

## Biological traits and predation capacity of four *Orius* species on two prey species

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### Abstract

Laboratory trials were carried out in order to determine biological traits and predation activity of four *Orius* species - the paleartic *Orius majusculus* (Reuter), *O. laevigatus* (Fieber) and *O. niger* Wolff and the nearctic *O. insidiosus* (Say) - using *Ephestia kuehniella* (Zeller) eggs and *Frankliniella occidentalis* (Pergande) adults as prey. The intrinsic rates of natural increase ( $r_m$ ) were calculated for the four *Orius* species on the two preys and the  $r_m$  was 0.094 (on *F. occidentalis*) and 0.068 (on *E. kuehniella*) for *O. laevigatus*, 0.097 (on *F. occidentalis*) and 0.080 (on *E. kuehniella*) for *O. majusculus*, 0.116 (on *F. occidentalis*) and 0.101 (on *E. kuehniella*) for *O. insidiosus*, 0.035 (on *F. occidentalis*) and -0.003 (on *E. kuehniella*) for *O. niger*, respectively. The kill-rate ( $k_m$ ), a parameter that we designed to take into account the age-specific predation both during the nymphal and the adult stages, was calculated in order to compare the predation capacity of the *Orius* species. The  $k_m$  on the prey species *F. occidentalis* was 0.23 for *O. laevigatus*, 0.21 for *O. majusculus*, 0.25 for *O. insidiosus*, 0.19 for *O. niger*, respectively. In all species, the females that fed on *E. kuehniella* showed greater longevity and higher reproduction than those fed on *F. occidentalis*. *O. niger* was the most difficult species to rear, both during immature stages and as adults. *O. niger* showed a high preimaginal mortality, high consumption of *E. kuehniella* eggs, low predation of *F. occidentalis* adults, long development time, low fecundity and low  $r_m$  on both preys. The development time of *O. majusculus* and *O. laevigatus* was similar when feeding on *F. occidentalis*. The total consumption of *E. kuehniella* eggs was significantly higher for *O. laevigatus*. *O. majusculus* showed a higher fecundity compared to *O. laevigatus* when fed *E. kuehniella* eggs, but no differences were recorded when both species were fed *F. occidentalis* adults. Most data for the nearctic *O. insidiosus* were similar to those of *O. laevigatus* and *O. majusculus*. Performance of *O. laevigatus* was best at 26 °C. A mass-rearing method for *O. laevigatus* was developed and the main quality control parameters for this species were defined.

**Key words:** life table, predation, *Frankliniella occidentalis*, Anthocoridae, *Orius laevigatus*, *Orius niger*, *Orius majusculus*, *Orius insidiosus*, *Ephestia kuehniella*, life-history.

### Introduction

Since the accidental introduction from the USA, western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera Thripidae), has disrupted Integrated Pest Management systems developed and applied successfully for several vegetable and ornamental crops in Europe (Tommasini and Maini, 1995). Among the natural enemies of this pest, several species belonging to the genus *Orius* (Rhynchota Anthocoridae) appeared to be promising candidates for biological control (Riudavets, 1995). In Italy, wild populations of indigenous *Orius* species, *O. majusculus* (Reuter), *O. laevigatus* (Fieber) and *O. niger* Wolff, limit *F. occidentalis* outbreaks, especially during summer. The nearctic species *O. insidiosus* (Say) has been released in Europe by several natural enemy producers for control of *F. occidentalis*.

Several studies have been conducted to obtain knowledge about *Orius* species. In table 1 the main biological characteristics found in the literature are summarized for the *Orius* species subject of the present study. Similar biological characteristics for other paleartic and nearctic *Orius* species are available in the literature, but are not summarized here: *O. tristicolor* (White) (Salas-Aguilar and Ehler, 1977; Stoltz and Stern, 1978), *O. albidipennis* (Reuter) (Tawfik and Ata, 1973a; Zaki, 1989; Carnero *et al.*, 1993), *O. limbatus* Wagner (Carnero *et al.*, 1993) and *O. minutus* L. (Lichtenauer

and Sell, 1993). Studies for these species concentrated on development time and/or fecundity at different temperature regimes and when offered different types of prey. *O. tristicolor* and *O. minutus* were studied as predators of *F. occidentalis*, while the other species were fed with *Ephestia kuehniella* (Zeller) (MFM).

Until 1992, research was carried out mainly for the nearctic species *O. insidiosus* and *O. tristicolor* as predators of *F. occidentalis*. Later, several studies included paleartic species as *O. majusculus* and *O. laevigatus*. No specific studies on the biology of *O. niger* were done before this research project started. Generally, the effect of temperature on development time, fecundity and longevity were studied. Most authors agree that temperature and food play an important part in the development time and adult activity of *Orius* spp. Isehour and Yeargan (1981a), Kingsley and Harrington (1982), McCaffrey and Horsborough, (1986) and Bush *et al.* (1993) studied bionomics of *O. insidiosus*. Alauzet *et al.* (1990; 1992), Fischer *et al.* (1992), Rudolf *et al.* (1993), Alvarado *et al.* (1997) and Riudavets and Castañé (1998) worked on *O. majusculus* and only recently aspects of the biology of *O. laevigatus* were studied (Rudolf *et al.*, 1993; Tavella *et al.*, 1994; Alauzet *et al.*, 1994; Tommasini and Benuzzi, 1996; Cocuzza *et al.*, 1997a, 1997b; Alvarado *et al.*, 1997; Riudavets and Castañé, 1998; Tommasini, 2003; Tommasini and van Lenteren, 2003). Studies on the last three

**Table 1.** Earlier published data on biological characteristics of *Orius* spp. (+ ample data, +/- only few data, – no data).

<i>Orius</i> Species	Prey species	Immature development	Immature mortality	Fecundity	Longevity	Predation capacity	$r_m$	Source
<i>O. insidiosus</i>	c, d, f	+	+	–	–	–	–	1, 2, 3, 4
	f	–	–	+	–	+	–	17
	d, e	–	–	+	+	–	–	3, 4, 18
	a	+	–	+	–	–	–	9
	b	+	+/-	+	+/-	–	+	20
	b, g, n	+	–	+	+	+	–	22
<i>O. majusculus</i>	g	+	–	–	–	+	–	21
	a	+	–	–	–	–	–	9
	a	+	+	+	+	+	+	10
	a, m	+	–	–	–	+	–	8
	b	+	–	+	–	–	–	5, 7
	b	+	–	+	+	–	–	6
<i>O. laevigatus</i>	l	+	–	–	–	–	–	5
	g	+	–	–	–	+	–	21
	a	+	–	–	–	–	–	9
	a	+	+	+	+	+	+	10, 23, 25
	a*	–	–	–	–	+	–	16
	b	+	–	+	+	–	–	11, 12, 15, 16
<i>O. niger</i>	b	–	–	+	+	–	–	24
	i, j	+	–	+	+	–	–	15
	g, h, k	+	–	+	+	+/-	–	13
	g, h, k	+	–	–	–	–	–	14
	g	+	–	–	–	+	–	21
	?	–	–	–	+/-	–	–	19

Prey species: a = *F. occidentalis* (nymphs), a\* = *F. occidentalis* (adult), b = *E. kuehniella* (eggs), c = *Panonychus ulmi* (Kock), d = *Heliothis virescens* (F.), e = *H. obsoleta* (F.) (eggs), f = *Sericothrips variabilis* (Beach) (larvae, adult), g = *Aphis gossypii* Glover, h = *Spodoptera littoralis* Boisduval (eggs), i = *Tribolium confusum* Duval (paralyzed larvae), j = *Phthorimaea operculella* (Zeller) (larvae), k = *Tetranychus telarius* L., l = *Rhopalosiphum padi* (L.), m = *Tyrophagus putrescentiae* Schrank, n = *Caliothrips phaseoli* (Hood).

Sources: 1 = McCaffrey and Horsburg, 1986, 2 = Isenhour and Yeargan, 1981a, 3 = Bush *et al.*, 1993, 4 = Kiman and Yeargan, 1985, 5 = Alauzet *et al.*, 1990, 6 = Fischer *et al.*, 1992, 7 = Alauzet *et al.*, 1992, 8 = Hussein *et al.*, 1993, 9 = Castañé and Zalom, 1994, 10 = Riudavets, 1995, 11 = Alauzet *et al.*, 1994, 12 = Tavella *et al.*, 1994, 13 = Tawfik and Ata, 1973a, 14 = Tawfik and Ata, 1973b, 15 = Zaki, 1989, 16 = Vacante and Tropea Garzia, 1993, 17 = Isenhour and Yeargan, 1981b, 18 = Barber, 1936, 19 = Akramovskaya, 1978, 20 = van den Meiracker, 1994, 21 = Alvarado *et al.*, 1997, 22 = Mendes *et al.*, 2002, 23 = Cocuzza *et al.*, 1997a, 24 = Cocuzza *et al.*, 1997b, 25 = Sanchez and Lacasa, 2002.

*Orius* species as predators of *F. occidentalis* are limited (Hussein *et al.*, 1993; Riudavets *et al.*, 1993, 1995; Riudavets, 1995; Vacante and Tropea Garzia, 1993a, b; Cocuzza *et al.*, 1997a; Tommasini, 2003). No comparisons were made of the development of several *Orius* species on different prey species.

Very few data are available about the life histories of *Orius* spp. Van den Meiracker (1994), studied the life history of *O. insidiosus*, Riudavets (1995) calculated the intrinsic rate of natural increase for *O. laevigatus* and *O. majusculus* when feeding on *F. occidentalis* nymphs at 25 °C and Alauzet *et al.* (1994) studied bionomics of *O. laevigatus*.

The best available single description of the population growth potential of a species under given conditions is still the intrinsic rate of natural increase ( $r_m$ ) (Southwood, 1966). It might also be a useful parameter to compare the capacity of parasitism of parasitoids, because in parasitoids each egg laid means that a host is killed (van Lenteren, 1986b). We propose to use a new parameter to compare the intrinsic predation capacity of predators: the kill-rate ( $k_m$ ). To determine the kill-rate,

the predation capability with *ad libitum* prey is measured for all stages of the predator over its immature and adult life span. With this kill-rate, the capability of a predatory species, in this case of *Orius* species, to reduce a pest species can be estimated during one generation of the predator. For a further explanation of the kill-rate, see the material and methods section.

Information about biological characteristics, including the kill-rate, is needed also for development of mass rearing methods. Methodologies for culturing Anthocoridae, including some *Orius* species, were reported by Samsøe-Petersen *et al.* (1989), Takara and Nishida (1981), Isenhour and Yeargan (1981a), Kiman and Yeargan (1985), Alauzet *et al.* (1990), van den Meiracker and Ramakers (1991), Hussein *et al.* (1993), Frescata *et al.* (1994), Castañé and Zalom (1994), van den Meiracker (1994), Blümel (1996) and Yano (1996). With new knowledge from this study, it is expected that the mass rearing of *Orius* species can be improved.

In this paper, biological characteristics of four *Orius* species (*O. majusculus*, *O. laevigatus*, *O. niger* and *O.*

*insidiosus*) and their predation capacity of two prey species (*F. occidentalis* and *E. kuehniella* eggs), are presented. The biological parameters studied (development time, mortality, sex ratio, female lifespan, fecundity and predation of *F. occidentalis* by each *Orius* species) were used to determine the intrinsic rate of natural increase ( $r_m$ ) and the kill-rate ( $k_m$ ) of each *Orius* species. This information is, among others, very useful to compare the prey reduction capacity and needed also to develop a mass rearing.

## Materials and methods

### Rearing of predators

Separate rearings of *Orius* species were set up in a climate room at  $26 \pm 1$  °C, RH  $75 \pm 10\%$  and  $16L \div 8D$ , using the three species most frequently found in Italy on plants infested by thrips (Tommasini, 2004), and the nearctic species *O. insidiosus*. *O. majusculus* was collected in northern Italy (Emilia-Romagna region; ca.  $44^\circ$  N latitude), *O. laevigatus* and *O. niger* were collected in southern Italy (Sicily; ca.  $37^\circ$  N latitude), while *O. insidiosus* was supplied by a natural enemy producer.

Identification of the field-collected predators was carried out in the laboratory. Egg-laying females ( $> 200$ ) were isolated in a plexiglass cylinder (4 cm high, 4 cm diameter), with a fine gauze lid on the top. The offspring of each female was checked in order to find at least one male, which was then identified after dissection with keys of Péricart (1972) and Herring (1966). Then, ca. 50 newly emerged adults of the same species were put together in larger plexiglass cylinders (9 cm high, 9 cm diameter) covered with fine cotton gauze to start pilot rearings (the so-named adult unit). To prevent cannibalism, some strips of paper were added to each cylinder, and water was supplied by adding moist cotton. Frozen eggs of the flour moth *E. kuehniella*, glued on paper with Arabic gum, were used to feed both nymphs and adults. This prey was successfully used for other Anthocoridae also by Samsoe-Petersen *et al.* (1989), Alauzet *et al.* (1990; 1992), Frescata *et al.* (1994) and van den Meiracker (1994). Bean pods were used as oviposition substrates like reported by Isenhour and Yeargan (1981a), van den Meiracker and Ramakers (1991), Riudavets *et al.* (1993), Tavella *et al.* (1994) and van den Meiracker (1994). Bean pods with *Orius* eggs were removed from the adult units three times per week and were placed in a new cylinder (the so-named nymphs unit) to start the pre-imaginal rearing. Food and water were supplied up to adult emergence.

### Pre-imaginal characteristics

The experiments were carried out in a rearing chamber at  $26 \pm 1$  °C,  $75 \pm 10\%$  RH and  $16L \div 8D$  photoperiod. Three palearctic species, *O. majusculus*, *O. laevigatus* and *O. niger*, and the nearctic species *O. insidiosus* were tested. All populations were reared in the laboratory for seven to ten generations before the start of the experiments.

More than 600 eggs per *Orius* species laid into bean pods during an interval of 6 hours were isolated in petri dishes. After hatching, which was checked every 3-4 hours, several first-instar nymphs were isolated in plexiglass cylinders (4 cm high, 4 cm diameter) covered by a plastic cap with small-mesh steel wire netting (200 mesh). Nymphs were fed *ad libitum* on either of two different species of preys, *i.e.* on *E. kuehniella* frozen eggs ( $>500$  eggs per *Orius* nymph) glued onto pieces of cardboard with Arabic gum, or on *F. occidentalis* adults ( $>40$  adults per *Orius* nymph) feeding on a piece of a bean pod. Mortality from egg hatch to adult emergence, development time and predation for each instar, and sex ratio of emerged adults were recorded for both species of prey. Nymphal development was checked every 3-4 hours until the adult stage. When exuviae were found, the number of *E. kuehniella* eggs or *F. occidentalis* adults consumed were counted for 35 predators of each *Orius* species and for both prey species. The natural mortality of *E. kuehniella* eggs and *F. occidentalis* adults was estimated by keeping an equal amount of prey at the same rearing conditions without predators (20 replications per prey).

### Adult characteristics

Newly-emerged pairs of *Orius* species (*O. majusculus*, *O. laevigatus*, *O. niger* or *O. insidiosus*) were isolated in transparent plexiglass cylinders (9 cm high, 9 cm diameter), capped with a wad of fine cotton. Every two days, adults were fed *ad libitum* on frozen *E. kuehniella* eggs ( $>500$  per *Orius* pair) glued onto pieces of cardboard with Arabic gum, or on *F. occidentalis* adults ( $>80$  adults per *Orius* pair). At the same time, a bean pod was placed in each cylinder, to provide a substrate for oviposition of the predators and as food for *F. occidentalis*. Survival of *Orius* females, and the number of eggs laid were checked. Dead males were replaced with fresh ones. Starting from the day of emergence, the predation of the *Orius* pairs was calculated once a week by counting the number of prey consumed during 24 hours. The natural mortality of *E. kuehniella* eggs and of *F. occidentalis* adult was estimated by keeping an equal amount of prey at the same conditions without predators (12 replications per prey type).

### Effect of temperature on the development and fecundity of *O. laevigatus*

The main biological parameters of *O. laevigatus* were studied at several constant temperatures. The experiment was carried out by using predators reared in the laboratory for ca. 18 generations. Experimental rearings of *O. laevigatus* were set up at different constant temperatures (14, 22 and 30 °C), RH  $75 \pm 10\%$  and  $16L \div 8D$  (at 14 °C the photoperiod was set at  $12L \div 12D$ ). The egg development time, the total immature development time, the fecundity and female longevity were recorded. More than 500 eggs of *O. laevigatus* were isolated in petri dishes for each temperature regime. Eggs were laid on bean pods during a 24-hours interval. Egg-hatching and adult emergence were checked twice a day. Groups of 20 newly-hatched nymphs were isolated in transparent plexiglass

cylinders (9 cm high, 9 cm diameter) capped with a wad of fine cotton. Twice a week, predators were fed with frozen *E. kuehniella* eggs glued onto pieces of cardboard with Arabic gum. After emergence *Orius* pairs were isolated (>30 pairs per temperature regime) in smaller plexiglass cylinders (4 cm high, 4 cm diameter). Survival and oviposition of females were checked three times per week, and dead males were replaced with fresh ones. Total development time against temperature were calculated, considering also the data recorded during previous experiment at 26 °C with the same species. Furthermore, our data were combined with those of Alauzet *et al.* (1994) who studied *O. laevigatus* at a different constant temperature when fed with *E. kuehniella* eggs, to define the threshold temperature of development for each instar as well as for the total development time and pre-oviposition period.

#### Calculation of the intrinsic rate of natural increase $r_m$ and the intrinsic kill-rate $k_m$

Life table parameters were studied following the methodology explained by Southwood (1966). Age in day (including immature stages) ( $x$ ), age-specific survival (including immature mortality) ( $l_x$ ), age-specific fertility ( $m_x$ ), estimated as the expected number of female eggs produced per females alive at age  $x$ , were determined in order to calculate the net reproductive rate ( $R_0 = \sum_x l_x m_x$ ) and the intrinsic rate of natural increase  $r_m$  ( $r_m = \ln R_0/T$ ), where  $T$  is the generation time ( $T = \sum_x l_x m_x x / R_0$ ) and  $x$  the age expressed in units of time (a class unit is composed from an interval of 4 days). The kill-rate ( $k_m$ ) of the four *Orius* species when fed with *F. occidentalis ad libitum*, was calculated using the same formula of  $r_m$  but substituting the age-specific fertility ( $m_x$ ), with the age-specific predation both during the nymphal and the adult stages. Thus  $k_m = \ln K_0/T_k$ , where  $T_k$  (generation time) is the period during a generation where the predator may prey ( $T_k = \sum_x l_x K_x x / K_0$ ) and  $K_0$  is the net consumption rate ( $K_0 = \sum_x l_x K_x$ ), *i.e.* the number of preys killed ( $K_x$ ) during a generation of the predator, corrected by natural mortality.

#### Statistical analysis

Each predator, or pair of predators of the four *Orius*

species feeding on one of the two prey species, was considered as an experimental unit. The pre-imaginal mortality (expressed as % of adult emerged), the sex ratio (% of females) as well as the total development time of females and males at the different temperatures, were analysed by the chi-square test ( $p < 0.05$ ). The embryonic and post-embryonic development time for each prey species as well as at each temperature, the predation capacity on *E. kuehniella*, the pre-oviposition time and total fecundity, were compared with the Kruskal-Wallis test followed by the distribution free multiple comparison test (Dunn's procedure valid for unequal sample size). The predation capacity on *F. occidentalis* for young *Orius* instars and the adult pairs of *Orius* were compared by ANOVA and the Tukey test. The performance of the same species when fed on different prey was compared by using the Mann-Whitney U test.

## Results

### Pre-imaginal characteristics

#### Development and immature mortality

All four species completed the development on both prey species, *E. kuehniella* eggs and *F. occidentalis* adults (table 2 and 3). Diet affected the development time of all four *Orius* species: *F. occidentalis* adults as prey induced a faster development of all *Orius* species compared to *E. kuehniella* eggs as prey. *O. niger* had the longest egg development period. The other three species had similar development times. During immature development (table 2), *E. kuehniella* eggs induced a significantly higher mortality than *F. occidentalis* adults in all species, except for *O. insidiosus* where mortality with the two prey species was similar. No significant differences were found in the sex ratio for all the *Orius* species on both prey species (table 2). The development times recorded for all the pre-imaginal instars of the four *Orius* species are given in table 3. Differences among species were recorded in the total post-embryonic development time when *E. kuehniella* was used as prey: it increased from *O. insidiosus* (10.8 days) to *O. niger* (13.0 days). The same differences were recorded when the predators were fed with *F. occidentalis* adults.

**Table 2.** Pre-imaginal mortality and sex ratio at emergence of four *Orius* species on two different prey species.

Species	No. nymphs	Mortality (%)	No. Females emerged	No. Males emerged	Sex ratio (% females)
Prey: <i>Ephestia kuehniella</i> eggs					
<i>O. majusculus</i>	77	59.7	12	19	38.7 a
<i>O. laevigatus</i>	183	78.1	23	17	57.5 a
<i>O. niger</i>	189	93.7	5	7	41.7 a
<i>O. insidiosus</i>	83	37.3	25	27	48.1 a
Prey: <i>Frankliniella occidentalis</i> adults					
<i>O. majusculus</i>	84	41.7	17	32	34.7 a
<i>O. laevigatus</i>	84	46.4	25	20	55.6 a
<i>O. niger</i>	103	42.7	25	34	42.4 a
<i>O. insidiosus</i>	84	46.4	23	22	51.1 a

**Table 3.** Development time (days) of four *Orius* species on two different prey species (means±SE).

Species	Eggs	1 <sup>st</sup> instar	2 <sup>nd</sup> instar	3 <sup>rd</sup> instar	4 <sup>th</sup> instar	5 <sup>th</sup> instar	Total development
Prey: <i>Ephestia kuehniella</i> eggs							
<i>O. majusculus</i>	4.2 ± 0.02 a	2.1 ± 0.03 b	1.8 ± 0.04 a	1.6 ± 0.05 a	1.9 ± 0.05 ab	3.6 ± 0.05 ab	15.4 ± 0.11 ab
<i>O. laevigatus</i>	4.2 ± 0.02 a	2.4 ± 0.04 c	1.7 ± 0.04 ab	1.8 ± 0.03 a	2.1 ± 0.03 b	3.8 ± 0.04 b	16.0 ± 0.14 bc
<i>O. niger</i>	4.8 ± 0.12 b	2.8 ± 0.13 c	2.0 ± 0.10 b	2.0 ± 0.06 b	2.2 ± 0.11 b	3.9 ± 0.12 b	17.8 ± 0.22 c
<i>O. insidiosus</i>	4.2 ± 0.02 a	2.0 ± 0.03 a	1.6 ± 0.05 a	1.6 ± 0.03 a	2.0 ± 0.03 a	3.6 ± 0.04 a	15.0 ± 0.10 a
Prey: <i>Frankliniella occidentalis</i> adults							
<i>O. majusculus</i>	4.0 ± 0.01 a	2.1 ± 0.03 a	1.6 ± 0.03 a	1.6 ± 0.06 b	2.1 ± 0.05 c	3.7 ± 0.07 b	15.1 ± 0.11 b
<i>O. laevigatus</i>	4.1 ± 0.02 b	2.3 ± 0.04 b	1.7 ± 0.02 b	1.6 ± 0.05 b	1.9 ± 0.03 b	3.6 ± 0.07 ab	15.1 ± 0.11 b
<i>O. niger</i>	4.6 ± 0.03 c	2.6 ± 0.05 c	1.8 ± 0.04 b	1.7 ± 0.04 c	2.0 ± 0.04 b	3.8 ± 0.07 c	16.5 ± 0.12 c
<i>O. insidiosus</i>	4.1 ± 0.02 b	2.1 ± 0.05 a	1.5 ± 0.06 a	1.5 ± 0.04 a	1.5 ± 0.05 a	3.4 ± 0.04 a	14.1 ± 0.07 a

### Predation

Because natural mortality of the prey was very low, the number of spontaneously collapsed *E. kuehniella* eggs (1.6±0.11 in 24 hours; means±SE), or the natural mortality of *F. occidentalis* adults (1.7±0.35 in 24 hours; means±SE) were not subtracted from the daily predation data. The amount of prey consumed by each instar during the pre-imaginal development is reported in table 4. It shows an increase in predation rates from the first (9.6 prey eaten) to the fifth instar (34.4 preys eaten) for all species on the two prey species. Differences among the four species were found in the total predation of *E. kuehniella* egg. *O. niger* and *O. laevigatus* consumed significantly more eggs than *O. majusculus* and *O. insidiosus*. Slight differences were found in

the predation capacity on *F. occidentalis* adults. On average *O. majusculus* ate the highest number and significantly more thrips than *O. insidiosus* and *O. niger*.

### Adult characteristics

#### Fecundity and longevity

Females of the four species mate several times during their reproductive life. The average longevity, pre-ovipositional period and the total oviposition per female of the four *Orius* species fed on *E. kuehniella* eggs or on *F. occidentalis* adults is presented in tables 5 and 6. In all four *Orius* species, the females fed on *E. kuehniella* lived significantly longer and showed higher rates of total oviposition than *Orius* females fed on *F. occidentalis*.

**Table 4.** Pre-imaginal predation capacity expressed as number of prey eaten during the instars of four *Orius* species on two different prey species (means±SE).

Species	1 <sup>st</sup> instar	2 <sup>nd</sup> instar	3 <sup>rd</sup> instar	4 <sup>th</sup> instar	5 <sup>th</sup> instar	Total immature predation
Prey: <i>Ephestia kuehniella</i> eggs						
<i>O. majusculus</i>	7.7 ± 0.3 a	13.4 ± 0.8 a	13.5 ± 0.7 a	23.4 ± 0.9 a	40.7 ± 1.6 a	99.4 ± 2.7 a
<i>O. laevigatus</i>	19.4 ± 1.0 b	23.9 ± 1.3 b	30.6 ± 1.8 b	35.2 ± 1.8 b	65.3 ± 4.1 b	174.6 ± 8.6 b
<i>O. niger</i>	21.2 ± 1.5 b	30.9 ± 3.7 b	38.1 ± 2.4 b	27.9 ± 2.9 a	66.9 ± 3.9 b	183.5 ± 8.0 b
<i>O. insidiosus</i>	9.1 ± 0.3 a	12.7 ± 0.6 a	14.3 ± 0.7 a	22.6 ± 1.0 a	37.0 ± 2.3 a	94.3 ± 3.5 a
Prey: <i>Frankliniella occidentalis</i> adults						
<i>O. majusculus</i>	5.2 ± 0.3 bc	5.7 ± 0.2 ab	8.4 ± 0.3 b	8.8 ± 0.3 b	17.5 ± 1.1 a	45.7 ± 1.1 b
<i>O. laevigatus</i>	5.4 ± 0.2 c	7.7 ± 0.3 c	7.6 ± 0.4 ab	6.3 ± 0.4 a	15.6 ± 0.7 a	42.6 ± 0.9 ab
<i>O. niger</i>	4.3 ± 0.4 ab	6.0 ± 0.3 b	8.6 ± 0.2 b	6.8 ± 0.5 a	15.4 ± 0.8 a	41.1 ± 1.5 a
<i>O. insidiosus</i>	4.1 ± 0.2 a	4.9 ± 0.3 a	7.0 ± 0.4 a	6.7 ± 0.4 a	16.4 ± 0.04 a	39.2 ± 1.0 a

**Table 5.** Pre-oviposition period, total fecundity and longevity (Means ± SD) of four *Orius* species reared at 26 °C when fed with *E. kuehniella* eggs.

Species	No.	Pre-oviposition period (days)	Total fecundity (eggs/female)	Longevity of females (days)
<i>O. majusculus</i>	63	4.6 ± 3.9 ab	174.0 ± 106.0 c	47.0 ± 21.8 b
<i>O. laevigatus</i>	64	3.2 ± 1.8 a	118.6 ± 75.1 b	38.6 ± 18.5 a
<i>O. niger</i>	29	6.7 ± 4.4 b	54.1 ± 59.8 a	50.0 ± 18.2 b
<i>O. insidiosus</i>	65	3.7 ± 6.2 a	144.3 ± 76.8 bc	42.3 ± 14.0 ab

**Table 6.** Pre-oviposition period, total fecundity and longevity (Means  $\pm$  SD) of four *Orius* species reared at 26 °C when fed with *F. occidentalis* adults.

Species	No.	Pre-oviposition period (days)	Total fecundity (eggs/female)	Longevity of females (days)	Longevity of males (days)
<i>O. majusculus</i>	36	2.8 $\pm$ 2.7 a	87.1 $\pm$ 50.6 b	19.7 $\pm$ 7.7 a	16.6 $\pm$ 6.9 a
<i>O. laevigatus</i>	42	2.7 $\pm$ 1.1 a	55.6 $\pm$ 50.4 b	18.0 $\pm$ 9.7 a	18.9 $\pm$ 12.1 a
<i>O. niger</i>	36	6.8 $\pm$ 5.2 b	16.2 $\pm$ 26.1 a	18.5 $\pm$ 11.3 a	18.6 $\pm$ 11.0 a
<i>O. insidiosus</i>	46	2.5 $\pm$ 1.3 a	65.7 $\pm$ 56.8 b	17.1 $\pm$ 8.5 a	20.1 $\pm$ 12.8 a

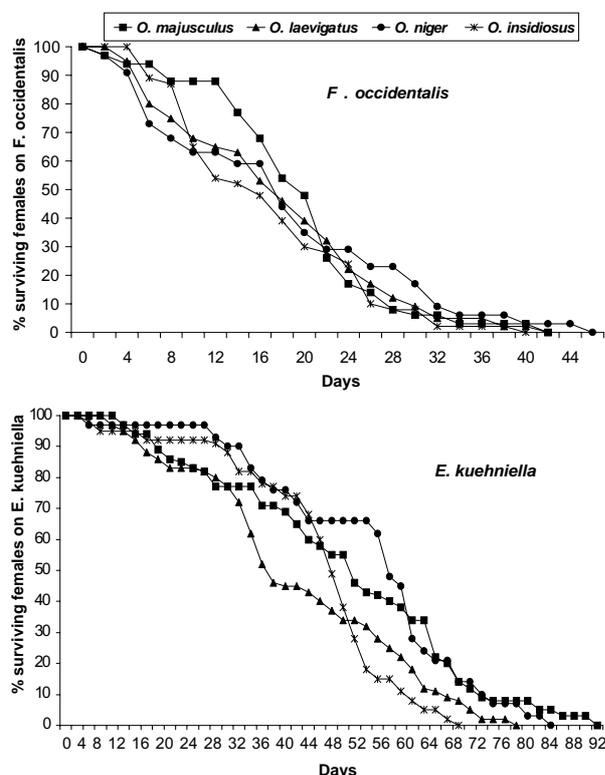
When predators were reared on *E. kuehniella* eggs, the pre-oviposition period was longer than when reared on *F. occidentalis*. The difference was largest for *O. majusculus*, which showed a delay of about 2 days (tables 5 and 6). *O. niger* showed the longest pre-oviposition period (6.8 days) on both prey species. No differences in pre-oviposition period were found among the other three species.

*O. majusculus* laid the highest number of eggs when fed with *E. kuehniella* eggs, but it was not significantly different from *O. insidiosus*. *O. insidiosus* did not show difference in oviposition activity compared to *O. laevigatus* on both prey species. *O. niger* laid the lowest number of eggs, both with *E. kuehniella* and *F. occidentalis* as prey. Among the three species *O. majusculus*, *O. laevigatus* and *O. insidiosus*, total fecundity was similar when thrips were used as prey (table 6).

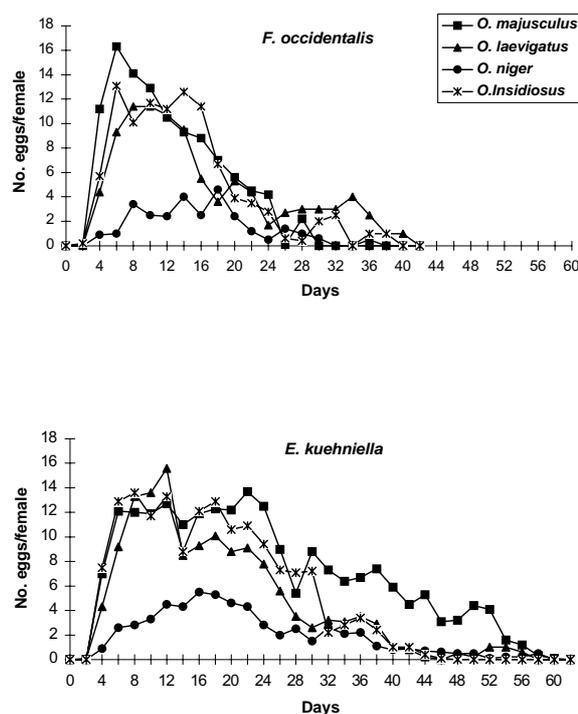
The age-specific survival for each species is shown in figure 1. Sixty percent of the females survived till the 28th day after emergence. Maximum survival was 90 days for *O. majusculus* on *E. kuehniella* eggs. Among the species fed on the same prey, significant differences in longevity were found among the species with *E.*

*kuehniella* as prey, but not with *F. occidentalis* as prey (tables 5 and 6). Different life spans were recorded for each species when fed with different prey. The highest longevity was recorded for both *O. majusculus* and *O. niger* when fed with *E. kuehniella* eggs. With *F. occidentalis* as prey no differences in longevity were found. The longevity of males was recorded for the four *Orius* species with *F. occidentalis* as prey, and no differences were found among the species (Kruskal Wallis,  $P > 0.05$ ). Only the females of *O. majusculus* lived longer than males. No difference was recorded in male and female longevity of *O. laevigatus* and *O. niger*. The males of *O. insidiosus* lived longer than the females.

Oviposition patterns of *Orius* females are presented in figure 2. Females usually began to oviposit between 2-5 days after emergence, although sporadic cases of earlier oviposition were found. *O. majusculus*, *O. laevigatus* and *O. insidiosus* showed a high oviposition rate with both prey species. Oviposition rates in females fed on *F. occidentalis* started to decline ca.10 days earlier than females fed on *E. kuehniella* (day 16 and day 26 respectively). Differences were less marked in *O. niger*, because of its overall lower oviposition.



**Figure 1.** Longevity of four *Orius* species fed on adults of *Frankliniella occidentalis* or *Ephestia kuehniella* eggs.



**Figure 2.** Oviposition of four *Orius* species fed on adults of *Frankliniella occidentalis* or *Ephestia kuehniella* eggs.

**Table 7.** Predation by pairs of four *Orius* species fed on two different prey species. Different letters show significant differences between the data of the same day ( $P < 0.05$ ); Kruskal-Wallis test, followed by distribution-free multiple comparison; Dunn's procedure valid for unequal sample size (Mean  $\pm$  SE).

Species	Prey: <i>Frankliniella occidentalis</i>								
	1 <sup>st</sup> day	8 <sup>th</sup> day	16 <sup>th</sup> day	24 <sup>th</sup> day	8 <sup>th</sup> day	16 <sup>th</sup> day	24 <sup>th</sup> day	32 <sup>nd</sup> day	
<i>O. majusculus</i>	21.6 $\pm$ 2.3 a	20.3 $\pm$ 1.8 a	23.3 $\pm$ 2.6 a	26.4 $\pm$ 5.6 a	21.9 $\pm$ 0.9 a	81.4 $\pm$ 3.7 a	57.4 $\pm$ 4.7 a	49.9 $\pm$ 3.7 a	57.6 $\pm$ 4.2 a
<i>O. laevigatus</i>	27.6 $\pm$ 3.0 a	22.7 $\pm$ 2.4 a	27.8 $\pm$ 2.3 a	20.9 $\pm$ 3.0 a	33.3 $\pm$ 1.4 b	75.3 $\pm$ 7.0 a	59.8 $\pm$ 5.0 a	41.2 $\pm$ 3.6 a	54.8 $\pm$ 2.5 a
<i>O. niger</i>	24.5 $\pm$ 2.5 a	25.0 $\pm$ 1.7 a	21.2 $\pm$ 0.9 a	17.0 $\pm$ 2.3 a	22.3 $\pm$ 1.1 a	76.6 $\pm$ 9.3 a	56.8 $\pm$ 6.2 a	52.2 $\pm$ 2.8 a	48.4 $\pm$ 2.7 a
<i>O. insidiosus</i>	21.7 $\pm$ 2.4 a	29.8 $\pm$ 3.1 a	25.3 $\pm$ 1.9 a	20.0 $\pm$ 1.9 a	24.2 $\pm$ 1.3 a	88.6 $\pm$ 7.6 a	61.7 $\pm$ 5.2 a	49.6 $\pm$ 2.0 a	54.1 $\pm$ 4.5 a
Species	Prey: <i>Ephestia kuehniella</i>								
	1 <sup>st</sup> day	8 <sup>th</sup> day	16 <sup>th</sup> day	24 <sup>th</sup> day	32 <sup>nd</sup> day	40 <sup>th</sup> day	48 <sup>th</sup> day	56 <sup>th</sup> day	
<i>O. majusculus</i>	21.9 $\pm$ 0.9 a	81.4 $\pm$ 3.7 a	57.4 $\pm$ 4.7 a	49.9 $\pm$ 3.7 a	57.6 $\pm$ 4.2 a	47.8 $\pm$ 1.9 ab	58.8 $\pm$ 2.2 a	55.8 $\pm$ 2.4 b	
<i>O. laevigatus</i>	33.3 $\pm$ 1.4 b	75.3 $\pm$ 7.0 a	59.8 $\pm$ 5.0 a	41.2 $\pm$ 3.6 a	54.8 $\pm$ 2.5 a	44.6 $\pm$ 1.3 ab	55.2 $\pm$ 2.0 a	57.6 $\pm$ 2.9 b	
<i>O. niger</i>	22.3 $\pm$ 1.1 a	76.6 $\pm$ 9.3 a	56.8 $\pm$ 6.2 a	52.2 $\pm$ 2.8 a	48.4 $\pm$ 2.7 a	55.9 $\pm$ 3.3 b	53.9 $\pm$ 2.3 a	45.1 $\pm$ 1.9 a	
<i>O. insidiosus</i>	24.2 $\pm$ 1.3 a	88.6 $\pm$ 7.6 a	61.7 $\pm$ 5.2 a	49.6 $\pm$ 2.0 a	54.1 $\pm$ 4.5 a	40.6 $\pm$ 1.9 a	51.8 $\pm$ 3.5 a	52.4 $\pm$ 1.5 ab	

### Predation

The predation per *Orius* pair during 24 hours, which was checked at 8 day intervals, is shown in table 7. Significant differences in predation among the four species were registered only at the beginning and the end of life of the predators when fed on *E. kuehniella*. No differences in predation were found with *F. occidentalis* as prey. All the predators ate a larger number of *E. kuehniella* eggs than *F. occidentalis* adults. It should be realised, however, that *E. kuehniella* eggs are smaller than *F. occidentalis* adults, so one *F. occidentalis* adult provides more food than one *E. kuehniella* egg. On average, the daily predation of the *Orius* species was 25 eggs of *E. kuehniella* and 22 adults of *F. occidentalis*.

### Life tables

The life tables of the four *Orius* species are shown in table 8 and 9. The intrinsic rate of natural increase ( $r_m$ ) of all the predators was higher when they were fed *F. occidentalis* adults than *E. kuehniella* eggs (table 8). The type of prey has a strong influence on the  $r_m$ , which was expected as these differences were also observed for development time, fecundity and longevity of the four *Orius* species. *O. niger* showed the lowest rate of natural increase ( $r_m$ ), as well the lowest net reproductive rate ( $R_0$ ) of the *Orius* species for both types of prey. The highest  $r_m$  was found for *O. insidiosus*. *O. insidiosus* showed a  $R_0$  value three times higher than *O. laevigatus* and almost double of that of *O. majusculus* when the predators were fed with *E. kuehniella*. *O. majusculus* and *O. laevigatus* fed with *F. occidentalis* showed a similar  $r_m$  and  $R_0$ . Excluding *O. niger*, the other three *Orius* species showed a lower difference in the  $R_0$  when they were fed with *F. occidentalis* compared to *E. kuehniella*.

Kill-rate ( $k_m$ ) is a parameter that take into account the age-specific predation both during the nymphal and the adult stages. It was calculated in order to compare the predation capacity of the *Orius* species. The kill-rates ( $k_m$ ) of the four *Orius* species fed with *F. occidentalis* were from highest to lowest: 0.25 for *O. insidiosus*, 0.23 for *O. laevigatus*, 0.21 for *O. majusculus* and 0.19 for *O. niger*. The values of  $k_m$  are generally proportional to the net predation rates ( $K_0$ ) and inverse to the generation time ( $T_k$ ).

**Table 8.** Generation time (T), net reproductive rate ( $R_0$ ) and intrinsic rate of natural increase ( $r_m$ ) of four *Orius* species reared at 26 °C on two preys (MFM = *E. kuehniella* eggs; WFT = *F. occidentalis* adults).

Species	Prey	$R_0$	T	$r_m = \ln R_0/T$
<i>O. majusculus</i>	WFT	12.5	26.0	0.097
<i>O. majusculus</i>	MFM	18.4	36.4	0.080
<i>O. laevigatus</i>	WFT	12.7	26.9	0.094
<i>O. laevigatus</i>	MFM	10.1	34.0	0.068
<i>O. niger</i>	WFT	3.0	30.8	0.035
<i>O. niger</i>	MFM	0.9	38.7	-0.003
<i>O. insidiosus</i>	WFT	17.9	24.9	0.116
<i>O. insidiosus</i>	MFM	30.1	33.6	0.101

**Table 9.** Predation period ( $T_k$ ), net predation rate ( $K_0$ ) and kill-rate ( $k_m$ ) of four *Orius* species reared at 26 °C on *F. occidentalis* adults.

Species	$K_0$	$T_k$	$k_m = \ln K_0/T_k$
<i>O. laevigatus</i>	68.8	18.3	0.23
<i>O. majusculus</i>	62.9	19.9	0.21
<i>O. niger</i>	59.4	21.0	0.19
<i>O. insidiosus</i>	76.5	17.2	0.25

### Effect of the temperature on the development and fecundity of *O. laevigatus*

There were two reasons to carry out this experiment only with *O. laevigatus*. First, the *Orius* species most frequently found in the Mediterranean area were *O. laevigatus* and *O. niger* (Tommasini, 2004), but *O. niger* showed a very low intrinsic rate of increase. Second, a southern European strain of *O. laevigatus* does not go into diapause (Tommasini and van Lenteren, 2003) and it is, therefore, a better candidate for control of *F. occidentalis* in winter than the other *Orius* species.

### Development time

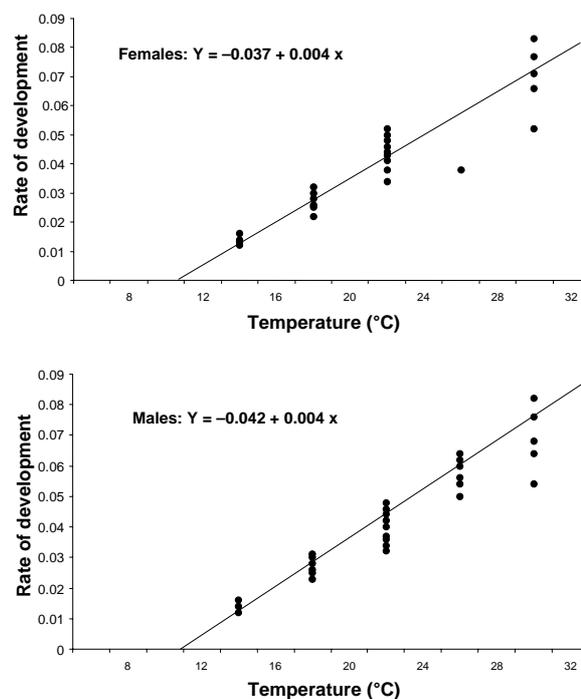
The equations of the rate of development against temperature were calculated with the data of Alauzet *et al.* (1994). It was assumed that the mean developmental rates, *i.e.* the reciprocal of development times, were linearly related to the temperature between 15 and 30 °C (table 10 and figure 3). The threshold value for overall development was 11.3 °C, which is higher than that of *F. occidentalis* (9.4 °C - Gaum *et al.*, 1994). The slope of the regression of *O. laevigatus* and for *F. occidentalis* appear quite similar. The instars L1, L2, L3 and L4 seem more sensitive to temperature than the egg stage and L5. Their rates of development accelerated faster with the increase of the temperature than the egg stage and L5. The egg stage was least sensitive, showing the lowest threshold temperature (9.2 °C). The highest threshold temperature was found during the pre-ovipositional period (14.2 °C).

The egg development periods and the total development times of *O. laevigatus* are given in table 11. Differences in both egg and total development time were found at the three temperatures, with an inverse relation between development time and temperature. No differences were found in the development times of males and females at the same temperature. Sex ratios were the same at different temperatures. Immature mortality was influenced by temperature, mortality was lowest at 22 °C (table 11). Table 12 provides the rate of development of *O. laevigatus* at 5 temperatures. Here, the threshold temperature (9.8 °C) was lower than the threshold temperature calculated from the data of Alauzet *et al.* (1994) (11.3 °C).

### Adult activity

The shortest pre-oviposition period was recorded at 30 °C and the longest one at 14 °C (table 13). At 14 °C

only 30% of the females laid eggs, and only 1 egg per female was laid. The highest fecundity (172.8 eggs/female) and percentage of egg-laying females (94.6%) was recorded at 22 °C. The percentage of egg-laying females at 30 °C was lower, but not significant, than that at 22 °C. Table 13 also provides the female's longevity at the three temperatures. The highest longevity was observed at 14 °C, where few females lived more than 100 days and one female even lived 214 days.



**Figure 3.** Rate of total development time of females and males of *O. laevigatus* respectively (Alauzet *et al.*, 1994).

**Table 10.** Parameter values for rate of development ( $y = a + bx$ , and  $y = 1/\text{day}$ ) of *O. laevigatus* reared on *E. kuehniella* (based on data of Alauzet *et al.*, 1994).

Stage	A	b	R <sup>2</sup>	T <sub>0</sub> (°C)
Egg	-0.1306	0.0142	0.99	9.2
L1	-0.2737	0.0255	0.99	10.7
L2	-0.5081	0.0425	0.93	12.0
L3	-0.5277	0.0444	0.98	12.0
L4	-0.2842	0.0288	0.97	9.9
L5	-0.2152	0.0184	0.97	11.7
Total development	-0.0619	0.0055	0.99	11.3
Pre-oviposition time	-0.3744	0.0264	0.93	14.2

**Table 11.** Development time, sex ratio and percentage of emergence of *O. laevigatus* at different temperatures (Means ± SE) when reared on *E. kuehniella* eggs.

Temp. (°C)	No. eggs	Egg development time (days)	Nymphal development time (days)	Total development time females (days)	Total development time males (days)	Immature mortality (%)	Sex ratio (% females)
14	1101	15.8 ± 0.2 c	59.4 ± 5.0 c	75.2 ± 5.1 c	76.7 ± 5.0 c	93.8	56.6
22	1248	5.3 ± 0.5 b	15.4 ± 2.3 b	20.7 ± 2.2 b	20.7 ± 2.2 b	52.2	51.1
30	1328	2.9 ± 1.0 a	10.4 ± 1.5 a	13.3 ± 1.5 a	12.8 ± 1.3 a	85.6	58.6

**Table 12.** Rate of development of males and females (Means  $\pm$  SD) of *O. laevigatus* reared at different temperatures on *E. kuehniella* eggs (data at 18 °C determined by Tommasini and van Lenteren, 2003).

Temperature (°C)	No. of eggs	Egg stage	Nymphal stage	Total rate of development
14	66	0.063 $\pm$ 0.004	0.017 $\pm$ 0.001	0.013 $\pm$ 0.001
18	60	–	–	0.026 $\pm$ 0.002
22	588	0.190 $\pm$ 0.015	0.066 $\pm$ 0.010	0.049 $\pm$ 0.005
26	40	0.239 $\pm$ 0.008	0.085 $\pm$ 0.006	0.063 $\pm$ 0.003
30	111	0.344 $\pm$ 0.041	0.100 $\pm$ 0.013	0.076 $\pm$ 0.007
$T_0$ (°C)		11,1	8,8	9,8
$R^2$		0.90	0.77	0.88
$y = a + bx$		$y = -0.20 + 0.02x$	$y = -0.04 + 0.01x$	$y = -0.04 + 0.01x$
P		<0.001	<0.001	<0.001

**Table 13.** Pre-oviposition period, fecundity, longevity and percentage of egg-laying females of *O. laevigatus* at different temperatures (Means  $\pm$  SD) reared on *E. kuehniella* frozen eggs.

Temperature (°C)	No.	Pre-oviposition period (days)	Total fecundity (eggs/female)	Egg-laying females (%)	Female longevity (days)
14	26	53.3 $\pm$ 39.7 c	1.0 $\pm$ 2.2 a	30.0	75.6 $\pm$ 53.4 b
22	33	8.9 $\pm$ 8.3 b	172.8 $\pm$ 107.5 c	94.6	62.2 $\pm$ 29.2 b
30	41	2.9 $\pm$ 6.0 a	77.0 $\pm$ 66.9 b	80.4	18.0 $\pm$ 10.1 a

In figure 4, the fecundity of *O. laevigatus* reared at three different constant temperatures is shown. At 30 °C 80% of females laid eggs after 4 days from emergence. At 22 °C 80% of females laid eggs after 16 days from emergence, while at 14 °C oviposition remained low as well as the percentage of egg-laying females. At 14 °C the photoperiod was 12L:12D and this photoperiod may have strongly reduced the fecundity (Tommasini and van Lenteren, 2003).

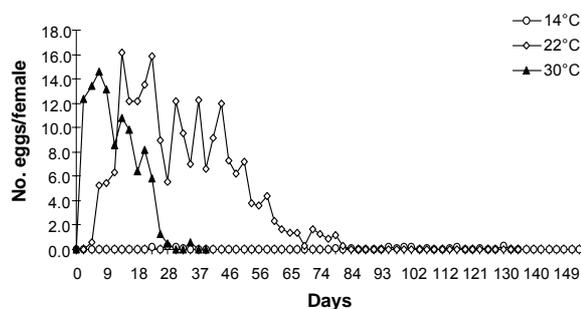
In figure 5 the survival of females at different temperatures is shown.

## Discussion

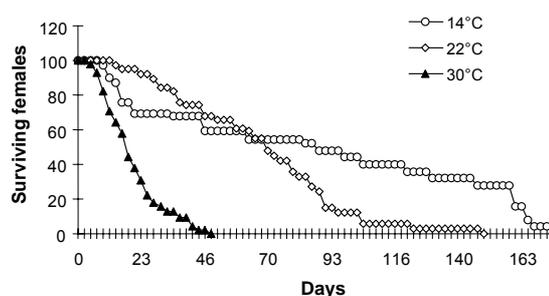
### Pre-imaginal characteristics

This study showed that the type of prey can strongly influence the rate of development and mortality of *Orius* species. *F. occidentalis* adults as food source resulted in a lower pre-imaginal mortality than *E. kuehniella* eggs for the European *Orius* species. Kiman and Yeargan (1985) found differences in the mortality during development time of *O. insidiosus* with different prey, and, contrary to our results, thrips was the poorest food among the types of prey tested. The present data on the development time of *O. insidiosus* are similar to those recorded by Kiman and Yeargan (1985) (15.8 days), who reared this species at 24 °C on *Sericothrips variabilis* (Beach). They are also similar to data of McCaffrey and Horsburgh (1986) who reared *O. insidiosus* on *Panonychus ulmi* (Koch) at 23 and 29 °C (18.8 and 9.5 days, with an interpolated average of 14.2 days at a temperature of 26 °C). *O. insidiosus* showed a longer development time when fed with eggs of *Heliothis vi-*

*rescens* (Fabr.) at 24 and 28 °C, with 20.0 and 12.7 days, respectively (Isenhour and Yeargan, 1981a). Bush *et al.* (1993) and Kiman and Yeargan (1985) recorded a shorter development time of *O. insidiosus* when fed on *H. virescens* eggs (11.1 days at 25 °C and 13.4 days at 24 °C respectively). Only van den Meiracker (1994)



**Figure 4.** Age-dependent fecundity of *Orius laevigatus* reared at three different constant temperatures.



**Figure 5.** Survival of *Orius laevigatus* females reared at three different constant temperatures and fed with *Ephestia kuehniella* eggs.

studied *O. insidiosus* fed with *E. kuehniella* eggs at 25 °C and he found a decrease in the nymphal development time of 3.6 and 4.9 days in females and males respectively, when he reared this species for 3 years in the laboratory. However, the data of van den Meiracker (1994) show a longer nymphal development time (17.2 days) than that found in the present study where we fed *O. insidiosus* with the same prey. When *F. occidentalis* nymphs were provided as prey *O. insidiosus* showed a faster development time (9.8 days at 25 °C) (Castañé and Zalom, 1994) than in our experiment.

The development time of *O. laevigatus* on *E. kuehniella* eggs was studied at a variable temperature between 24 and 28 °C by Zaki (1989), at 25 °C by Alauzet *et al.* (1994) and at 4 fluctuating thermoperiods by Tommasini and Benuzzi (1996). The nymphal development time was 14.8 (Zaki, 1989) and 13.1 days (Alauzet *et al.*, 1994) respectively at 24-28 °C and 25 °C, slightly longer than our result at 26 °C. Similar development time data were recorded by Tavella *et al.* (1994) (10.6 days) at 25 °C. On other prey, *O. laevigatus* showed a longer nymphal period of 13 and 16 days compared with *E. kuehniella* eggs as food (Tawfik and Ata, 1973a, b; Zaki, 1989). Riudavets (1995) studied the development time of *O. laevigatus* and *O. majusculus* at 25 °C when fed with nymphs of *F. occidentalis* and reported a slightly longer development for both predators (17.5 and 16.7 days respectively) in comparison with our data.

Husseini *et al.* (1993) found that *O. majusculus* completed its development in 15.2 days at 25.5 °C, similarly to our results when *F. occidentalis* is used as prey. On *E. kuehniella* eggs, the development of *O. majusculus* was studied at 25 °C also by Fischer *et al.* (1992) and Alauzet *et al.* (1990), who both reported a similar development period (ca. 15 days), although Alauzet *et al.* (1992) recorded a much longer development time (21.3 days) at 25 °C.

All species completed their development when fed with *F. occidentalis* adults. *O. majusculus* consumed significantly more thrips than *O. insidiosus* and *O. niger*. Our data support the findings of Riudavets (1995) who showed that *O. majusculus* and *O. laevigatus* can complete their development when fed only with *F. occidentalis* nymphs (total consumption rates of 62.2 and 54.1 respectively). The higher amount of prey killed recorded by Riudavets (1995) in comparison with our data can be explained by both the different stage of the prey offered and the greater difficulty for *Orius* species to catch adults than nymphs (Salas-Aguillar and Ehler, 1977).

Vacante and Tropea Garzia (1993) recorded that the last instar of *O. laevigatus* consumed a similar amount of nymphs or adults at 20 °C (11.0 nymphs and 11.8 adults), but large differences have been recorded for consumption rate in the previous instars. Isenhour and Yeargan (1981b) recorded that *O. insidiosus* shows strong differences in the predation of adults or nymphs of *S. variabilis*, mostly during the young instars of the predator (4.4 larvae vs. 1.9 adult for the first instar; 10.3 larvae vs. 5.3 adults in the third instar and 14.0 larvae vs. 10.8 adults in the fifth instar). According to Husseini

*et al.* (1993), *O. majusculus* showed no difference in the development time when fed with *F. occidentalis* adults (15.4±0.1 days) or with *F. occidentalis* nymphs (15.2±1.2 days).

In conclusion, *Orius* nymphs can complete their development on both *E. kuehniella* eggs and thrips, although the prey species and stage do influence *Orius* mortality and development time.

#### Adult characteristics

Pre-oviposition time, longevity and fecundity of the four *Orius* species are strongly influenced by the prey. This was earlier reported by other authors (Zaki, 1989; Tawfik and Ata, 1973a; Kiman and Yeargan, 1985; Alauzet *et al.*, 1990; Bush *et al.*, 1993).

*Orius* females showed better performance when fed with *E. kuehniella* eggs than with *F. occidentalis* adults, while mortality of juvenile *Orius* instars was lower when feeding on *F. occidentalis*. Pre-oviposition periods similar to our findings were recorded by Riudavets (1995) for both *O. majusculus* (3.8 days) and *O. laevigatus* (3.3 days) with *F. occidentalis* nymphs as food. *O. majusculus* showed the highest fecundity when fed with *E. kuehniella* eggs. This agrees with other authors who, on the same prey, recorded 184.7 eggs/female with ivy as oviposition substrate (Alauzet *et al.*, 1990) and 236.9 eggs on geranium leaves (Alauzet *et al.*, 1992). Our data on fecundity are similar to those found from Riudavets (1995) (176.6 eggs/female) who fed *O. majusculus* on *F. occidentalis* nymphs. Fischer *et al.* (1992) found a higher fecundity on *E. kuehniella* eggs (328.1 eggs/female).

Tavella *et al.* (1994) results on the fecundity of *O. laevigatus* are similar to ours when reared on *E. kuehniella* eggs (104.6 eggs/female). Others found higher fecundities when *O. laevigatus* was reared on *E. kuehniella* (Zaki, 1989), 160 eggs/female; Alauzet *et al.* (1994), 158 eggs/female; Cocuzza *et al.* (1997b), 183.7 eggs/female; Vacante and Tropea Garzia (1993), 141 eggs/female). Riudavets (1995) also recorded a higher fecundity (164 eggs/female) when *O. laevigatus* was reared on *F. occidentalis* nymphs. Both *O. laevigatus* and *O. majusculus* fed with *F. occidentalis* nymphs lived longer (45.1 and 46.1 respectively) (Riudavets, 1995) than fed with *F. occidentalis* adults, 18.5 and 18.2 days respectively.

Few data are available about the fecundity of *O. insidiosus* on the same two prey species as we used. Castañé and Zalom (1994) recorded 75.6 eggs/female with *F. occidentalis* nymphs. Kiman and Yeargan (1985) recorded 20.3 eggs/female when fed with *S. variabilis* and 103.1 eggs/female when fed with *H. virescens*. Bush *et al.* (1993) found 121.1 eggs/female when fed with *H. virescens* eggs. Barber (1936) counted 114 eggs/female with *H. obsolate* (F.) eggs as prey and Isenhour and Yeargan (1981b) found 106.4 eggs/female using *S. variabilis* (1st instar larvae) as prey.

Similar to our findings with *E. kuehniella* eggs as prey, Alauzet *et al.* (1994) found that *O. laevigatus* laid 80% of the total amount of eggs during the initial 16 days of adult life at 30 °C. Also Riudavets (1995), who reared *O. laevigatus* and *O. majusculus* on *F. occiden-*

*talis* nymphs at 25 °C recorded most egg-laying from the 7th to the 28th day. Castañé and Zalom (1994) found most oviposition from the 3rd to the 17th day for *O. insidiosus*.

Fisher *et al.* (1992) recorded a high longevity (52 days) for *O. majusculus* reared at 25 °C. For *O. laevigatus*, Tavella *et al.* (1994) observed a shorter longevity (23 days) when reared under similar conditions, while Cocuzza *et al.* (1997b) found a female's longevity (41.9 days) similar to that we recorded when predator is reared on *E. kuehniella* eggs. Zaki (1989) reported a longevity of 34.5 days, Alauzet *et al.* (1994) 34 days, while Vacante and Tropea Garzia (1993) found 40.5 days which is similar to our data. A shorter lifespan of *O. insidiosus* was recorded by Kiman and Yeargan (1985) (14.3 days) feeding the predators on the thrips *S. variabilis*. According to Tawfik and Ata (1973a) and Zaki (1989), the females of *O. laevigatus* live longer than males (32.3 and 9.9 days for females and males respectively on *A. gossypii*, 18.2 and 10.5 days on *S. littoralis* eggs, and 34.5 and 29.5 days on *E. kuehniella* eggs). As described in the previous paragraph, different results were recorded in the present study for all the four *Orius* species tested when *F. occidentalis* was used as prey.

Temperature affects the development time and lifespan of *Orius* spp. and particularly of *O. laevigatus*, which was also recorded by Alauzet *et al.* (1994), who studied *O. laevigatus* at 15, 20, 25 and 30 °C. At 30 °C, development of *O. laevigatus* was fast, but its lifespan was short and fecundity lower. At temperatures of a few degrees lower the species showed its best performance. For 18, 25 and 32 °C, Tavella *et al.* (1994) arrived at the same conclusions, although they recorded a lower fecundity (53.2 eggs/female at 32 °C) and a longer pre-oviposition period (3.8 days at 32 °C) than we did. They found a lower mortality during the pre-imaginal instars, probably due to the different methods used. Similar results were observed by Sanchez and Lacasa (2002), who studied *O. laevigatus* and *O. albidipennis* at 4 temperatures (20, 25, 30 and 35 °C). They used non-linear models to explain reproduction and female survivorship in relation to temperature. For *O. laevigatus* they found the lower thermal development threshold at 11.3 °C, while the upper reproductive threshold was estimated at 35.5 °C.

The life-history characteristics of a natural enemy in comparison with that of the pest, are important ecological aspects to be considered in the evaluation of a potential natural enemy for biological control (van Len-

teren, 1986b). Our data on four *Orius* species can provide a general basis for such a comparison with the life history of *F. occidentalis* (table 14). These data were used to define quality control parameters, mass rearing of *Orius*, the kill-rates of predators and to achieve information for biological control of thrips pest species.

*O. niger* was unable to develop and reproduce efficiently on *F. occidentalis*, and, in addition, the rearing of *O. niger* on the factitious prey *E. kuehniella* was not successful. The three other *Orius* species showed a net reproductive rate ( $R_0$ ) higher than *F. occidentalis* reared on bean leaves and cucumber, with the exclusion of *O. laevigatus* reared on *E. kuehniella*. Van den Meiracker (1994) followed the changes in the intrinsic rate of natural increase and the net reproductive rate in a population of *O. insidiosus* reared at 25 °C when fed with *E. kuehniella* eggs over several years. The intrinsic rate of natural increase ( $r_m$ ) increased over time mainly due to the decrease of the development time (0.131/day after ca. 1 year from field collection and 0.169/day after 3 years). The  $R_0$  also decreased (86.3 and 73.0, after 1 and 3 years, respectively). Van den Meiracker's values for  $R_0$  and  $r_m$  were higher than those we recorded for the same species, but van den Meiracker reared *O. insidiosus* under different conditions and used a different method to calculate  $r_m$  (the Sekita method). The intrinsic rates of natural increase of *O. laevigatus* and *O. majusculus* given by Riudavets and Castañé (1998) were higher than the data found in the present study, but also in this case the formula used was different (presumably they did not consider pre-imaginal mortality). Also Cocuzza *et al.*, (1997a) found a higher  $r_m$  (0.105) for *O. laevigatus* reared on *F. occidentalis* at 25 °C than we did, and they showed that the  $r_m$  was decreasing when temperature increased or decreased ( $r_m = 0.051$  and 0.0099 at 35 °C and 15 °C, respectively). An important conclusion is that *Orius* spp. apparently change their performance over time dependent of environmental condition.

For predators, the intrinsic rate of natural increase ( $r_m$ ) gives information about the speed of predator population development only. It does not tell how much prey they kill. This is quite different in parasitoids, where the  $r_m$  both provides information about the growth rate of the parasitoid population as well as its capability to reduce the pest population, because for each parasitoid egg laid, generally one pest insect is killed (van Lenteren, 1988). Janssen and Sabelis (1992) tried to find a way to compare intrinsic rate of natural increase of

**Table 14.** Generation time,  $R_0$  and  $r_m$  of *F. occidentalis* reared at 25 °C on different crops.

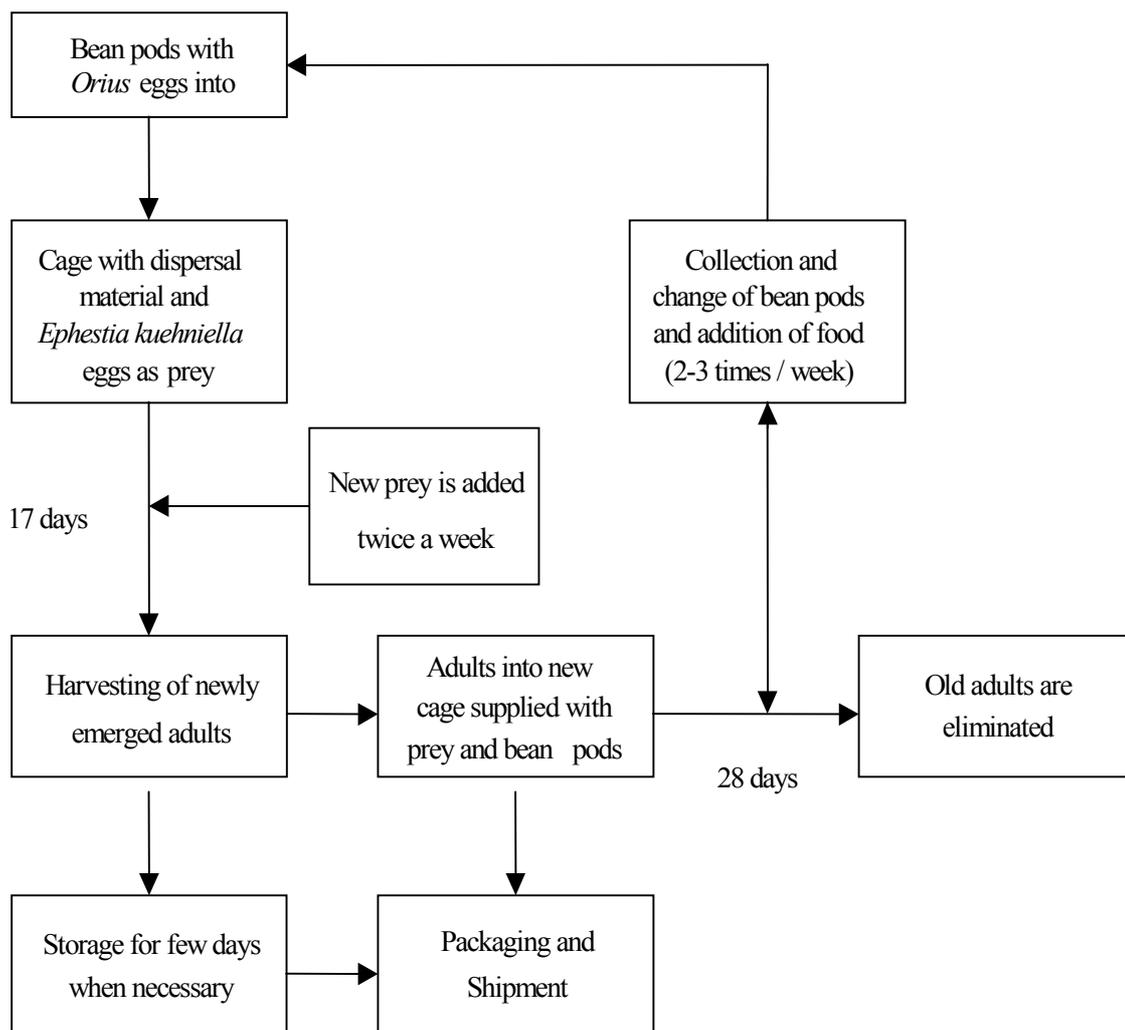
Crop	$R_0$	T	$r_m = \frac{\ln R_0}{T}$	References
Chrysanthemum	99.5	26.9	0.171	Robb, 1989
Bean leaves	12.2	17.9	0.139	Brødsgaard, 1991, 1994
Bean leaves	34.7	25.3	0.140	Gerin <i>et al.</i> , 1994
Cucumber	6.0	4.6	0.300	Gaum <i>et al.</i> , 1994
Cucumber	22.1	20.1	0.166	van Rijn <i>et al.</i> , 1995
Chrysanthemum (flower)	91.3	32.0	0.141	Katayama, 1997

predators (phytoseiid mites) with that of their prey species (spider mites) and they concluded that the predation rate is the important characteristic to obtain an indication for the capability of biological control. However, they did not investigate the matter further. Therefore, we propose to calculate the kill-rate  $k_m$  to compare the predation capacity of the *Orius* species. This kill-rate is a new parameter that takes into account the age-specific predation both during the nymphal and the adult stages. Our data show that the native species *O. laevigatus* has the highest  $k_m$ . As the values for the rate of population increase did not differ a lot for *O. laevigatus* and *O. majusculus*, *O. laevigatus* is suggested to be used as natural enemy for *F. occidentalis* control because of its higher kill-rate. We should realise that in addition to the kill-rate, searching efficiency in the field is another important and critical criterion for comparison of predator performance (van Lenteren, 1988).

Based on the biological data reported in this paper, a mass rearing method for *Orius* species was developed, which is reported in the appendix and figure 6.

## Conclusions

*O. niger* appears to be unsuitable for biological control of *F. occidentalis*, because it is difficult to mass rear, develops slowly, has a very low  $r_m$  and has a low predation rate on *F. occidentalis*. *O. laevigatus* and *O. majusculus* showed similar development when fed on *F. occidentalis*. However, when evaluated based on the kill-rate ( $k_m$ ), *O. laevigatus* has a higher value ( $k_m = 0.28$ ) than *O. majusculus* ( $k_m = 0.25$ ). So although *O. insidiosus*, *O. laevigatus* and *O. majusculus* can all develop and reproduce on *F. occidentalis* and *E. kuehniella*, we propose to use for thrips control in Mediterranean Europe the species *O. laevigatus*, as it has the highest kill-rate, does not go into diapause in winter (Tommasini and van Lenteren, 2003) and is a native species which reduces risks of negative effects on non-target species (van Lenteren *et al.*, 2003). We also conclude that for successful biological control multiple releases of *Orius* are necessary, because the development time of the predator is much longer than that of the prey.



**Figure 6.** Flow-chart of rearing system of *Orius* spp..

## Appendix

### Mass rearing of *O. laevigatus*

An important problem in mass rearing of potentially cannibalistic predators is the provision of an adequate amount of prey. Natural prey are often difficult and expensive to rear, thus the use of factitious prey is preferred. Our research showed that *O. majusculus*, *O. laevigatus* and *O. insidiosus* can easily be reared on frozen eggs of *E. kuehniella*, but not *O. niger*, because of its high pre-immature mortality, long development time and low fecundity. Based on the better performance of *O. majusculus*, *O. laevigatus* and *O. insidiosus* when reared on *E. kuehniella* eggs than on *F. occidentalis*, we conclude that this factitious prey is more profitable for mass-rearing than *F. occidentalis*. *E. kuehniella* frozen eggs are also more simple to use and less expensive. Kiman and Yeargan (1985) studied various diets for *O. insidiosus*, and they concluded that this *Orius* species required arthropod prey to complete the development time quickly, and that mites were a more suitable diet than thrips. Vacante *et al.* (1997) and Cocuzza *et al.* (1997b) confirmed that also *O. laevigatus* can develop faster with a diet based on *E. kuehniella* rather than only on pollen.

On the basis of the biological data reported above, a mass rearing of *O. laevigatus* was set up, starting from ca. 1000 wild predators collected on Sicily (South Italy) and identified with morphological keys of Tommasini (Tommasini, 2004).

Environmental conditions, food and ovipositional substrate were the same as used in the pilot rearing described in the material and methods section above. The rearing units used were transparent plastic boxes (3.6 dm<sup>3</sup> in volume), with holes for aeration closed with fine steel netting on the sides and on the top. To reduce cannibalism during the juvenile instars, a certain amount of buckwheat (ca. 1.5 dm<sup>3</sup>) was put on the bottom of each box. Each rearing unit started from ca. 1,500 eggs of *O. laevigatus* laid into French bean pods, and the whole cycle was completed in the same box. Twice a week, bean pods with eggs of the predator were collected and food and water were supplied. Adults were kept for oviposition in these boxes for ca. 4 weeks. A brief description of the rearing process is shown in figure 6. A similar rearing-method was carried out successfully for *O. laevigatus* and *O. majusculus* by Blümel (1996).

The mass-rearing of the predator has been improved in co-operation with the Italian mass producer of natural enemies, Bioplanet in Cesena ([www.Bioplanet.it](http://www.Bioplanet.it)). It is now possible to produce up to 100,000 adult predators per week. They are packed in plastic bottles for shipment and release in several vegetable and ornamental crops grown in greenhouses and in open fields. The total production in 1994 was 1.5 million adult predators and increased considerably in the following years.

Quality control methods have been developed for the rearing process and for product control of *Orius* spp. (van Lenteren, 1986a, 1986b, 2003; Tommasini and Bolckmans, 1998).

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