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van den Meiracker, R.A.F.

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Induction and termination of diapause in *Orius* predatory bugs

R. A. F. van den Meiracker
Research Institute for Plant Protection (IPO-DLO), P.O. Box 9060, 6700 GW Wageningen, The Netherlands/Department of Pure and Applied Ecology, Section Population Biology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands

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Abstract

Photoperiodic induction of reproductive diapause at 18 °C was investigated in four *Orius* [Heteroptera: Anthocoridae] species. *Orius insidiosus* (Say) displayed a long-day response with a critical photoperiod between L11:D13 and L12:D12. Diapause in this species was terminated rapidly when the temperature and/or the daylength were increased. *Orius majusculus* (Reuter) also displayed a long-day response. The critical photoperiod fell between L14:D10 and L16:D8. Diapause in this species was not terminated within 14 days when both temperature and daylength were increased. In *Orius albidipennis* (Reuter) no diapause could be induced at photoperiods varying from L8:D16 to L16:D8. In *Orius tristicolor* (White) a high proportion of diapause was found at all photoperiods tested.

The effect of temperature on photoperiodic induction of diapause was studied in *O. insidiosus* at L10:D14. Diapause occurred at 18 °C, 21 °C and 25 °C, but not at 30 °C. Again, diapause was terminated rapidly after transfer to 25 °C/L16:D8. Exposing only the nymphal instars 1–5 to short daylength was not enough to induce diapause in the whole population of *O. majusculus*. *Orius* predatory bugs are used as biocontrol agents against western flower thrips, *Frankliniella occidentalis* (Pergande) [Thysanoptera: Thripidael, in greenhouses. The consequences of photoperiodic induction of diapause for the success of early season releases of *Orius* are discussed.

Introduction

Orius predatory bugs are important natural enemies of western flower thrips, *Frankliniella occidentalis* (Pergande), a major pest species in many greenhouse crops in Europe. In 1991 and 1992 *O. insidiosus* has been applied against this pest in 90–95% of the sweet pepper area in the Netherlands (van Schelt, 1993). Concern about the early season establishment of introduced *Orius* predatory bugs was the incentive to investigate diapause in this genus. Many greenhouse crops in the Netherlands are planted as early as December. Therefore, photoperiodic induction of diapause in *Orius* predatory bugs may inhibit their successful application against thrips early in the growing season. Quiescence is not likely to hamper population build-up of *Orius* in greenhouses, since temperatures are usually maintained at a level that is high enough for development and reproduction of *Orius*. However, if the short daylengths of December act as a stimulus for induction of diapause, population build-up will cease. Under greenhouse conditions in the Netherlands western flower thrips does not enter diapause.

In temperate zones many *Orius* species are known to hibernate as adults in dry and protected places, e.g., *O. insidiosus* (Garman & Jewett, 1914; McGregor & McDonough, 1917; Marshall, 1930; Iglinsky & Rainwater, 1950), *O. tristicolor* (McGregor & McDonough, 1917; Anderson, 1962), *O. minutus* (L.) and *O. majusculus* (Collyer, 1953), and *O. niger* Wolff (Bailov, 1929). The majority of bugs coming out of hibernation consists of mated females, but males occur occasionally (Collyer, 1953; Anderson, 1962). The role of diapause in hibernation has been studied in two *Orius* species. Ruberson *et al.* (1991) investigated photoperiodic induction of reproductive diapause in *O. insidiosus*. Diapausing females exhibited poorly developed ovaries and well developed fat bodies. Kingsley & Harrington (1982) studied termination of diapause in field-collected females of this species. Induction of diapause has also been examined in two North American populations of *O. tristicolor* (Gillespie & Quiring, 1993).

The objective of this study was to investigate the effect of photoperiod on the induction of diapause in four important *Orius* species which have already been used in practice: *O. insidiosus*, *O. tristicolor*, *O. majusculus* and *O. albidipennis*. The effect of various photoperiods on reproduction was studied at 18 °C. Furthermore the effect of temperature was tested at L10:D14 in *O. insidiosus*. It was also investigated whether diapause in *Orius* could be terminated by an increase in temperature or daylength. Rapid termination of diapause after such increases would be an advantage in terms of pest control. Finally it was determined which developmental stages are sensitive to photoperiodic induction of diapause. This may enable better timing of the release of *Orius* early in the growing season.

Materials and methods

Origin of predatory bugs. O. insidiosus used in this study originated from Georgia (U.S.A.). It has been reared in the laboratory for two years preceding this study. *O. majusculus* was collected from sweet pepper in a greenhouse in the Netherlands, and was reared in the laboratory for one year. *O. albidipennis*, collected from sweet pepper in a greenhouse on the Canary Islands, was reared in the laboratory for five months. *O. tristicolor* was collected in an orchard adjacent to a strawberry field in California (U.S.A.), and was reared in the laboratory for four months.

Rearing of predatory bugs. Orius was reared on eggs of *Ephestia kuehniella* Zeller at 25 °C, 75% r.h., and L16:D8. Bean pods (*Phaseolus vulgaris* L.) were used as oviposition sites. See for rearing details van den Meiracker & Ramakers (1991).

Experiment 1. To investigate the effect of photoperiod on the induction of diapause, *O. insidiosus*, *O. majusculus*, *O. albidipennis*, and *O. tristicolor* were tested at different photoperiods. This experiment was carried out at 18 ± 0.5 °C, which corresponds with the current mean temperature in vegetable greenhouses early in the season. Bean pods with *Orius* eggs of 0–24 h old, were distributed over rearing jars, which were placed at different photoperiods: L8:D16, L10:D14, L11:D13, L12:D12, L13:D11, or L16:D8. For *O. majusculus* a jar was also placed at L14:D10. The r.h. was kept at 75%. The nymphs were treated as in the rearing. From each of these jars 48 nymphs of *O. insidiosus* and *O. majusculus* were collected as fifth instars. They were put separately in 25 ml glass pots with snap caps, lined with filter paper. Ventilation of these pots was provided by a hole in the cap covered with fine nylon gauze. A small piece of bean pod was added to each pot for moisture. *E. kuehniella* eggs were provided on small pieces of filter paper (25 × 7 mm). Pieces of bean pod and filter papers with *E. kuehniella* eggs were replaced every second day.

The 25 ml pots were checked for adult eclosion daily, and developmental time was determined. Newly eclosed males were added to pots with newly eclosed females, until 20 pairs were made up per species at each photoperiod. Pieces of bean pod from pots with adults were checked for *Orius* eggs every second day during two weeks, which is approximately twice the preoviposition period at 18 °C. Females that did not oviposit within two weeks after adult eclosion were considered to be in diapause. This arbitrary two week-criterium can be justified, because comparisons between treatments are made in a relative way. In case oviposition was commenced within two weeks the preoviposition period was determined.

Subsequently, pots with diapausing females were placed at 25 ± 0.5 °C and L16:D8 to investigate if diapause could be terminated. Females that oviposited within two weeks after this switch were considered to have terminated diapause. Again, this arbitrary period of two weeks is justified by the fact that only relative comparisons are made.

O. albidipennis and *O. tristicolor* were treated in the same way, except that pairs were directly made up of newly eclosed adults from the rearing jars, and that termination of diapause was not investigated.

Experiment 2. The effect of temperature on the photoperiodic induction of diapause in *O. insidiosus* was studied at a short daylength of L10:D14 and 75% r.h.. This experiment was carried out at four different temperatures: 18.0 ± 0.5 °C, 21.0 ± 0.5 °C, 25.0 ± 0.5 °C, and 30.0 ± 0.5 °C. The same procedure as in experiment 1 was followed. The percentage diapause was determined two weeks after adult eclosion. Pairs that were previously kept at 21 °C, 25 °C, and 30 °C, were then placed at 25 °C/L16:D8 to find out if diapause could be terminated within two weeks.

Pairs that were kept at 18 °C until two weeks after adult eclosion, were then subjected to three different treatments to investigate the separate influence of increases in daylength and temperature on termination of diapause. In the first treatment the photoperiod was switched to L16:D8. In the second treatment the temperature was raised to 25.0 ± 0.5 °C. Temperature and photoperiod in the third treatment were left unchanged. Diapause incidence was determined again after two weeks.

Experiment 3. To determine in which developmental stages diapause can be induced by short daylength, *O. majusculus* was reared from egg to adult at 18.0 ± 0.5 °C and 75% r.h. Upon hatching nymphs were separately put in 25 ml glass pots. Food and moisture were supplied as in experiment 1. In four treatments a basic photoperiod of L16:D8 was temporarily switched to L10:D14 during a specific period of development: egg stage, instars 1–3, instars 3–5 and instars 1–5. In a control treatment the photoperiod was kept at Ll6:D8 continuously. Data of experiment 1, of females kept at L16:D8 and L10:D14 continuously, were also used to make comparisons. Percentage diapause was determined two weeks after adult eclosion.

Sensitivity to photoperiod was also studied in newly emerged adults of *O. insidiosus* and *O. majusculus* collected from the rearing (25 °C/L16:D8). Males and females were put in 25 ml pots in pairs and were further treated as in experiment 1. Of both species a control group was kept under rearing conditions (25.0 ± 0.5 °C/L16:D8) and a group was placed at 18.0 ± 0.5 °C/L10:D14 to mimic the switch from rearing conditions to early season greenhouse conditions. Oviposition was checked for two weeks.

Statistical analysis. Developmental times and preoviposition periods at different photoperiods (experiment 1) or temperatures (experiment 2) were compared, using the Kruskal-Wallis one-way analysis of variance by ranks. When significant differences were found, means were separated using the Wilcoxon two-sample test. Developmental times of females and males were also compared using the Wilcoxon two-sample test. Differences in diapause incidence between the four treatments and the controls of experiment 3 were tested with the Fisher exact test. In all tests α was taken 0.05. In the case of multiple comparisons α was corrected to $\alpha' = 1 - (1 - \alpha)^{1/n}$ (n denotes the number of comparisons).

Results and discussion

Effect of photoperiod on developmental time and preoviposition period. Although developmental times of *O. insidiosus* (Table 1) and *O. majusculus* (Table 2) differed significantly between photoperiods at 18 °C, no consistent trend was visible. During experiment 1 the temperature at the 12L:12D treatment was actually 17 °C instead of 18 °C. This unintended deviation of 1 °C probably caused a delay in development of 4 to 5 days (Tables 1 & 2). The differences in developmental time between the other photoperiods were much smaller, but may have been caused by (much smaller) deviations in temperature as well. In both species males developed faster than females (Tables 1 & 2).

Photoperiodic control of developmental time is a well known phenomenon in many insects (Beck, 1980; Saunders, 1982). Although no straightforward relation between photoperiod and developmental time was found in the present study, Ruberson *et al.* (1991) found that nymphs of *O. insidiosus* developed faster at L10:D14 than at longer daylengths (at 20 °C). Askari and Stern (1972) found that development in *O. tristicolor* was faster at L12:D12 than at L16:D8 (at 25.5 °C). An accelerating effect of short daylengths on developmental time has also been observed in other Heteroptera, e.g. *Palomena angulosa* Motschulsky (Hori, 1986; 1987; 1988) and *Eysarcoris lewisi* Distant (Hori & Inamura, 1991). This may reflect a trade-off between reaching the diapausing stage before the onset of unfavourable conditions and acquiring metabolic reserves (for reproduction or hibernation). In other Heteroptera a decelerating effect of short daylengths on developmental time has been found, e.g., *Dolycoris baccarum* L. (Conradi-Larsen & Sømme, 1973), *Nezara viridula* L. (Ali & Ewiess, 1977), and *Carbula humerigera* Uhler, which undergoes nymphal diapause (Kiritani, 1985). In *Pyrrhocoris apterus* L. nymphal development was strongly protracted at photoperiods near the critical photoperiod for diapause induction (Saunders, 1983).

The preoviposition period of nondiapausing *O. insidiosus* was rather constant at different photoperiods at 18 °C (Table 1). Ruberson *et al.* (1991) found that the preoviposition period in *O. insidiosus* was inversely related to daylength. They checked for

Table 1. Developmental time (from oviposition to adult eclosion) and preoviposition period of nondiapausing *O. insidiosus* at 18 °C at different photoperiods, and preoviposition time for females that terminated diapause after a switch to 25 °C/L16:C8. Means in days ± s.d. (*n*)

Photoperiod	Developmental time[1] Females[2]	Developmental time[1] Males[2]	Preoviposition period[3]	Preoviposition time after switch[3]
L8:D16	31.6±1.5 (26)^{a}	30.5±1.4 (22)^{a}	6.5±0.7 (2)	4.8±2.3 (15)
L10:D14	30.0±1.2 (24)^{bc}	29.1±1.0 (24)^{b}	8.0±0.0 (2)	5.4±1.5 (18)
L11:D13	29.3±0.9 (31)^{c}	28.1±0.9 (16)^{c}	8.0±2.0 (3)	4.1±2.4 (16)
L12:D12[4]	35.0±1.0 (27)	34.7±1.1 (21)	10.1±2.6 (12)	5.1±5.1 (5)
L13:D11	30.8±1.4 (29)^{ab}	29.7±1.3 (18)^{ab}	7.9±2.5 (11)	4.2±2.9 (3)
L16:D8	30.0±2.3 (22)^{bc}	29.6±2.1 (24)^{abc}	6.7±1.2 (15)	1.5±0.0 (2)

[1] Developmental times of females and males differed significantly, except at L12:D12 and L16:D8.

[2] Significant difference between photoperiods, means followed by the same letter are not significantly different.

[3] No significant difference between photoperiods.

[4] 17 °C (see text); omitted from comparisons between photoperiods.

Table 2. Developmental time (from oviposition to adult eclosion) and preoviposition period of nondiapausing *O. majusculus* at 18 °C at different photoperiods. Means in days ± s.d. (*n*)

Photoperiod	Developmental time[1] Females[2]	Developmental time[1] Males[2]	Preoviposition period
L8:D16	30.8±1.8 (28) ^{b}	29.4±1.1 (19) ^{ab}	5.0±0.0 (2)
L10:D14	30.0±1.5 (22) ^{b}	28.9±1.1 (26) ^{b}	
L11:D13	28.6±1.5 (21) ^{c}	26.9±1.2 (27) ^{c}	
L12:D12[3]	34.3±1.4 (22)	32.9±1.5 (26)	10.5±0.7 (2)
L13:D11	31.1±1.6 (12) ^{ab}	28.8±1.0 (36) ^{b}	7.0 (1)
L14:D10	30.9±1.6 (28) ^{b}	30.4±1.8 (17) ^{a}	10.0 (1)
L16:D8	32.9±2.9 (25) ^{a}	29.7±1.8 (20) ^{ab}	6.9±2.3 (11)

[1] Developmental times of females and males differed significantly, except at L14:D10.

[2] Significant difference between photoperiods, means followed by the same letter are not significantly different.

[3] 17 °C (see text); omitted from comparisons between photoperiods.

oviposition until 22 days after adult eclosion at 20 °C, while in the present study this was done until 14 days after adult eclosion at 18 °C. This may have affected the determination of the preoviposition period, as is discussed later. In the relatively few nondiapausing *O. majusculus* females, the preoviposition period was about as long as in *O. insidiosus* (Table 2).

Effect of photoperiod on diapause incidence. O. insidiosus exhibited a long-day response to photoperiod (type I of Beck, 1980) at 18 °C (Fig. 1a). The critical daylength fell between 11 and 12 h. This is shorter than reported for *O. insidiosus* from Arkansas (U.S.A.), where it fell between 12 and 13 h at 20 °C (Ruberson *et al.*, 1991). Below the critical daylength and at L16:D8 the proportion of ovipositing females was stable several days before diapause incidence was determined (Fig. 2a–c, f), as contrasted with L12:D12 and L13:D11 (Fig. 2d–e).

O. majusculus also exhibited a long-day response, with a critical daylength falling between 14 and 16 h light per day at 18 °C (Fig. 1b). Since only 55% oviposited at L16:D8, the critical daylength may be closer to 16 h. A similar response to photoperiod was recorded by Alauzet *et al.* (1992) in *O. majusculus* in France. Oviposition was absent or delayed at

Table 3. Developmental time (from oviposition to adult eclosion) and preoviposition period of nondiapausing *O. insidiosus* at L10:D14 at different temperatures. Means in days ± s.d. (*n*)

Photoperiod	Developmental time[1]		Preoviposition period[2]
	Females[2]	Males[2]	
18 °C	33.7±1.4 (86) ^{a}	32.5±1.5 (98) ^{a}	8.9±2.1 (9) ^{a}
21 °C	25.8±1.0 (21) ^{b}	23.9±0.8 (25) ^{b}	8.0±1.4 (2) ^{ab}
25 °C	16.7±0.9 (25) ^{c}	15.6±0.7 (22) ^{c}	7.7±3.6 (6) ^{ab}
30 °C	11.4±0.7 (27) ^{d}	10.8±0.6 (17) ^{d}	3.5±2.6 (23) ^{b}

[1] Developmental times of females and males differed significantly at all temperatures.

[2] Significant difference between temperatures, means followed by the same letter are not significantly different.

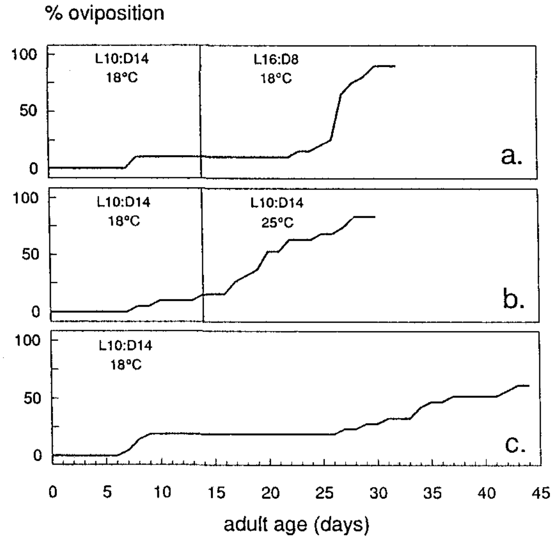

Fig. 4. Termination of diapause in *Orius insidiosus* induced at 18 °C/L10:D14. Cumulative onset of oviposition: a. increase of daylength at adult age of 14 days ($n = 20$), b. rise of temperature at adult age of 14 days ($n = 20$), c. no change of conditions ($n = 21$).

The bugs in the 18 °C/10L:14D treatment of experiment 2 were subjected to three different treatments to study termination of diapause. When the daylength was increased the percentage of ovipositing females started to increase after nine days, and finally attained 90% (Fig. 4a). The mean preoviposition time after the increase in daylength was 12.7 days (s.d. = 1.7, $n = 16$) in females that failed to oviposit before. Photoperiodic termination of diapause has been observed in many species (Tauber *et al.*, 1986; Danks, 1987; etc.), and is not uncommon in Heteroptera. In field-collected diapausing females of *Pyrrhocoris apterus*, *Aelia acuminata* (L.), *Jalysus spinosus*, *Lygaeus equestris* (L.), *Anasa tristis* and *Microvelia douglasi* diapause was ended soon after transfer to long-day conditions, whereas diapause was maintained for a substantial period under short-day conditions (Hodek, 1971; 1974a; Elsey, 1974; Solbreck & Sillén-Tullberg, 1981; Nechols, 1988; Muraji *et al.*, 1989). Laboratory-induced diapause has been terminated by long-day conditions in *Pyrrhocoris apterus* (Hodek, 1968), *Oncopeltus fasciatus* (Dingle, 1974b), *Aelia acuminata* (Hodek & Honěk, 1981), *Riptortus clavatus* (Numata & Hidaka, 1982; 1983), *Anasa tristis* (Fielding, 1988), *Dolycoris baccarum* (Hodková *et al.*, 1989), *Microvelia douglasi* (Muraji & Nakasuji, 1990), *Podisus maculiventris* Say (Volkovich *et al.*, 1991), and *Corythucha cydoniae* (Neal *et al.*, 1992).

When the temperature was raised to 25 °C the percentage of ovipositing females started to increase earlier (three days after the rise), but the increase proceeded more gradual (Fig. 4b). Two weeks after the rise 83% was ovipositing. The mean preoviposition time after the rise of the temperature was 6.8 days (s.d. = 3.7, $n = 12$) in females that failed to oviposit before. Although recorded less often than photoperiodic termination, termination by increasing temperatures has also been reported (Tauber *et al.*, 1986; Danks, 1987; Hodek & Hodková, 1988; Zaslavski, 1988). A similar result as in *O. insidiosus*, was obtained by Dingle (1974b), who ended diapause in *Oncopeltus fasciatus* by a temperature increase from 23 °C to 27 °C (under short day conditions). It should be noted that in *O. insidiosus* a switch took place between two diapause-promoting conditions, whereas *O. fasciatus* did not respond to photoperiod at 27 °C. In field-collected *Lygaeus equestris* diapause was terminated after transfer to 30 °C, but not after transfer to 23 °C and short days (Solbreck & Sillén-Tullberg, 1981). Partial termination by high or increasing temperatures was found in *Pyrrhocoris apterus* (Hodek, 1968; 1974b), *Aelia acuminata* (Hodek & Honěk, 1981), *Riptortus clavatus* (Numata & Hidaka, 1982), and *Dolycoris baccarum* (Hodek & Hodková, 1993).

When females were kept at 18 °C/10L:14D continuously, 20% oviposition occurred 9 days after adult eclosion (Fig. 4c). This number did not increase until 27 days after adult eclosion. The percentage of ovipositing females then gradually increased to 62% after 43 days. The mean preoviposition period of the females that failed to oviposit in the first weeks was 34.7 days (s.d. = 5.4, $n = 9$). Completion of diapause without specific cues (such as an increase in temperature or daylength) has also been found in *Oncopeltus fasciatus* (Dingle, 1974b), *Carbula humerigera* (Kiritani, 1985), and *Dolycoris baccarum* (Hodková *et al.*, 1989), and may have been found in other Heteroptera, if experiments with sufficient duration would have been done.

When a synchronizing cue is absent, diapause usually ends over a broad span of time (Tauber *et al.*, 1986). This applies for *O. insidiosus* kept at 18 °C/10L:14D continuously. Increases of the temperature and the daylength affect termination of diapause in a different way. Whereas extension of daylength seems to have a accelerating as well as a synchronizing effect on termination, a rise of temperature only accelerates termination (cf. Fig. 2b for the simultaneous effect of both cues).

Females that experienced 18 °C/L10:D14 continuously, fell apart in two distinct groups (Fig. 4c): those that did not enter diapause and oviposited after approximately eight days and those that entered diapause and subsequently terminated diapause after several weeks. This pattern may be typical for daylengths of 11 h and shorter at 18 °C (Fig. 2a–c). At L12:D12, however, the proportion of ovipositing females gradually increased during the two weeks after adult eclosion (Fig. 2d). At L13:D11 and L16:D8 the oviposition curve becomes increasingly steeper (Fig. 2e–f). Probably a certain proportion of the females enters a short diapause, which is ended within two weeks after adult eclosion. This proportion apparently decreases with increasing daylength. When numbers of ovipositing females increase gradually, the proportion of diapause will depend on the point of time on which it is determined. This would, in turn, affect the determination of the preoviposition period (of nondiapausing females). Ruberson *et al.* (1991) recorded diapause eight days later than in this study. This may explain why different relations between daylength and preoviposition period were found in both studies (as mentioned before).

Stages sensitive to photoperiod. Fig. 5 shows diapause incidence in *O. majusculus*, when kept at short daylength during certain stages of development. Compared to the females that were reared at a long daylength continuously, no increase in diapause incidence was found when only the eggs or the first three instars were kept at short daylength. A slight increase could be seen when the instars 3–5 or 1–5 were kept at short daylengths. However none of the four treatments differed significantly from the control at long daylength continuously (L16:D8, data of experiment 1 and 3 combined). On the contrary, diapause incidence in each of the four treatments was significantly lower than in the control at short daylength continuously. To induce diapause in the whole population diapause-promoting daylengths may be required early in the adult stage as well.

To determine which developmental stages of *O. insidiosus* are most sensitive to photoperiod, the method applied for *O. majusculus* is probably not suitable, because diapause in *O. insidiosus* adults can be terminated rapidly by extending daylength. Therefore, it is likely that oviposition will always occur when only pre-imaginal stages are exposed to short daylengths.

No diapause could be induced in adults of *O. insidiosus* and *O. majusculus* that developed under rearing conditions of 25 °C/L16:D8: all females kept under such conditions as well as those transferred to short-day conditions (18 °C/L10:D14) commenced and continued to lay eggs during the course of the experiment (two weeks, $n = 17$–20).

Sensitivity in *O. majusculus* resembles sensitivity in *Podisus maculiventris*. In this pentatomid sensitivity to photoperiod was very low in early nymphal instars and adults, but diapause incidence was high when the instars 2–5 experienced short days (Volkovich *et al.*, 1992). Adults of different ages of *Nezara viridula* did not enter diapause when transferred to short daylength (Ali & Ewiess, 1977). In *Oncopeltus fasciatus* sensitivity disappeared shortly after adult eclosion (Dingle, 1974b). On the other hand, many Heteroptera retain their sensitivity as adults. *Pyrrhocoris apterus*, *Dolycoris baccarum*, *Riptortus clavatus*, *Anasa tristis*, *Microvelia douglasi* and *Corythucha cydoniae* remain sensitive as sexually mature adults (Hodek, 1968; Babrakzai & Hodek, 1987; Numata & Hidaka, 1982; Fielding, 1988; Muraji & Nakasuji, 1990;

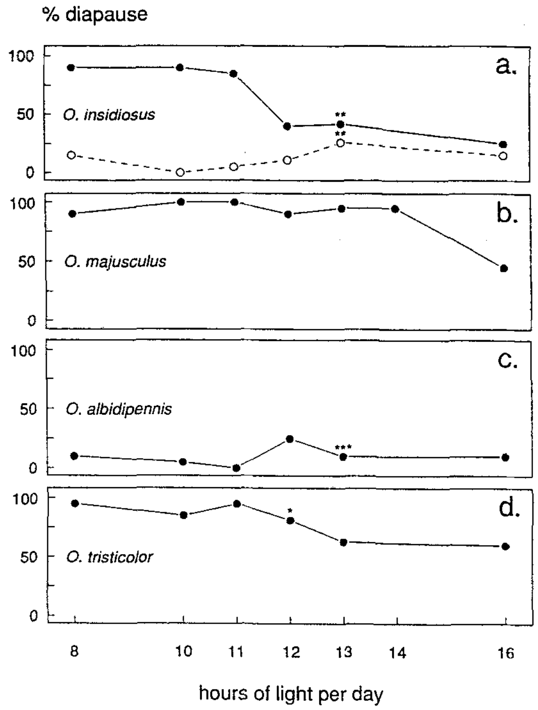

Fig. 1. Effect of photoperiod on diapause incidence in four *Orius* species at 18 °C. —•— diapause incidence 14 days after adult eclosion, —o— diapause incidence 28 days after adult eclosion with conditions changed to 25 °C/L16:D8 14 days after adult eclosion ($n = 20$, except where indicated: * $n = 16$, ** $n = 18$, *** $n = 19$). At L12:D12 the temperature was actually 17 °C (see text).

daylengths of 14 h and shorter, whereas normal oviposition occurred at L16:D8.

In *O. albidipennis* diapause incidence at 18 °C was very low (Fig. 1c). The highest proportion of diapause (25%) occurred at L12:D12, when the temperature was 17 °C. It may well be that at even lower temperatures the proportion of diapause will further increase.

Most of the females of *O. tristicolor* entered diapause at all photoperiods (Fig. 1d). However. at L12:D12, L13:D11 and L16:D8 the proportion of diapause was lower, and numbers of ovipositing females were still increasing after two weeks (in contrast with L8:D16, 10:14D and L11:D13). Gillespie & Quiring (1993) also studied diapause induction in a Californian population of *O. tristicolor*, and found a more typical long-day response, with a critical daylength of about 12 h. Instead of a constant temperature, they used different day and night temperatures of 25 °C and 15 °C respectively, which may explain the discrepancy with the present data.

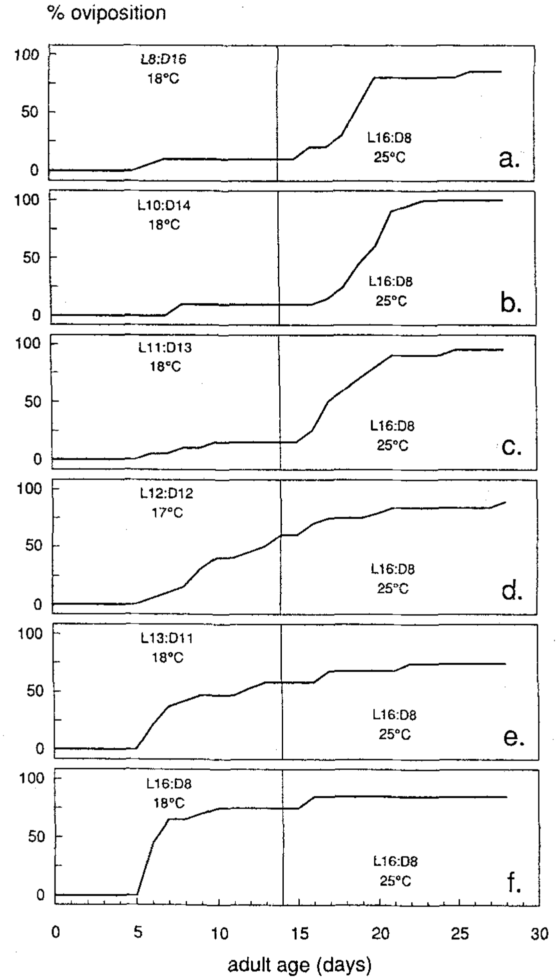

Fig. 2. Cumulative onset of oviposition in *Orius insidiosus* during four weeks after adult eclosion at 18 °C at different photoperiods. Two weeks after adult eclosion conditions were switched.

In many Heteroptera diapause incidence is practically 100% and 0% at daylengths below and above the critical daylength, respectively. Examples are *Jalysus spinosus* (Say) (Elsey, 1974), *Nezara viridula* (Ali & Ewiess, 1977), *Riptortus clavatus* Thunberg (Numata & Hidaka, 1982), *Pyrrhocoris apterus* (Saunders, 1983), *Carbula humerigera* (Kiritani, 1987), *Microvelia douglasi* Scott (Muraji *et al.*, 1989), *Eysarcoris lewisi* (Hori & Inamura, 1991), *Corythucha cydoniae* (Fitch) (Neal *et al.*, 1992), and *Leptocorisa oratorius* F. (Ito & Noor, 1993). The photoperiodic response curve of *O. insidiosus* at 18 °C is different in two ways. First, 25–42% diapause occurs at daylengths above the critical daylength (see also Ruberson *et al.*, 1991). It may be that a part of the population undergoes an obligatory diapause (Zaslavski, 1988). The same may apply to *O. tristicolor* (Fig. 1d), where this part may consist of the majority of the population, thus overshadowing the response curve of the part that is sensitive to daylength. The fraction that consistently enters diapause at long days may decrease with increasing temperature (Zaslavski, 1988). Second, 10–15% of the *O. insidiosus* population did not enter diapause at daylengths below the critical daylength. Diapause incidence at short days was not zero in *O. majusculus* and *O. tristicolor* either. This offers prospects for artificial selection of nondiapause lines. Selection for nondiapause has already been achieved in other Heteroptera, like *Aelia* spp. (Hodek & Honěk, 1970; Honěk, 1972) and *Oncopeltus fasciatus* (Dallas) (Dingle, 1974a).

Insects often show geographical variation in photoperiodic response, and examples of this phenomenon are also known in the Heteroptera (Beck, 1980; Danks, 1987). Usually the critical daylength declines with latitude. Gillespie & Quiring (1993) found a decline of about three hours in critical daylength when comparing *O. tristicolor* populations from British Columbia (49 °N, Canada) and California (38 °N, U.S.A.). Besides in North America, *O. insidiosus* and *O. tristicolor* also occur in Central and South America (Herring, 1966). *O. majusculus* is known from Scandinavia in the north to Asia Minor in the south (Péricart, 1972). Strains of these species from lower latitudes may have shorter critical daylengths, or even lack a photoperiodic response, and therefore they could be of great value for biological control in greenhouses at higher latitudes.

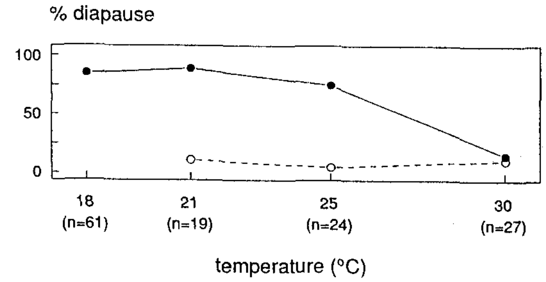

Fig. 3. Effect of temperature on diapause incidence in *Orius insidiosus* at L10:D14. —●— diapause incidence 14 days after adult eclosion, —○— diapause incidence 28 days after adult eclosion with conditions changed to 25 °C/L16:D8 14 days after adult eclosion.

Effect of temperature on diapause incidence. Temperature clearly affected developmental time (from oviposition to adult eclosion) in *O. insidiosus* (Table 3). Diapause incidence at L10:D14 was influenced by temperature: most of the females entered diapause at 18 °C, 21 °C, and 25 °C, while diapause incidence was low at 30 °C (Fig. 3). At 30 °C most females start laying eggs after two or three days. The preoviposition period of nearly all nondiapausing females was seven days or more at 18 °C, 21 °C, and 25 °C (Table 3). Constant temperatures are mostly reported to affect the photoperiodic response curve in two ways. First, temperature can modify the critical daylength. Second, temperature can modify the degree to which an insect responds to photoperiod (Beck, 1980; Saunders, 1982; Tauber *et al.*, 1986; etc.). Both modifications have been found in Heteroptera. In *Carbula humerigera* and *Anasa tristis* DeGeer the critical daylength decreases with increasing temperature (Kiritani, 1987; Fielding, 1988). Dingle (1974b) found a long-day response to photoperiod in *Oncopeltus fasciatus* at 23 °C, whereas at 27 °C the photoperiodic response was almost abolished. The photoperiodic response may have been suppressed in *O. insidiosus* at 30 °C in the present study. However, it cannot be excluded that the critical daylength has been shifted to below 10 h. At 21 °C and 25 °C the critical daylength may have become shorter than at 18 °C, but obviously not shorter than 10 h.

Termination of diapause. In the second part of experiment 1 termination of diapause was investigated. Diapause in *O. majusculus* was never terminated within two weeks after conditions were switched to 25 °C/L16:D8. In *O. insidiosus*, on the contrary, diapause was usually terminated within two weeks after conditions were switched to 25 °C/L16:D8: diapause incidence decreased in all treatments, reaching values of 0–26% (dashed line in Fig. 1a). The proportion of ovipositing females increased soon after the switch (Fig 2a–f). The mean preoviposition time after this switch (in females that failed to oviposit in the first two weeks) was four or five days, except in those females that experienced L16:D8 continuously (Table 1). In females of *O. insidiosus*, which were kept at L10:D14 at temperatures of 21 °C, 25 °C, and 30 °C until an adult age of 14 days (experiment 2), diapause incidence decreased to 5–11% when conditions were switched to 25 °C/L16:D8 (dashed line in Fig. 3). Kingsley & Harrington (1982), who collected diapausing *O. insidiosus* females in the field, also observed quick termination of diapause when both temperature and daylength were increased (relative to field conditions). However, when either only the temperature or only the daylength was increased, termination occurred in no more than 25%.

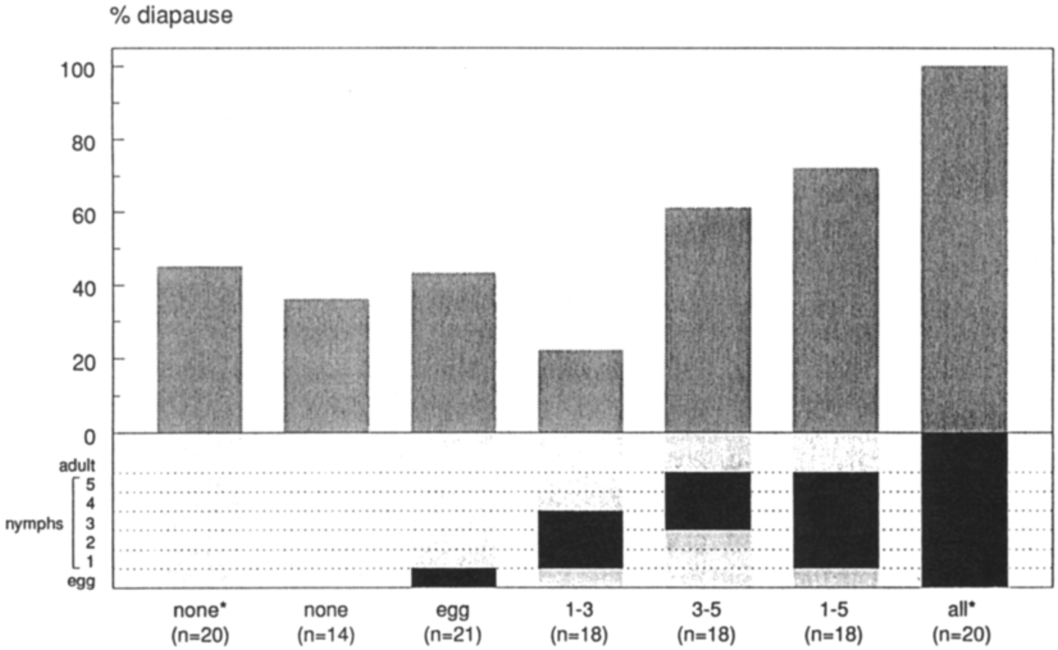

Fig. 5. Developmental stages of *Orius majusculus* sensitive to photoperiodic induction of diapause at 18 °C. Diapause incidence 14 days after adult eclosion, at L16:D8, or L10:D14 during specific developmental stages (indicated black in the lower part of the figure). The treatments marked with * originate from experiment 1.

Neal *et al.*, 1992). Sensitivity even persists in most of these species after completion of diapause in the field (Hodek, 1974b; 1977; Numata, 1987; Fielding, 1988; Muraji *et al.*, 1989). After hibernation a temporary loss of sensitivity can occur, like in *Aelia acuminata* (Hodek, 1977; 1979). Since photoperiodic sensitivity in *O. insidiosus* and *O. majusculus* adults was observed for two weeks only, it cannot be excluded that oviposition would have ceased, had the experiment been continued.

Consequences for biological control. Of the species tested, *O. albidipennis* is the most suitable for introductions throughout the year, since diapause could not be induced photoperiodically in this species at 18 °C. However, it cannot be excluded that diapause will occur at lower temperatures. *O. majusculus* cannot be advised for early season introductions, since diapause is induced at daylengths of 14 hours and shorter at 18 °C. In Switzerland a native strain of *O. majusculus* did not establish well in cucumber greenhouses, until after mid-April (Fisher *et al.*, 1992). Problems may also arise with *O. insidiosus*, although a successful introduction of this species was achieved in the Netherlands at the end of January (van den Meiracker & Ramakers, unpubl.). In contrast with *O. majusculus*, termination of diapause in *O. insidiosus* could be accelerated by raising the temperature or extending the daylength. This may enhance the success of spring introductions of the latter. Higher temperatures will probably advance the time at which a successful greenhouse introduction of *O. insidiosus* is possible, although at 25 °C the critical daylength still fell above 10 h. Chambers *et al.* (1993) extended the early season photoperiod using tungsten bulbs in sweet pepper. This resulted in good thrips control by *Orius laevigatus* (Fieber) in February and March, whereas establishment of the predator failed in absence of supplementary lighting. Later in the growing season less problems are to be expected in *O. insidiosus*, since van den Meiracker & Ramakers (1991) found reproductive activity until mid-October. At about this time the crops are cleared out in the Netherlands.

Orius predatory bugs that have been reared under diapause-averting conditions (25 °C/L16:D8), persist in ovipositing for at least two weeks after transfer to diapause-promoting conditions (18 °C/L10:D14). This will ensure the production of a next generation when adults are released in a greenhouse. However, this next generation might enter diapause when daylengths are still too short.

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