the reproductive capacity and survival enables one to compare data with similar average values, which differ in their temporal distribution (Tingle & Copland, 1989).

The fact that both species showed an increase in the sex ratio favouring females at temperatures close to their lower and upper thresholds (Kontodimas et al., 2004) is an important advantage of the survival of the species at these temperatures. Summaries of the life tables for each species and temperature are presented in Tables 4 and 5, and the life table parameters calculated for each species in Table 6. Differences between the species in the adaptation to temperature are indicated by their intrinsic rates of natural increase (r_m). As expected, life table parameters were sensitive to temperature in both species. Neverthe-

Enkegaard and Analytis parameters in Table 2. Both models gave a satisfactory fit at 20, 25 and 30°C for *N. includens* and 20 and 25°C for *N. bisignatus,* respectively, for which the data were less variable than at the other temperatures. The coefficient of nonlinear regression (R^2) and the residual sum of squares (RSS) were used as criteria of goodness of fit. The higher the R^2 and lower the RSS the better the fit (Kontodimas et al., 2004).

The description of the age specific survival of female adults (l_x) using the Weibull frequency distribution is pre-

TABLE 6. Life table parameters of *Nephus includens* and *Nephus bisignatus*.

Tempera-ture (°C)	Net reproductive value $R_0 = \Sigma(l_x \cdot m_x)$	Intrinsic rate of increase (r_m) $\Sigma(e^{r_m \cdot x} \cdot l_x \cdot m_x) = 1$	Mean generation time $T_c = \frac{\Sigma(x \cdot l_x \cdot m_x)}{R_0}$	$T = \frac{\ln R_0}{r_m}$	Doubling time $DT = \frac{\ln 2}{r_m}$	Finite rate of increase $\lambda = e^{r_m}$
			N. includens			
15	8.0	0.014	153.1	149.3	49.7	1.01
20	32.2	0.041	90.3	84.6	16.9	1.04
25	60.7	0.083	56.4	49.4	8.3	1.09
30	32.6	0.086	47.9	40.4	8.0	1.09
32.5	20.7	0.077	45.1	39.0	9.0	1.08
35	2.6	0.024	40.6	39.7	29.3	1.02
			N. bisignatus			
15	13.9	0.017	157.2	151.8	40.0	1.017
20	26.4	0.035	106.8	94.7	20.07	1.035
25	31.3	0.060	66.0	57.1	11.49	1.062
30	15.2	0.051	62.0	53.3	13.58	1.052
32.5	3.6	0.024	55.0	52.7	28.31	1.025

less, *N. includens* performed better than *N. bisignatus* in almost all cases except 15°C. The highest net reproductive rate (R_0) was recorded at 25°C in *N. includens* (60.7 females/female) and the highest intrinsic rate of increase (r_m) at 30°C. The respective values in *N. bisignatus* were recorded at 25°C. The higher value of (r_m) for *N. includens* at temperatures between 25–32.5°C is due to the greater survival of immature stages, which indirectly influence net reproductive rate (R_0) (Persad & Khan 2002). Reproductive value (V_x) for both species was highest at 25°C, with seven day old females of *N. includens* having an expected remaining life time (E_x) of 55 days, and twelve day old females of *N. bisignatus* an expected remaining life time (E_x) of 59 days. However, in *N. includens* the reproductive value (V_x) remained at a high level (>15 females/female) until the 25th day of their life and 20th day in *N. bisignatus*. Life history parameters need to be determined in the laboratory, which usually involved rearing them under constant conditions, despite the fact that insects are subjected to more complex and fluctuating conditions in their natural environment. Nevertheless, life tables remain a very useful tool for evaluating the effectiveness of natural enemies for controlling pests under various climatic conditions and in different habitats (Birch 1948, Jervis & Copland 1996). The parameter r_m is of especial interest because it integrates the effects of mortality and fertility in a single value.

In inundative releases of a biological control agent, its reproductive value (V_x) and expected remaining life time (E_x) are important. Probably the best time to release an agent is at its maximum reproductive value. Our results show that this occurs in early summer in central Greece. On the other hand, a release at the end of summer should consider whether the expected remaining life time (E_x) of the natural enemy is sufficiently long for it to become established over winter. Maximum value of *Vx* also was recorded for newly emerged adults or 15 day old adults. The biological meaning of this result is that these individuals will produce more progeny in the next generation than their co-specifics of other age classes. Thus, it is concluded that newly emerged adults are the ideal individuals for release.

A comparison of the population parameters (R_0, r_m, T_c, *DT*) indicates that *N. includens* is capable of developing high populations in temperatures ranging between 20–32.5°C. Temperatures 15–20°C are considered to be more suitable for "storage" of *N. includens*, based on the reproductive value (V_x) and expected remaining life time (E_x). The results of the current study provide information that will help facilitate the more effective control of mealybug pests by these coccinellid predators. The above results, in combination with data on development at constant temperatures and on their predatory activity (Kontodimas, 2004; Kontodimas et al., 2004), shows that *N. includens* could be an effective predator of *P. citri*, at least, in warm, southern temperate regions.

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