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Modelling population dynamics of *Orius laevigatus* and *O. albidipennis* (Hemiptera: Anthocoridae) to optimize their use as biological control agents of *Frankliniella occidentalis* (Thysanoptera: Thripidae)

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Abstract

Orius laevigatus (Fieber) and *O. albidipennis* (Reuter) play an important role in the control of *Frankliniella occidentalis* (Pergande) in crops and natural vegetation in the Mediterranean area. The biological parameters of the two anthocorids were studied and modelled in relation to temperature to optimize their use in thrips control programmes. Development times and reproductive parameters of *O. laevigatus* and *O. albidipennis* were determined at 20, 25, 30 and 35°C. Pre-imaginal development times ranged from 34.6 and 37.2 days at 20°C to 12.3 and 10.2 days at 35°C in *O. laevigatus* and *O. albidipennis*, respectively. The lower thermal development threshold was significantly higher for *O. albidipennis* (14.2 ± 0.9°C) than for *O. laevigatus* (11.3 ± 0.7°C). No significant differences in fecundities between the two anthocorids were observed at 20, 25 and 30°C. At 35°C, *O. albidipennis* had a significantly higher fecundity than *O. laevigatus*. Non-linear models were used to explain reproduction and female survivorship in relation to temperature. The upper reproductive thresholds were estimated at 40.9 ± 0.3 and 35.5 ± 0.1°C for *O. albidipennis* and *O. laevigatus*, respectively. The different optimum temperatures may explain, at least in part, the different distributions of the two species in the Palaeartic region and their population dynamics in greenhouses and natural vegetation in the south of Spain. The estimation of r_m as a function of temperature showed high variability between years. Three release rates of 0.75–0.25 *Orius* per plant are recommended from early March to mid May to deal with thrips outbreaks in pepper crops.

Introduction

Orius laevigatus (Fieber) and *Orius albidipennis* (Reuter) (Hemiptera: Anthocoridae) are commonly found on cultivated and wild plants in the Mediterranean region of Europe. The two species play an important role in the regulation of populations of western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), in crops and wild vegetation (Tavella *et al.*, 1991; Vacante & Tropea-Garzia, 1993; Lacasa *et al.*, 1996; Sanchez *et al.*, 1997, 2000). Throughout the world, this thrips is a key pest of ornamental and vegetable crops, largely because of its high efficiency in transmitting tomato spotted wilt virus (TSWV) (Sakimura, 1962; Wijkamp *et al.*, 1995).

Diapause induced by short photoperiod is one of the overwintering strategies developed by some species with a northern distribution such as *Orius insidiosus* (Say), *Orius tristicolor* (White) and *Orius majusculus* (Reuter) (Hemiptera:

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Anthocoridae) (Ruberson *et al.*, 1991; Van den Meiracker, 1994). This response to day-length has been reported to be a limiting factor in integrated pest management programmes (IPM) (Gillespie & Quiring, 1993). In *O. laevigatus* photoperiodic diapause induction has been observed in populations from northern Europe but not in southern populations (Tommasini & Nicoli, 1996). No response to photoperiod has been found in *O. albidipennis* (Van den Meiracker, 1994; Chyzik *et al.*, 1995). Therefore, as southern populations of *O. laevigatus* and *O. albidipennis* are not limited by daylength, temperature may be considered the abiotic factor with the greatest influence on their population dynamics.

In the south of Spain, winter is usually mild and *O. laevigatus* is active all the year round (Lacasa *et al.*, 1996). Little is known about the overwintering biology of *O. albidipennis*. However, low and high temperatures could limit the activity of the two anthocorids in winter and summer. Although development and reproduction of the two species have been studied at several temperatures (Alauzet *et al.*, 1994; Tommasini & Benuzzi, 1996; Cocuzza *et al.*, 1997b), these data do not allow comparison of the limiting effects of temperature on the two species. Little information is available for *O. albidipennis*. In most cases, authors have used populations of different origin and the information is dispersed in works whose goal was other than the study of the effect of the temperature. With *O. laevigatus* most of the work has been done with northern populations, or with populations of unknown origin (i.e. commercial suppliers), and the information about southern populations is limited and dispersed. The origin of the population must be considered, because the response of the species may change with latitude as an adaptation to different climatic conditions (Campbell *et al.*, 1974). There are no comparative data sets that allow calculation of thermal thresholds and modelling of the development and reproduction of *O. laevigatus* and *O. albidipennis* as a function of temperature.

Models are important analytical tools for predicting, evaluating, and understanding the dynamics of populations of pest and beneficial organisms. In the Mediterranean zone, *O. laevigatus* and *O. albidipennis* are of a great economic importance. They are commonly released in protected pepper crops for biological control of *F. occidentalis*, or spontaneously colonize the crops when the use of insecticides is restricted (Tavella *et al.*, 1991; Vacante & Tropea-Garzia, 1993; Sanchez *et al.*, 1997, 2000). Growing seasons extend for most of the year and the environmental conditions of the crop fluctuate greatly over the whole period. Low temperature may limit the establishment of populations of these predators in winter and early spring. In summer, high temperatures (usually above 30°C for more than 12 h a day and maxima of 42°C) may reduce population growth (Sanchez *et al.*, 2000). Therefore, the availability of a model to predict population dynamics of the two species relative to temperature may be a very useful tool for management purposes. The model can be used to select the appropriate *Orius* species for the local environmental conditions. Data from population dynamics may be also used to establish optimum release strategies in order to enhance western flower thrips control.

The objective of the present work was to optimize the use of *O. laevigatus* and *O. albidipennis* in IPM crops where the anthocorids are used against *F. occidentalis*. Development and reproduction of the two species were studied at several temperatures. The experimental data were used to model the development time, reproduction and intrinsic rate of natural increase (r_m) of the two species in relation to temperature. The probability of thrips outbreaks and the density of *Orius* that reduced thrips outbreaks were determined from study of the population dynamics of these two species on greenhouse pepper crops. Modelling population dynamics of *O. laevigatus* and *O. albidipennis* was used to provide rates and dates of release for effective control of *F. occidentalis* under greenhouse conditions.

Materials and methods

Mass rearing

Orius laevigatus and *O. albidipennis* were collected from pepper crops and surrounding vegetation in the south-east of Spain in 1996. Cultures of both species were maintained in independent chambers at 23°C, 70–80% r.h and L14:D10 photoperiod. Leaves of geranium *(Pelargonium peltatum* Soland in Ait (Geraniaceae)) were used as a substrate for egg-laying. Nymphs were fed with sterilized *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) eggs and adults with honeybee pollen and moth eggs.

Trial conditions

Development time and mortality of the pre-imaginal instars, and daily fecundity and mortality of the adults were determined at four constant temperatures: 20 ± 1, 25 ± 1, 30 ± 1 and 35 ± 1°C, 70–80% r.h and L14:D10 photoperiod. Groups of five to ten females were placed at each temperature in plastic jars with a *Pelargonium* leaf for egg-laying. The females were removed 24 h later and the eggs were counted and observed daily for eclosion. Newborn nymphs were kept individually in 'Penna cage' cells using pepper leaves as a substrate (Lacasa & Llorens, 1998). Sterilized *E. kuehniella* eggs were supplied *ad libitum*. For *O. laevigatus*, 58, 73, 34 and 70 nymphs were followed to adulthood at 20, 25, 30, 35°C, respectively. For *O. albidipennis* 64, 83, 32 and 87 nymphs were observed through to adulthood at 20, 25, 30, 35°C, respectively. Nymphs were observed daily for exuviae, which were removed from the cells. Teneral adults were sexed and male and female pairs were placed in 80 cm^3 screened-lid plastic jars. Adults were fed *ad libitum* with *E. kuehniella* eggs and honeybee pollen and *Pelargonium* leaves provided for egg-laying. Leaves were changed daily and eggs counted. Approximately 30 pairs of *O. laevigatus* and *O. albidipennis* were studied at each temperature.

Data analysis

Development and reproduction

Development times of the pre-imaginal instars, total development time, adult longevity, fecundity, pre- and oviposition times were compared between *O. laevigatus* and *O. albidipennis* using a two-factor ANOVA (Species × Temperature). Differences among means in the ANOVA were distinguished with the Tukey test. Data were $\log_{10}$ transformed and only individuals that completed the total development were included in the analysis. Female and male development times were combined together as no significant differences were found between sexes either for *O. laevigatus* (two factor ANOVA. Sex: F = 0.734; df = 1, 211; $P = 0.392$. Temperature: F = 1815; df = 3, 211; $P < 0.001$) or *O. albidipennis* (two factor ANOVA. Sex: F = 0.819; df = 1, 249; $P = 0.819$. Temperature: F = 2081; df = 3, 249; $P < 0.001$).

The relationship between the development rate (y) and temperature was calculated by linear regression ($Y = a + bT$). The thermal constant (K) was calculated as $1/b$ and the development thresholds (T_o) as $-a/b$. The standard error (SE) of K was calculated as (SE of b)/b^2 and the SE of T_o with the equation:

$$SE(T_0) = \bar{y} \,/\, b\sqrt{s^2 \,/\, N \cdot \bar{y}^2 + (SE(b)\,/\,b)^2}$$

(Campbell *et al.*, 1974). The development threshold, thermal constant and the slope of the thermal equation were compared (t-test) between the two species and with published values.

The intrinsic rate of natural increase (r_m) was calculated with the equation $\Sigma l_x m_x e^{-r_m x} = 1$ derived by Lotka (1907, 1913 in Krebs, 1985). The net reproduction rate ($R_0 = \Sigma l_x m_x$), the average generation time ($G = \Sigma_0^{\max} x l_x m_x \,/\, R_0$), the finite capacity of increase ($\lambda = e^{r_m}$) and the doubling population time ($D = \ln 2 \,/\, r_m$) were also calculated. In these equations x is the age of the female; l_x is the proportion of living females at age x and m_x is the number of females produced by each female at age x. A 1:1 sex ratio was used to calculate the demographic parameters. Considering the assay of each temperature as a repeat, the sex ratio was not significantly different from 1:1, for *O. laevigatus* (t = 0.703; df = 1, 3; P = 0.532) or for *O. albidipennis* (t = 0.941; df = 1, 3; P = 0.416).

Modelling of the reproduction

The time elapsed from mating to the start of oviposition (P) was described in relation to temperature (T) with a logistic equation:

$$P = a \,/\, (1 + \exp(-b(T - c)))$$

where a, b and c are the regression parameters. Daily oviposition (Ov) was described by a model composed of an analytical function developed by Logan *et al.* (1976) and an exponential equation:

$$(Ov = \alpha\left\{\left[1 + k\exp(-\rho T)\right]^{-1} - \exp(-\tau)\right\}$$
$$(x - P)\exp[-(d + eT)(x - P)])$$

Logan *et al.* (1976) developed the analytical model to explain development and oviposition in *Tetranychus mcdanieli* (Mcgregor) (Acari: Tetranychidae) and it successfully described the rate of increase in temperature-dependent processes in several arthropods such as *Dacus dorsalis* Hendel (Diptera: Tephritidae) and *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). The parameters in the model have biological interpretation. x is time, $\tau = (T_M - T) \,/\, \Delta T$, where T_M is the lethal maximum temperature in degrees Celsius above a base temperature (T_b), T is the temperature in degrees above T_b and ΔT the temperature range over which 'thermal breakdown' has an overriding effect (Logan *et al.*, 1976). Based on the reproduction data reported by other authors (Alauzet *et al.*, 1994; Cocuzza *et al.*, 1997b), T_b was established at 15°C for both *O. laevigatus* and *O. albidipennis*. T_M and ΔT were initially set visually. Subsequent analyses were done by a non-linear least square technique to fit T_M and ΔT, and to calculate the regression parameters α, k, ρ, d and e. The complete reproduction (R) model was given by the following expression:

$$\begin{cases} \text{If} \;\; x \le P \Rightarrow R = 0 \\ \text{If} \;\; x > P \Rightarrow R = Ov \end{cases}$$

Female survivorship (S) was described as a function of time (x) and temperature (T) by the Gompertz function for both *O. laevigatus*:

$$S = a\exp\{b\exp[(c + dT)(e + fx)]\}$$

and *O. albidipennis*:

$$S = a\exp\{b\exp[(c + dT)x\,)]\}$$

where a, b, c, d, e and f are regression parameters. A similar equation was used by Tsai & Wang (1996) to explain the survival of females of *Bemisia argentifolii* Bellows & Perring (Hemiptera: Aleyrodidae). The models were fitted to the experimental data by non-linear least-square technique using Systat (Wilkinson *et al.*, 1992).

The r_m was predicted between a lower and an upper threshold. The lower threshold for the r_m prediction was set at a temperature close to that of the adult development threshold (12°C for *O. laevigautus* and 15°C for *O. albidipennis*). The upper threshold was set at a temperature close to the upper reproduction threshold estimated using the reproduction models (35°C for *O. laevigatus* and 40°C for *O. albidipennis*). The thermal equation was used to calculate the duration of the pre-imaginal instars and the models described above for daily oviposition and female survivorship. The mortality of the pre-imaginal instars was the average of that at 20, 25, 30 and 35°C.

Temperature records from five growing seasons recorded in greenhouses from the Campo de Cartagena (Murcia, Spain) were used to model the daily r_m of *O. laevigatus* and *O. albidipennis*. Temperature was recorded with a thermohygrograph during the growing seasons of 1995 to 1998. A digital thermometer (Hobo®, Onset Computer Corporation) was used to record temperature at intervals of six times per hour in 1999. The thermohygrograph paper bands were read with a digital panel with software developed *ad hoc*. In both cases, temperature records were averaged over hourly intervals every day. The r_m was calculated hourly for *O. laevigatus* and *O. albidipennis* and the 24 values were averaged to estimate the daily $r_{m.}$ The r_m was estimated daily as a function of greenhouse temperature records and the differences between the r_m of the two species were plotted against time.

Release strategies for Orius laevigatus *and* O. albidipennis *in greenhouses pepper crops*

Orius release rates were calculated based on a study of the population dynamics of *F. occidentalis*, *O. laevigatus* and *O. albidipennis* carried out over several years in greenhouses in Campo de Cartagena (Murcia, Spain) and based on our models of the population dynamics. These three species were monitored in six experimental and 12 commercial greenhouses from 1995 to 1999. In all greenhouses, *O. laevigatus* was released to control *F. occidentalis*. *Orius albidipennis* was also used in 12 of the greenhouses. Other natural enemies or chemical products compatible with IPM were used to control other pests or fungal diseases. In all greenhouses, *F. occidentalis* and *Orius* spp. were monitored weekly by taking three and six samples of ten randomly distributed flowers from experimental and commercial greenhouses, respectively. Thrips and *Orius* spp. extraction was done with Berlese funnels with a 25 W lamp for 24 h. Individuals were collected in 10% alcohol, counted and identified under a stereo microscope. The number of flowers was counted on ten randomly selected plants in the experimental greenhouses and on 30 randomly selected plants in commercial greenhouses. As *Orius* spp. are located mainly on flowers (Shipp *et al.*, 1992; Sanchez *et al.*, 1998), an approximation of the number of *Orius* per plant was given by multiplying the average number of flowers per plant by the number of *Orius* individuals per flower. Temperature and humidity were monitored with digital data logger thermometers (Hobo®) or paper band thermohygrographs.

In all greenhouses the date when an outbreak of *F. occidentalis* peaked and the number of *Orius* per plant that reduced a thrips outbreak were recorded. Theoretical rates and dates of *Orius* release were based on the number of *Orius* per plant that controlled thrips outbreaks in the greenhouses. The *Orius* threshold needed to control a thrips outbreak was set at the highest number of *Orius* per plant that successfully reduced thrips outbreaks in greenhouses. The theoretical population growth of *Orius* spp. after release was assumed to be exponential and calculated by the expression ($N_{t+1} = \lambda N_t$), where t is the time in days, N_{t+1} and N_t are the number of *Orius* per plant at time $t+1$ and t respectively and λ is the finite capacity of increase at time t. Hourly temperature records from 1995 to 1999 were averaged and r_m and λ calculated daily as explained above. This approach to calculating the population growth of *Orius* spp. implies several assumptions: (i) initial *Orius* spp. population increase is exponential; (ii) emigration or immigration does not occur; (iii) all other parameters apart from temperature (e.g. food resources) are at their optimum; and (iv) interspecific or intraspecific competition does not occur.

Results

Development, reproduction and demographic parameters

Development times from eggs to adult ranged from 34.6 and 37.2 days at 20°C to 12.3 and 10.2 days at 35°C for *O. laevigatus* and *O. albidipennis*, respectively (table 1).

Table 1. Development times (days ± SD) and survivorship of the pre-imaginal instars of *Orius laevigatus* and *O. albidipennis* at 20, 25, 30, 35°C.

		O. laevigatus		*O. albidipennis*	
T(°C)	Instar	Development time (days)	Survivorship (%)	Development time (days)	Survivorship (%)
20	Egg (n)	7.4 ± 0.8a(152)	87.2	7.9 ± 0.8b (98)	87.7
	n	58		64	
	N1	5.6 ± 1.1a	91.2	6.7 ± 1.9b	94.2
	N2	4.0 ± 0.7a	98.1	4.5 ± 1.1a	88.6
	N3	4.1 ± 0.8a	98.9	4.6 ± 0.7a	95.1
	N4	4.9 ± 0.7a	96.0	5.2 ± 0.8a	98.8
	N5	8.6 ± 0.9a	96.3	8.9 ± 0.9a	96.5
	N1–N5	27.1 ± 2.3a	81.8	29.6 ± 2.7b	75.6
	Adult	34.6 ± 2.3a	71.2	37.2 ± 2.8b	67.1
25	Egg (n)	4.3 ± 0.5a (125)	98.3	4.0 ± 0.4b (121)	96.9
	n	73		83	
	N1	3.3 ± 0.9a	89.9	4.0 ± 0.8b	96.0
	N2	2.4 ± 0.6a	95.9	2.3 ± 0.6a	97.7
	N3	2.6 ± 0.5a	95.7	2.5 ± 0.6a	97.7
	N4	2.8 ± 0.6a	92.0	2.5 ± 0.6b	100
	N5	4.9 ± 0.7a	98.7	4.5 ± 0.7b	98.8
	N1–N5	16.1 ± 1.2a	74.9	15.7 ± 1.3a	90.5
	Adult	20.5 ± 1.3a	73.7	19.6 ± 1.4b	87.7
30	Egg (n)	3.0 ± 0.7a (34)	93.5	3.1 ± 0.4a (57)	91.9
	n	34		32	
	N1	2.5 ± 0.5a	94.6	2.5 ± 0.6a	99.0
	N2	1.7 ± 0.5a	97.1	1.8 ± 0.6a	99.1
	N3	1.9 ± 0.5a	100	1.7 ± 0.7a	99.1
	N4	2.2 ± 0.6a	100	2.1 ± 0.8a	99.1
	N5	3.9 ± 0.7a	100	3.3 ± 0.8b	99.0
	N1–N5	12.2 ± 1.1a	91.9	11.3 ± 1.3b	95.4
	Adult	15.2 ± 1.1a	85.9	14.4 ± 1.3a	87.8
35	Egg (n)	2.4 ± 0.5a (70)	96.0	2.1 ± 0.3b (107)	97.5
	n	70		87	
	N1	2.0 ± 0.4a	90.1	1.8 ± 0.5b	98.2
	N2	1.5 ± 0.5a	92.1	1.1 ± 0.4b	99.1
	N3	1.5 ± 0.5a	95.1	1.1 ± 0.3b	97.2
	N4	1.8 ± 0.5a	93.3	1.6 ± 0.5b	98.0
	N5	3.1 ± 0.4a	100	2.6 ± 0.5b	91.8
	N1–N5	9.9 ± 0.7a	73.8	8.2 ± 0.8b	85.1
	Adult	12.3 ± 0.8a	70.7	10.2 ± 0.9b	83.0

n, number of individuals; N, nymphal instar. The same letter after the means denotes no significant differences between the two species in the same instar (Tukey-test, $P > 0.05$).

Development times of the two species were significantly different at all temperatures studied, except at 30°C, with a significant interaction between species and temperature (two factor ANOVA. Species: F = 61.3; df = 1, 494; $P < 0.001$. Temperature: F = 6104; df = 3, 494; $P < 0.001$. Species × temperature: F = 75; df = 3, 494; $P < 0.001$). Preimaginal survivorship of *O. laevigatus* and *O. albidipennis* was similar at all temperatures studied (table 1). The development threshold and the thermal constant for adults of *O. laevigatus* were 11.3°C and 285.7 ± 11.5 degree days (DD) respectively (table 2). The eggs had the highest threshold (12.8°C) and those of the nymphs were similar to the adults. The thermal constant (212.8 ± 12.8 DD) and development threshold (14.2°C) for *O. albidipennis* were significantly lower than those of *O. laevigatus* (table 2; t-test, $P < 0.05$). In *O. albidipennis*, the thresholds for eggs, first, second and third-instar nymphs (14.4–16°C) were higher than those of fourth and fifth-instar nymphs (12.5–13.5°C) though the differences were not significant (table 2; t-test, $P > 0.05$).

The extent of oviposition at 20, 25 and 30°C ranged from 150 to 83 eggs per female in *O. laevigatus* and 130 to 92 eggs per female in *O. albidipennis* (table 3). At 35°C the fecundity of *O. laevigatus* (19 eggs per female) was significantly lower than that of *O. albidipennis* (91 eggs per female) (table 3, Tukey test, $P < 0.001$). The highest rate of oviposition (3.6 and 3.1 eggs per female for *O. laevigatus* and *O. albidipennis*, respectively) took place approximately 20 days after mating in the two species at 20°C and shortened to 5 days at 35°C (figs 1 and 2). At 35°C the oviposition peak was higher for *O. albidipennis* (7.2 eggs per female) than for *O. laevigatus* (1.7 eggs per female). The longevity of females was greatly reduced as temperature increased. At 20°C the longevity of *O. laevigatus* females (70 days) was significantly longer than that of *O. albidipennis* females (56 days), while at 35°C *O. albidipennis* females lived longer (11.6 days) than those of *O. laevigatus* (7.7 days). Five females of *O. laevigatus* that did not lay any eggs at 35°C were transferred to another chamber at 25°C and L14:D10, five days after mating (an interval almost twice as long as the pre-oviposition time at 35°C). The reproductive parameters of these females were similar to those at 25°C. Three females laid eggs the day after they were transferred and the other two started at days 4 and 9. The average fecundity was 130 eggs per female and the life span was 26.8 days.

The intrinsic rate of natural increase (r_m) of *O. laevigatus* rose from 0.059 to 0.135 between 20 and 30°C (table 4, fig. 3). Thus, from 20 to 30°C the population doubling time (D) was reduced from 11.8 to 5.1 days. At 35°C, the r_m decreased strongly (0.042) and consequently the doubling time climbed to 16.5 days. The r_m of *O. albidipennis* increased progressively from 0.051 to 0.195 between 20 and 35°C (table 4). This implies a reduction in population doubling time (D) from 13.6 days at 20°C to 3.5 days at 35°C.

Modelling oviposition, females survivorship and r_m

In the two species, females started laying eggs at 6, 2, 1 and 1 days after mating at 20, 25, 30 and 35°C, respectively (figs 1 and 2). The logistic model:

$$P = 64.828 \ / \ (1 + \exp(0.194(T - 8.14)))$$

explained 97.3% of the variability of the experimental data, where P is the start of oviposition and T is temperature. In *O.*

Table 2. Thermal equation and development threshold temperature (T_0) ± SE of the pre-imaginal instars and adult of *Orius laevigatus* and *O. albidipennis*.

	O. laevigatus						*O. albidipennis*					
Instar	Equation		T_0 (°C)		r^2	P	Equation		T_0 (°C)		r^2	P
Egg	-0.2435+0.0190T	a	12.8 ± 0.6	a	0.995	0.002	–0.3235+0.0224T	a	14.4 ± 1.5	a	0.967	0.011
N1	-0.2271+0.0207T	a	11.0 ± 0.9	a	0.991	0.003	–0.3964+0.0266T	b	14.9 ± 0.8	b	0.989	0.004
N2	-0.3188+0.0292T	a	10.9 ± 1.5	a	0.977	0.007	–0.6219+0.0416T	b	15.0 ± 1.6	b	0.961	0.013
N3	-0.3262+0.0284T	a	11.5 ± 0.2	a	0.999	0.000	–0.7416+0.0465T	b	16.0 ± 1.6	a	0.953	0.016
N4	-0.2595+0.0237T	a	10.9 ± 0.9	a	0.991	0.003	–0.3578+0.0287T	a	12.5 ± 2.0	a	0.955	0.015
N5	-0.1380+0.0131T	a	10.5 ± 1.3	a	0.984	0.005	–0.2505+0.0187T	b	13.5 ± 0.7	b	0.994	0.002
Adult	-0.0397+0.0035T	a	11.3 ± 0.7	a	0.995	0.002	–0.0665+0.0047T	b	14.2 ± 0.9	b	0.989	0.003

r^2, regression coefficient; P, probability level; N, nymphal instar. In the equations T = temperature in °C. The same letter denotes no significant differences between the slope of the thermal equation or development threshold for each instar of the two species (t-test, $P > 0.05$).

Table 3. Average ± SE of fecundity, fertility, pre-oviposition and oviposition period, adult longevity and sex-ratio of *Orius laevigatus* and *O. albidipennis* at four temperatures.

		O. laevigatus				*O. albidipennis*		
	20°C	25°C	30°C	35°C	20°C	25°C	30°C	35°C
n	32	31	27	29	32	28	37	35
Fecundity	150 ± 16a	133 ± 14a	83 ± 9a	19 ± 4a	93 ± 14a	130 ± 13a	92 ± 13a	91 ± 10b
Fertility (%)	75	87	85	31	77	75	78	49
Pre-oviposition period*	12.8 ± 1.2a	7.3 ± 0.9a	4.0 ± 0.7a	3.1 ± 0.2a	12.6 ± 1.4a	3.7 ± 0.5a	2.1 ± 0.3a	1.3 ± 0.1a
Oviposition period*	37.3 ± 3.1a	19 ± 1.7a	13 ± 1.1a	3.8 ± 0.5a	25.4 ± 2.9b	18.2 ± 1.5a	11.6 ± 1.3a	8.9 ± 0.8a
Longevity (females)*	70.3 ± 4.0a	32.8 ± 2.3a	21.2 ± 1.7a	7.7 ± 0.8a	56.4 ± 3.8b	30.4 ± 2.2a	18.1 ± 1.5a	11.6 ± 0.8b
Longevity (males)*	33.7 ± 3.1a	16.1 ± 1.8a	9.4 ± 0.9a	4.9 ± 0.5a	49.7 ± 3.2b	20.8 ± 2.3a	11.7 ± 1.1a	8.3 ± 0.6b
Sex-ratio (females/male)	0.47	0.43	0.44	0.57	0.41	0.42	0.53	0.52

n, number of pairs; * measured in days.

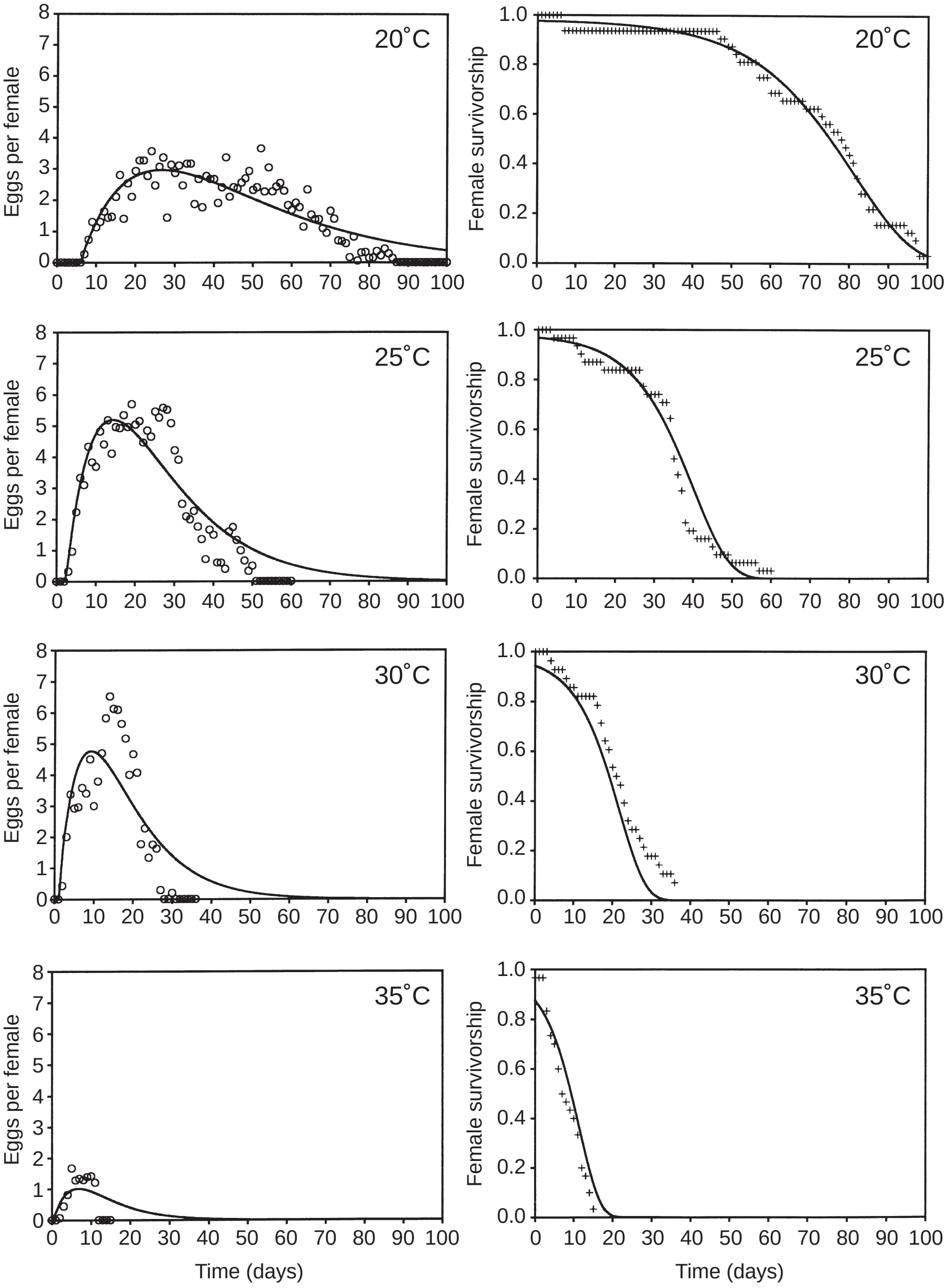

Fig. 1. Daily oviposition and survivorship of females of *Orius laevigatus* at 20, 25, 30 and 35°C. Symbols represent the experimental values and curves the prediction for oviposition and survivorship with the respective models.

laevigatus, the non-linear model satisfactorily explained the daily oviposition rate in relation to time and temperature ($r^2 = 0.792$) (table 5, fig. 1). The model predicted an increase in daily fecundity and reduction of the oviposition period as temperature increased and a subsequent sharp decrease as temperature approached the estimated upper threshold (35.5°C) (table 5, fig. 1). In *O. albidipennis*, the reproduction model explained 77% of the variability of the experimental data (table 5, fig. 2). The upper reproduction threshold estimated for *O. albidipennis* was 40.9°C. The female survivorship models explained 96.2 and 95.5% of the variability of the experimental data in relation to time and temperature in *O. laevigatus* and *O. albidipennis*, respectively (table 5, figs 1 and 2). The parameters and coefficient of regression (r^2) for oviposition and females survivorship models are shown in table 5. The predicted r_m described accurately the trend of the experimental values through a wide range of temperature (fig. 3). The maximum r_m was predicted at 30 and 35°C for *O. laevigatus* and *O. albidipennis*, respectively.

The estimation of the daily differences in the intrinsic rate of natural increase (r_m) between *O. laevigatus* and *O. albidipennis* based on greenhouses temperature records

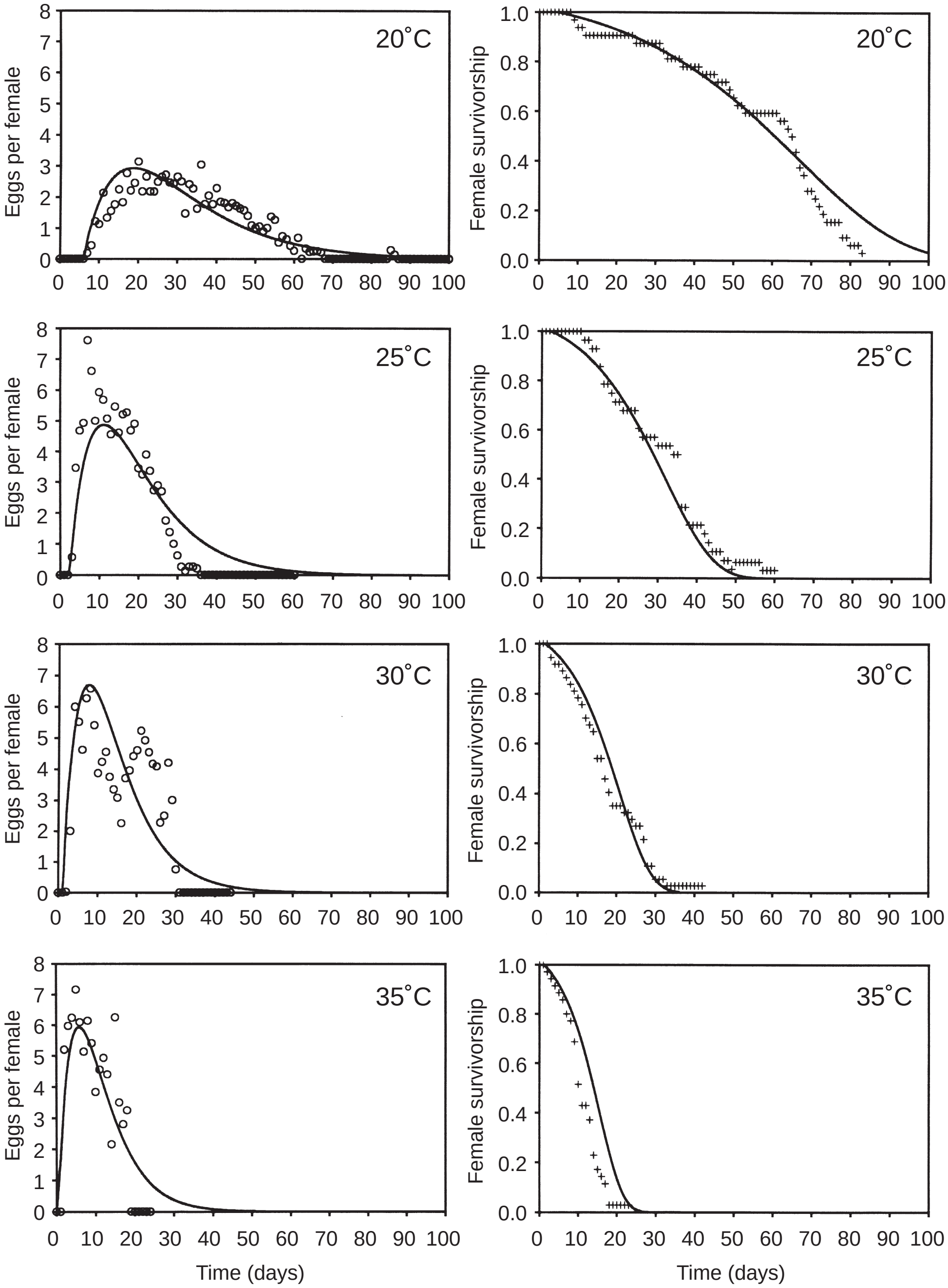

Fig. 2. Daily oviposition and survivorship of females of *Orius albidipennis* at 20, 25, 30 and 35°C. Symbols represent the experimental values and curves the prediction for oviposition and survivorship with the respective models.

showed a high variability between years (fig. 4). Overall, it was observed that the r_m values of the two species were similar from January to May while the differences in the r_m increased during the summer months (fig. 4).

Release strategies for Orius laevigatus *and* O. albidipennis

The proportion of greenhouses with *F. occidentalis* outbreaks was plotted fortnightly (fig. 5). None of the greenhouses had *F. occidentalis* outbreaks before April or after June. The highest proportion of outbreaks was observed during the first two weeks of May (33%). Thereafter, the proportion of greenhouses with thrips outbreaks declined progressively (fig. 5). The average number of *Orius* individuals per plant necessary to reduce moderate to high thrips outbreaks (18.4 thrips per flower) was 1.9 ± 0.3. The highest number necessary to reduce a thrips outbreak was 5.7 *Orius* per plant. To develop *Orius* release strategies the most conservative approach was

Table 4. Demographic parameters of *Orius laevigatus* and *O. albidipennis* at 20, 25, 30, 35°C.

	O. laevigatus						*O. albidipennis*					
T (°C)	n	R_o	G	D	r_m	λ	n	R_o	G	D	r_m	λ
20	32	46.1	64.9	11.8	0.059	1.061	32	26.6	63.7	13.6	0.051	1.053
25	31	42.6	35.6	6.6	0.105	1.111	28	42.8	30.5	5.6	0.123	1.131
30	27	30.5	25.3	5.1	0.135	1.145	37	31.5	22.2	4.5	0.155	1.168
35	29	2.1	18.1	16.5	0.042	1.042	35	22.8	16.0	3.5	0.195	1.216

n, number of females; R_o, net reproduction rate; G, generation time (days); D, population doubling time (days); r_m, intrinsic rate of natural increase; and λ, finite rate of increase.

Table 5. Parameters ± SE and regression coefficient (r^2) of the reproduction and female survivorship models of *Orius laevigatus* and *O. albidipennis*.

Survivorship			Oviposition		
Parameters	*O. laevigatus*	*O. albidipennis*	Parameters	*O. laevigatus*	*O. albidipennis*
a	0.982 ± 0.012	1.11 ± 0.0340	α	1.70 ± 0.04	7.87 ± 0.20
b	-0.0008 ± 0.0005	–0.0822 ± 0.0197	k	26.3 ± 1.3	24.2 ± 0.7
c	-2.50 ± 0.09	–0.128 ± 0.010	ρ	0.411 ± 0.008	0.212 ± 0.003
d	0.209 ± 0.008	0.0083 ± 0.0007	d	0.0126 ± 0.0009	0.0431 ± 0.0018
e	1.02 ± 0.06		e	0.00713 ± 0.0001	0.0071 ± 0.0002
f	0.039 ± 0.002		T_M	20.5 ± 0.1	25.9 ± 0.3
			ΔT	1.7 ± 0.4	5.8 ± 0.2
r^2	0.962	0.955	r^2	0.792	0.771

a, *b*, *c*, *d* and *f*, and α, k, ρ, d and e are regression parameters for the survivorship and oviposition models, respectively. T_M is the maximum temperature above base temperature (T_b= 15°C) and ΔT is the temperature range over which thermal breakdown has an overriding effect.

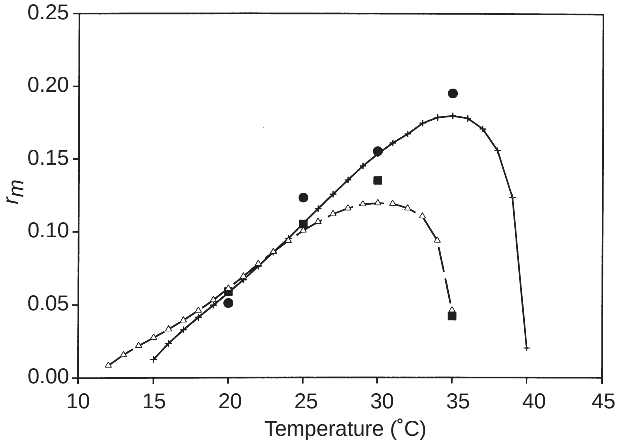

Fig. 3. Intrinsic rate of natural increase (r_m) for *Orius laevigatus* and *O. albidipennis* in relation to temperature. Symbols represent the experimental values and lines the predicted r_m. (*O. albidipennis*: experimental (●) and estimated (+) r_m; *O. laevigatus* experimental (■) and estimated (Δ) r_m).

chosen. Thrips outbreaks were assumed to take place as early as the beginning of April and as late as the last two weeks of June. *Orius* spp. threshold density to reduce *F. occidentalis* outbreaks was set at the highest level observed on the field (6 *Orius* per plant). *Orius* release rates and dates were designed to reach the threshold density at the beginning of April, the period of highest outbreak probability and the last two weeks of June (fig. 5). Rate and timing of release were considered acceptable if the predicted populations reached the desired *Orius* threshold five or six weeks after release. Under optimal conditions and exponential growth, an initial population of 0.75 *O. laevigatus* or *O. albidipennis* per plant released on 1 March was estimated to reach 6 *Orius* individuals per plant six weeks later for both species (fig. 5). If 0.5 individuals per plant of either species were released in mid March, populations were estimated to reach 6 *Orius* individuals per plant by the end of April, close to the period of highest probability of thrips outbreaks (fig. 5). In both releases the estimated population growths were similar for the two species, although *O. albidipennis* population growth was estimated to be a little higher than that of *O. laevigatus*. Releasing 0.25 *O. albidipennis* per plant on 10 May, the population was estimated to increase to more than 6 individuals per plant by mid June while *O. laevigatus* would not have reached this density until two weeks later (fig. 5).

Discussion

The results of this work show development and reproduction of *O. laevigatus* and *O. albidipennis* are greatly influenced by temperature. The differences in development times, thermal thresholds, and reproductive and demographic parameters indicate a different adaptation of the two anthocorids to temperature. The development and reproduction of the two species have been determined at different temperatures by several authors. For *O. laevigatus*, Cocuzza *et al.* (1997b) reported lower nymphal development time than ours at 25°C (14.1 ± 0.2 days. t = 8.22; df = 1, 101; $P < 0.001$) and similar at 35°C (10.1 ± 0.1 days. t = 8.22; df = 1,

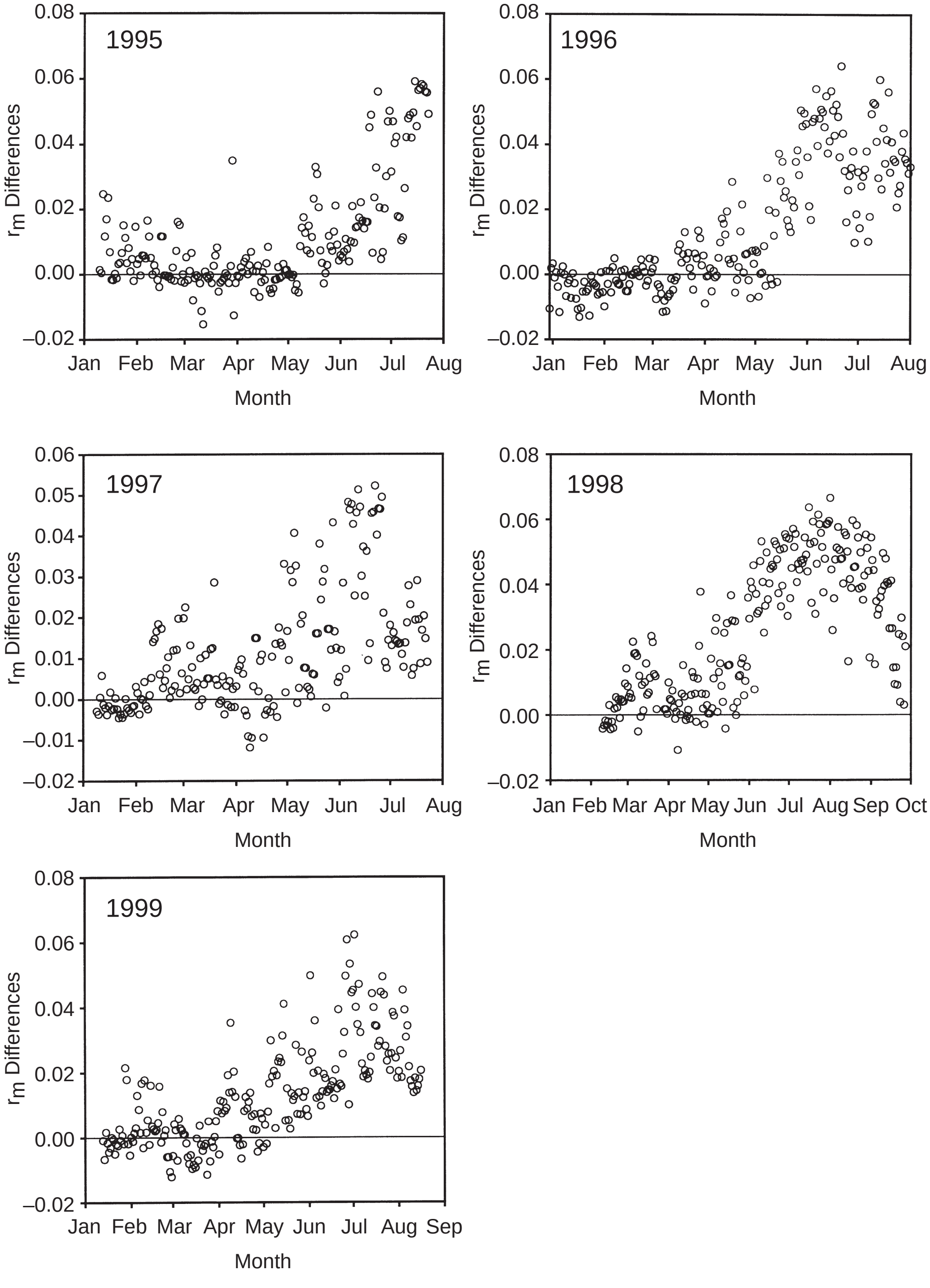

Fig. 4. Daily differences between the intrinsic rates of natural increase (r_m) of *Orius albidipennis* and *O. laevigatus*. r_m of the two species were calculated daily for the average temperature records of five years in pepper greenhouses.

106; P = 0.11). Alauzet *et al.* (1994) reported significantly lower development times than ours (t-test, $P < 0.001$) for the nymphal period (20.4, 13.2 and 9.3 days at 20, 25 and 30°C respectively). The lower thermal threshold (10.6°C) of *O. laevigatus* reported by Alauzet *et al.* (1994) was not significantly different from that determined in this work (t = 1.17, df = 6, P = 0.142). However, the thermal constant calculated using their data (247 ± 8.9 DD) was significantly lower than ours (285.7 ± 11.5) (t = 3.76, df = 6, $P < 0.001$).

Orius albidipennis nymphal development times observed by Cocuzza *et al.* (1997b) (13.2 ± 0.2 and 7.7 ± 0.1 days at 25 and 35°C respectively) were also significantly lower than those reported in this work (t-test, $P < 0.05$). No thermal thresholds have been reported before for *O. albidipennis*. However, the lower thresholds reported in this work for eggs and nymphs of the first stages agree with empirical observations of other authors. No eggs hatched when kept at 15°C for 25 days and a high mortality was recorded in the

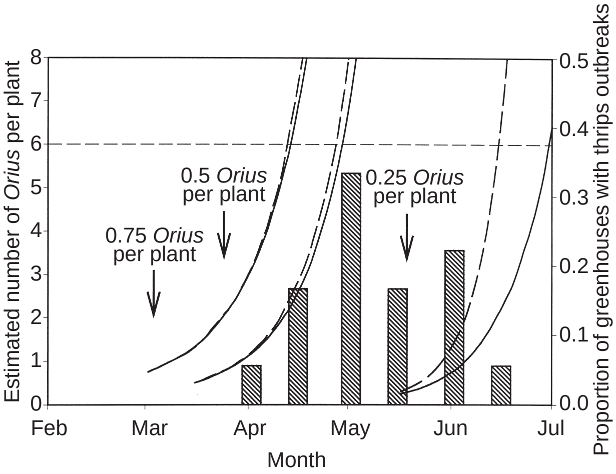

Fig. 5. Estimated release rates and population growth (curves) for *Orius laevigatus* (—) and *O. albidipennis* (– –) as a function of the five year temperature average in greenhouses where peppers were grown. The bars represent the proportion of greenhouse pepper crops having *Frankliniella occidentalis* outbreaks in the south-east of Spain, plotted fortnightly. The arrows represent *Orius* spp. releases. The dotted upper line represents the *Orius* threshold density considered necessary to reduce thrips outbreaks.

first nymphal instar (Carnero *et al.*, 1993; Chyzik *et al.*, 1995; Cocuzza *et al.*, 1997b).

The differences in development times recorded by authors might be a consequence of using populations with different origins adapted to local climatic conditions. This type of response was reported by Campbell *et al.* (1974) for *Acyrthosiphon pisum* (Harris), *Brevicoryne brassicae* (Linnaeus) (Hemiptera: Aphididae) and *Diaerietiella rapae* (M'Intosh) (Hymenoptera: Braconidae). Populations from a warm summer climate such as Berkeley, California, had longer development times and higher development thresholds than those from a cool climate such as Vancouver, British Columbia.

The reported fecundity of *O. laevigatus* at temperatures between 20 and 30°C varies greatly among authors, with values ranging from 67.8 to 160 eggs per female (Alauzet *et al.*, 1994; Tommasini & Benuzzi, 1996; Tommasini & Nicoli, 1996; Cocuzza *et al.*, 1997a,b). At 35°C the same decline in *O. laevigatus* fecundity was also noted by Cocuzza *et al.* (1997b). However, the exposure to temperatures above 35°C during part of the day may have only a temporary effect on female reproduction. Females that did not lay any eggs for days at 35°C initiated oviposition shortly after they were transferred to 25°C.

The reported fecundity between 20 and 30°C for *O. albidipennis* also varies among authors, with values ranging from 50.8 to 143 eggs per female (Zaki, 1989; Carnero *et al.*, 1993; Cocuzza *et al.*, 1997a,b). At low temperatures a great reduction in fecundity, more pronounced in *O. albidipennis* than in *O. laevigatus*, has been reported. At 15°C Alauzet *et al.* (1994) observed that 50% of the females of *O. laevigatus* died without laying eggs and the remaining half laid 60 eggs per female. At this temperature Cocuzza *et al.* (1997b) observed an average fecundity of 22.7 and 1.0 eggs per female in *O. laevigatus* and *O. albidipennis*, respectively.

The differences in the development threshold and the reproduction and demographic parameters in relation to temperature suggest that *O. laevigatus* is better adapted to low temperatures, while *O. albidipennis* is better adapted to high temperatures. The experimental results agree with the model's predictions. These estimate the temperature at which the r_m reaches its maximum and the upper reproduction threshold to be approximately 5°C higher for *O. albidipennis* than for *O. laevigatus*. The different response of the two anthocorids to temperature may explain in part why *O. albidipennis* has a southern distribution, with a northern limit on the south-east coast of Spain, while *O. laevigatus* is widespread in the Mediterranean basin and extends as far north as the UK (distribution data from Pericart, 1972). This can also explain why in the south-east of Spain *O. laevigatus* is more abundant than *O. albidipennis* during winter and spring while the latter species is more abundant in summer (Lacasa *et al.*, 1996). The same trends have been observed on sweet pepper grown in greenhouses in the south-east of Spain where the two species play an important role in controlling western flower thrips (Sanchez *et al.*, 1997).

The model used to explain the reproduction and female survivorship in relation to time and temperature described satisfactorily the variability of the experimental data. The trend of the intrinsic rate of natural increase (r_m) of *O. laevigatus* and *O. albidipennis* was also predicted satisfactorily using the thermal equation to estimate development times and the reproduction and female survivorship models. The estimated reproduction threshold for *O. albidipennis* (40.9°C) may look suspiciously low considering that r_m increased linearly from 20 to 35°C. However, the high proportion of females that did not lay eggs at 35°C (51%) justified the prediction of a reduction of reproduction above this temperature. The curvilinear shape predicted by these equations is considered to be characteristic of the relationship between activity rates of poikilothermic organisms and temperature (Mason & Mack, 1984). A similar trend has been described in *Pseudoplusia includens* (Walker) (Lepidoptera: Noctuidae) with a polynomial function that shows an increase in both fecundity and average oviposition rate from 17 to 32°C and a reduction at higher temperatures (Mason & Mack, 1984).

Modelling r_m as a function of the greenhouse temperature may be a good tool for optimizing the use of *O. laevigatus* and *O. albidipennis* in IPM programmes. The prediction of the r_m using greenhouse temperature records from five growing seasons showed how different the response of the two anthocorids could be depending on the temperature records of the year. The greenhouse environment may also be influenced by location, shape, structure and temperature regulation system. Based on the predicted population dynamics of *O. laevigatus* and *O. albidipennis* authors recommend releasing *O. laevigatus* from February to mid April and releasing *O. albidipennis* thereafter. Similar trends in population growth were estimated for releases of the two species scheduled for mid February and mid March, while the *O. albidipennis* population was estimated to grow much faster when releases were made in mid May. Use of *O. laevigatus* is also recommended at the beginning of the growing season because it is reported to prey on *F. occidentalis* at a higher rate than *O. albidipennis* (Cocuzza *et al.*, 1997b). This may result in a better control of the western flower thrips assuming the two species exhibit similar population growth during this time.

Choosing the right release time may improve the anthocorid's response and reduce the magnitude of thrips outbreaks. The ability of pollen-fed *O. laevigatus* and *O. albidipennis* to develop and reproduce successfully has been considered as an adaptation that allows for the release of predators before prey become abundant (Cocuzza *et al.*, 1997a; Vacante *et al.*, 1997). According to the data reported by Cocuzza *et al*. (1997a) and Vacante *et al*. (1997) an increase of the anthocorid populations should be expected after release if flowers are available on pepper crops. However, these expectations seem to disagree with the population dynamics observed on pepper crops over several successive years, where *Orius* spp. showed a clear prey-dependent response (Sanchez *et al.*, 1997, 2000; Sanchez, 1998). Populations remained at low levels or declined when prey were scarce and increased only when prey were available (Sanchez *et al.*, 1997, 2000; Sanchez, 1998). Therefore, the authors suggest periodical monitoring of *F. occidentalis* and release of *Orius* once the pest is present in the crop. If western flower thrips is present early in the growing season and environmental condition are favourable, outbreaks may be expected at the beginning of April. To deal with early outbreaks the authors suggest releasing 0.75 *O. laevigatus* per plant in early March. If the conditions are optimal, the population can be expected to increase sufficiently to reduce thrips numbers by the beginning of April. If the predator does not become established, another release of 0.5 *O. laevigatus* per plant in mid March is advised to deal with the period when thrips outbreaks are more likely to occur. If *O. albidipennis* does not colonize the crop naturally, a release of 0.25 individuals per plant is recommended in mid May. *Orius albidipennis* is better adapted than *O. laevigatus* to greenhouse summer conditions and it may not only keep thrips at a low level during summer time, but also contribute to the control of other arthropod pests. Use of both anthocorids is recommended, because it should considerably extend the efficacy of *Orius* predators through the entire growing season.

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