

Photoperiodic Sensitivity and Diapause in the Predator *Orius insidiosus* (Heteroptera: Anthocoridae)

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ABSTRACT Ontogenetic timing of photoperiodic sensitivity is critical in the life history of insects that rely on photoperiod as a token stimulus. The life stages of *Orius insidiosus* (Say) sensitive to photoperiod for diapause induction were investigated by transferring predators between short (10:14 [L:D] h) and long (14:10 [L:D] h) constant photoperiods (at 20°C) at various life stages. Bugs were considered to be in diapause if their preoviposition period exceeded 14 d after adult eclosion. The first three instars exhibited no clear sensitivity to photoperiod relative to diapause induction or intensity (as measured by preoviposition period). The fourth instar was somewhat sensitive, appearing to enhance the sensitivity of subsequent stages. In contrast, the fifth instar was highly sensitive to the short photoperiod. Exposure of bugs to short photoperiods during this instar induced diapause in at least 50% of the population. Likewise, the adult stage was sensitive to photoperiod during at least the first 14 d after eclosion. Exposure to short photoperiods during the early adult stage also appears to be necessary to induce diapause in ≈50% of the population. In addition, short photoperiod served to maintain diapause in adult females. Transferring diapausing adults from short to long photoperiods accelerated diapause termination relative to those remaining in short photoperiod.

KEY WORDS *Orius insidiosus*, photoperiod, diapause

PHOTOPERIOD IS A critical token stimulus for diapause induction in numerous insect species (Danilevsky 1965, Beck 1980, Tauber et al. 1986, Danks 1987). Photoperiod is a stable harbinger of predictable seasonal change, and can provide the insect with a vital opportunity to “prepare” physiologically and behaviorally for inclemencies. The efficacy of photoperiod as an anticipatory cue in the life history of an individual insect is dependent on the life stage or stages during which the insect is capable of perceiving the requisite photoperiodic changes, and the extent to which these stages overlap with the critical photoperiodic shifts.

The anthocorid *Orius insidiosus* (Say) is an important predator of numerous economically important pests (Quaintance and Brues 1905, Winburn and Painter 1932, Barber 1936, Iglinsky and Rainwater 1950, Isenhour et al. 1990). It is widely distributed across the United States and Canada (Herring 1966, Kelton 1978) and is currently available commercially for use against thrips (Glenister 1998). *O. insidiosus* overwinters as an adult in a state of reproductive diapause (Kingsley and Harrington 1982, Ruberson et al. 1991, Horton et al. 1998), with females generally surviving the winter much better than males (Elkassabany et al. 1996, Horton et al. 1998). Photoperiod plays a key role in diapause induction in this species,

as well as in other *Orius* species; diapause is induced if predators are reared under short-day conditions and is averted under long-day conditions (Ruberson et al. 1991, van den Meiracker 1994, Tommasini and Nicoli 1996, Nakashima and Hirose 1997, Kohno 1997, Horton et al. 1998). The life stages during which *O. insidiosus* is sensitive to diapause-inducing or -averting photoperiods have not been ascertained. Determining these sensitive stages is important for understanding the seasonal dynamics of this predator, as well as timing field or greenhouse releases or using diapause as a means of storing this species in commercial production.

Most species of predaceous Heteroptera overwinter as adults, typically in reproductive diapause (Ruberson et al. 1998). Photoperiod appears to play a primary role in diapause induction; and sensitivity to diapause-inducing photoperiods typically occurs in the late nymphal stages, sometimes extending into the adult stage (Ruberson et al. 1998). Among the Anthocoridae, *Orius majusculus* (Reuter) was found to be sensitive to photoperiod in its later instars, and probably in the adult stage as well, although this was not investigated (van den Meiracker 1994). The timing and duration of this sensitive period, particularly in relation to the occurrence of diapause-inducing conditions in the field, is critical in determining the probability for diapause in the insect. This may be particularly relevant for insects with relatively short generation times, such as *O. insidiosus* (Isenhour and Yeagan 1981, Bush et al. 1993), because rapid development may restrict the temporal window of sensi-

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Table 1. Photoperiodic regimens tested in experiment, and incidence of diapause and preoviposition periods for *O. insidiosus* in the respective regimens

Treatment no.	n (females)	N-I	N-II	N-III	N-IV	N-V	A 1-5	A 6-14	A >14	% diapause	Preoviposition periods (d) nondiapause/diapause
1	23									8.7	7.0 + 1.26
2	9	X								0	7.6 + 0.75
3	8	X	X							0	5.0 + 0.33
4	13	X	X	X						0	6.8 + 0.42
5	12	X	X	X	X					8.3	9.4 + 0.68/17.0 (n = 1)
6	24	X	X	X	X	X				54.2	13.0 + 0.40/23.2 + 3.66
7	7	X	X	X	X	X	X			100.0	25.5 + 6.57
8	9		X	X	X	X	X	X	X	100.0	46.9 + 4.24
9	12			X	X	X				91.7	12 (n = 1)/25.1 + 3.52
10	18			X	X	X	X			100.0	27.7 + 2.58
11	6			X	X	X	X	X		100.0	32.5 + 6.14
12	12			X	X	X	X	X	X	100.0	58.9 + 2.47
13	11				X	X				90.9	11 (n = 1)/29.5 + 3.65
14	24				X	X	X			95.8	10 (n = 1)/31.5 + 8.55
15	11				X	X	X	X		100.0	34.1 + 4.65
16	19					X				52.6	10.6 + 0.64/23.8 + 1.79
17	17					X				82.4	9 (n = 1)/28.4 + 3.53
18	10					X	X	X		100.0	39.0 + 12.87
19	22					X	X	X		54.5	8.8 + 0.97/49.3 + 9.49
20	24	X	X	X	X	X	X	X	X	100.0	40.3 + 2.47

Mean \pm SD days from adult emergence to first oviposition; single digits followed by a parenthetical (1) are values based on a single female.

Boxes containing Xs indicate the instars during which bugs were exposed to short (10:14 [L:D] h) photoperiod; empty boxes indicate instars during which bugs were exposed to long photoperiod (14:10 [L:D] h; 20°C). "N" followed by a Roman numeral denotes instar. "A" denotes adult, followed by the number of days after adult eclosion.

tivity and increase the probability of an individual bug missing the necessary photoperiodic cue(s).

The objective of this study was to determine those life stages of *O. insidiosus* that are sensitive to diapause-inducing photoperiods. A series of reciprocal transfers between short- and long-day conditions were made at various stages in the predators' development. The results also provided insights into the role of photoperiod in diapause maintenance in this predator.

Materials and Methods

Acquisition and Maintenance of Predators. *O. insidiosus* adults were collected by sweeping roadside flowering vegetation in Fayetteville, AR, (36.08° N, 94.16° W), and reared in the laboratory at 24 \pm 1°C and a photoperiod of 14:10 (L:D) h. Individual pairs were held in 30-ml diet cups provisioned with a piece of a snap bean pod, and eggs of the tobacco budworm, *Heliothis virescens* (F.) (\leq 24 h old). Bean pods served as a moisture source, as well as an oviposition substrate, for the bugs. Tobacco budworm eggs were used as prey. Bean pieces were removed from the diet cups every 2 d and replaced with fresh bean pieces. Likewise, *H. virescens* eggs were replaced at 2-d intervals. Collected bean pieces containing eggs were held in 50-ml shell vials, sealed with a cotton plug.

Upon hatching, *O. insidiosus* nymphs were provided with fresh bean pieces and *H. virescens* eggs. Nymphs were reared under the same temperature and photoperiodic conditions as those described above for the adults. After molting to the adult stage, bugs were paired and individual pairs were held as described above.

Experimental Procedures. *O. insidiosus* that had been in the laboratory for two or three generations were used in all experiments. A series of treatments was used to assess the response of the various life stages to long-day (constant 14:10 [L:D] h) and short-day (constant 10:14 [L:D] h) photoperiods (all at 20°C; see Table 1 for ontogenetic timing of exposures to respective photoperiods). These photoperiods were selected on the basis of previous experiments which demonstrated that at 14:10 (L:D) h diapause was generally averted, whereas at 10:14 (L:D) h it was induced in local Arkansas populations of *O. insidiosus* (Ruberson et al. 1991). These treatments involved transfers of the bugs between the two photoperiods at different life stages (*O. insidiosus* has five nymphal instars before the adult stage) to determine relative incidence of diapause induction as a function of the life stage(s) exposed to short or long photoperiods. Newly oviposited eggs were held in the photoperiod to which the first instar would be exposed. Insects were transferred between photoperiods within 24 h of molting to an instar. We reared 30–60 *O. insidiosus* individuals in each treatment. Within 24 h of adult emergence, pairs were constituted from bugs reared in the same treatment, and individual pairs were held as previously described. Bean pieces provided to paired predators were examined daily for the occurrence of eggs. First oviposition was noted for each female to assess the treatment effect on length of the preoviposition period. Collected eggs were held to determine viability. This was done to assure that only successfully mated females were used, thereby excluding mating status as a variable in assessing reproductive diapause. During the experiment, eggs laid by all ovipositing females were viable. Females that oviposited within

14 d of adult emergence (approximately double the normal preoviposition period at 20°C) were considered to be nondiapausing individuals, whereas females that initiated oviposition 15 or more days after adult emergence were classified as being in diapause. All females were held until they died or oviposited; however, mortality of bugs before oviposition was very low (<10% across treatments). Male diapause was not assessed, and it appears to be less relevant than that of females, because overwintering is predominantly accomplished by mated females (Elkassabany et al. 1996, Horton et al. 1998).

Data Analyses. Preoviposition periods and percent diapause were compared among treatments to assess the relative influence of the treatments on diapause incidence and intensity (as reflected by duration of the preoviposition period). Comparisons of preoviposition periods between specific treatments were made with the Kruskal–Wallis one-way analysis of variance, because of heterogeneous variances and variable distributions of the data (Sheskin 1997). Analyses of preoviposition periods were conducted separately for diapausing (preoviposition period ≥ 15 d) and nondiapausing individuals, as far as the data would permit. Such separations were not always possible, because in some cases there were too few individuals of one or the other type to permit reasonable analysis. Percentage of diapause was compared among treatments using a chi-square test, with rejection of the null hypothesis (equality of ranks between treatments) set at $P \leq 0.05$ (Sokal and Rohlf 1995).

Results

Sensitivity of First and Second Instars. No *O. insidiosus* entered diapause when exposed to short photoperiod only during the first or combined first and second instars, although a few predators exposed exclusively to constant long-day conditions did enter diapause (see treatments 1–3 in Table 1). In addition, the preoviposition periods were unaffected by exposure of the first or the first and second instars to short photoperiod (cf., treatments 2 and 3, Fig. 1; Table 1). Nor were preoviposition periods in predators held under short-day conditions during the first two instars plus subsequent nymphal stages different than those of bugs maintained in short photoperiod during their later nymphal or early adult stages, beginning at the third or fourth instars (cf., treatments 6, 9, and 13 [$\chi^2 = 5.697$, $P > 0.05$]; and treatments 7, 10, and 14 [$\chi^2 = 4.8452$, $P > 0.05$]). Based on these results, we conclude that the first two instars are not sensitive to diapause-inducing photoperiods.

Sensitivity of Third Instar. Predators exposed to short photoperiod during the first three instars did not exhibit a higher incidence of diapause than did those exposed only during the previous instars or those exposed only to long photoperiod through the first three instars (cf., treatments 1–4). Predators transferred to short photoperiod at the beginning of the third instar and then returned to long photoperiod 5 d after adult emergence exhibited approximately the same inci-

dence of diapause as those transferred to short photoperiod in the fourth instar and returned to long photoperiod 5 d after adult emergence (cf., treatments 10 and 14; Table 1). Further, the preoviposition periods for predators exposed to short photoperiod during any or all of the first three instars did not differ significantly ($H = 3.871$, $P > 0.05$; cf., treatments 2–4). Nor did diapause incidence increase when bugs were exposed to short photoperiod during the third and subsequent nymphal instars relative to exposure only during the fourth and fifth instars (cf., Treatments 9 and 13, respectively; and treatments 11, 15, and 18; Table 1). These results indicate a lack of sensitivity to photoperiod in the third instar relative to diapause.

Sensitivity of Fourth and Fifth Instars. Of predators exposed to short photoperiod from the egg stage through the fourth instar (transferred to long photoperiod at the beginning of instar 5), 8.3% entered diapause (treatment 5), which did not differ from the frequency of diapause observed in bugs held in the long-day control (treatment 1; Table 1). In contrast, if nymphs were exposed to 10:14 (L:D) h from the egg stage through the entire fifth instar, 54.2% entered diapause (Table 1). This rate of diapause induction is comparable to that obtained by exposing bugs to short photoperiod only during the fifth instar (52.6%; treatment 16), indicating very little sensitivity in the stages preceding the fifth instar. However, if the insects were exposed to short photoperiod during both the fourth and fifth instars (treatment 13), 90.9% of females entered diapause, indicating sensitivity to photoperiod during the fourth as well as the fifth instar.

Preoviposition periods also were affected by exposure of nymphs to short photoperiod during instars four and five (Fig. 1). Preoviposition periods for females exposed to short photoperiod only during the first through fourth instars differed significantly from those experiencing short photoperiods from the first through the fifth instar ($H = 33.106$, $P < 0.001$; cf., treatments 5 and 6; Fig. 1b), with the preoviposition periods being significantly longer for females exposed to short-day photoperiods during the first through fifth instars. There was no significant difference in preoviposition period for all females exposed to short-day photoperiod in only the first instar and those exposed to the same from the first to the fourth instar (cf., treatments 2 and 5; $H = 2.13$, $P > 0.05$). However, preoviposition periods of females exposed to short photoperiod from the first to the fourth instar were significantly longer than those of females exposed to this same photoperiod during instars 1–2 and 1–3 (cf., treatments 3, 4, and 5; $H = 20.803$, $P < 0.001$; Fig. 1A and B), indicating some response to photoperiod in the fourth instar. Further, preoviposition periods of diapausing females exposed to short photoperiod during the fourth and fifth instars were significantly longer than those of females exposed to short photoperiod only during the fifth instar (cf., treatments 13 and 16; $H = 7.209$, $P < 0.01$; Fig. 1D). No such effect was observed on predators experiencing short photoperiod during the adult stage in addition to the fourth

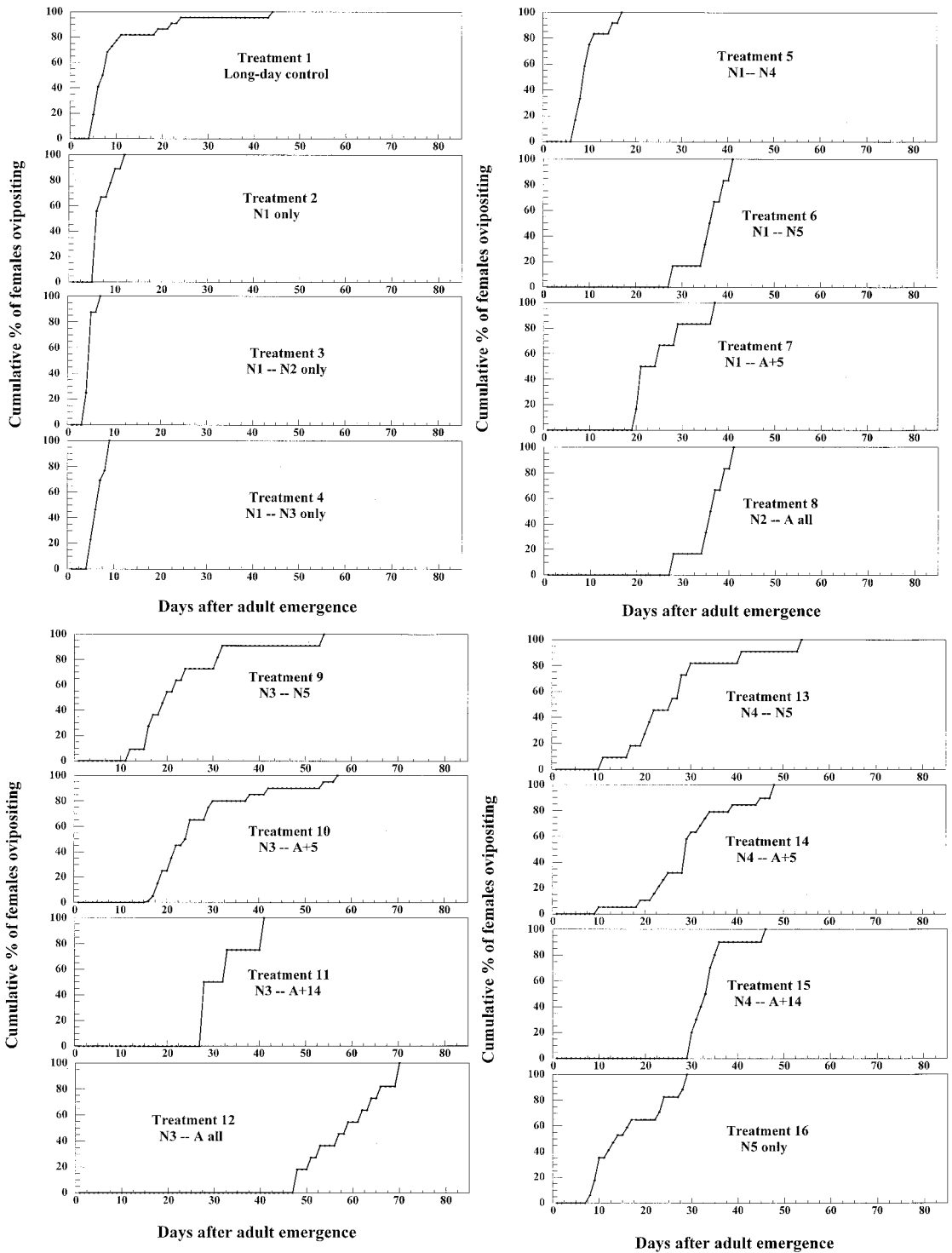


Fig. 1. Preoviposition periods of *O. insidiosus* exposed to short (10:14 [L:D] h) or long (14:10 [L:D] h) photoperiod during various life stages. Treatment numbers correspond to the treatments presented in Table 1. The graphs present the cumulative percentage of females ovipositing on progressive days after adult emergence.

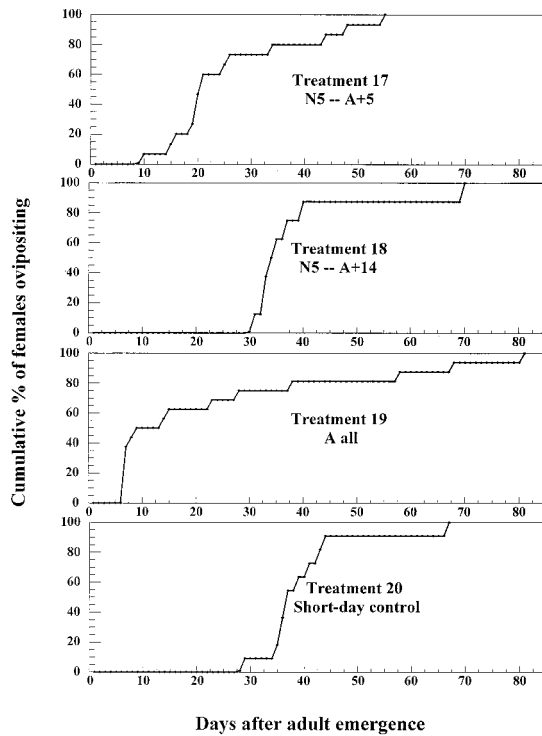


Fig. 1. Continued.

and/or fifth instars (cf., treatments 14 and 17, 15 and 18; $P > 0.10$ in both cases; Fig. 1 D and E).

These results demonstrate that *O. insidiosus* is sensitive to diapause-inducing photoperiods, at least to a limited degree, in the fourth instar, but is highly sensitive to such photoperiods during the fifth instar.

Sensitivity of Adult *O. insidiosus*. Diapause incidence for *O. insidiosus* transferred from long to short photoperiods upon adult emergence, and maintained in short photoperiod thereafter, was 54.5% (treatment 19; Table 1), which was equivalent with the frequency observed for females experiencing short photoperiod only during the fifth instar (52.6%; treatment 16; see above). Thus, adult *O. insidiosus* are sensitive to photoperiod for diapause induction. This is further demonstrated by comparing treatments 16, 17, and 18 (Table 1)—diapause incidence was significantly increased when adults were exposed to short photoperiod, relative to exposure only during the fifth instar ($\chi^2 = 6.012$, $P < 0.05$). When bugs were transferred into short photoperiod at the beginning of the fifth instar and transferred back to long photoperiod 5 and 14 d after molting to the adult stage, diapause incidence increased from 52.6% (for those exposed to short photoperiod only during the fifth instar) to 82.4 and 100% for females exposed to short photoperiod for 5 and 14 d as adults, respectively. This demonstrates that exposure of the adult stage to short photoperiod is necessary, though perhaps insufficient alone, to attain diapause in 100% of the population.

Duration of the preoviposition period (from adult emergence) also was significantly lengthened by in-

creased duration of adult exposure to the short photoperiod (cf., treatments 16, 17, and 18; $H = 8.993$, $P < 0.025$; Fig. 1). If only the days after transfer from short to long photoperiod are counted, however, the preoviposition periods are the same among the three treatments ($H = 1.032$, $P > 0.10$). Likewise, the preoviposition periods of female *O. insidiosus*, which entered diapause after being transferred from long to short photoperiod after adult emergence (54.5% of transferred females entered diapause; Table 1), did not differ significantly from those of females held under short photoperiod throughout their lives (100% of which diapaused; treatment 19 versus 20, $H = 0$, $P > 0.975$; Fig. 1).

Photoperiod and Diapause Maintenance. Preoviposition periods were prolonged by protracted exposure of adult females to short-day conditions, as noted above (Table 1; Fig. 1). After transfer from short to long photoperiods, the mean ranking of preoviposition periods from time of transfer did not differ significantly among females from the various treatments ($H = 1.032$, $P > 0.10$), indicating a role for short photoperiod in diapause maintenance. There was, however, a trend toward more synchronized preoviposition periods as females spent more of their adult lives under short-day conditions before transfer (cf., treatments 6 and 7; treatments 9, 10, and 11; treatments 13, 14, and 15; treatments 16, 17, and 18; Fig. 1).

Discussion

Our results demonstrate that *O. insidiosus* is somewhat sensitive to photoperiod in the fourth instar, and clearly from the fifth instar through at least the first 2 wk of the adult stage for diapause induction. Exposure to short photoperiods during the fourth instar did not appear to be critical for diapause induction. In contrast, exposure to short photoperiod during both the fifth instar and adult stages was critical to attain 100% diapause in the experimental population. The predaceous pentatomid *Podisus maculiventris* (Say) also was sensitive to photoperiod for diapause induction during the later nymphal stages, but only to a very limited extent in the adult stage (Volkovich et al. 1992). Our findings of photoperiodic sensitivity in the later nymphal stages also are similar to results obtained by Neal et al. (1992) with the lace bug *Corythucha cydoniae* (Fitch) and Yeargan and Barney (1996) with the nabids *Nabis americanus* Carayon and *Nabis roseipennis* Reuter.

The extent of photoperiodic sensitivity during the fourth instar is not obvious from our results. Experiencing short photoperiod during fourth instar did not enhance diapause induction for those bugs experiencing short photoperiods from the first through the fourth instar (treatments 2–5); indeed, the incidence of diapause for bugs exposed to short photoperiod during the first four instars did not differ from that observed in the long-day controls. However, experiencing short photoperiod during the fourth instar appeared to modify the photoperiodic response of the subsequent stages: diapause incidence for bugs expe-

riencing short photoperiod only during the fifth instar (treatment 16), or during the fifth instar and the first 5 d of the adult stage (treatment 17) was increased when predators were also exposed to short photoperiod during the fourth instar (treatments 13 and 14 versus 16 and 17, respectively; Table 1). Nevertheless, the results obtained for bugs experiencing short photoperiod during the fourth instar were quite variable (see, for example, Trt. 6 versus nine versus 13), and appeared to be a function of the other, later life stages also experiencing the short photoperiod. Thus, it appears that exposure to short photoperiod during the fourth instar serves principally to enhance the response in subsequent life stages, although the extent of this modification was inconsistent. For example, when bugs were exposed to short photoperiod for the entire nymphal period (treatment 6), 54.2% of the females entered diapause; however, when bugs were exposed to short photoperiod only during the fourth and fifth instars (treatment 13), diapause was induced in 90.9% of the females. It is possible that the radical shift from long (14 h light) to short photoperiod (10 h light) during the fourth instar in treatment 13 may have had an unusual effect on diapause induction in this treatment.

Adult females were sensitive to photoperiod during the first 2 wk after adult eclosion, and exposure to short photoperiod at least during the early period of the adult stage appears to be important for diapause induction in $\approx 100\%$ of the females. Exposure during the adult stage alone was insufficient to induce diapause in more than $\approx 50\%$ of the population. Thus, a combination of exposure during nymphal and adult stages is necessary to attain the highest incidence of diapause in the population. In contrast with our results, Neal et al. (1992) found that *C. cydoniae* reared in a short photoperiod (12:12 [L:D] h), then transferred to long photoperiod (14:10 [L:D] h) upon adult emergence, failed to enter diapause. However, the preoviposition period was protracted relative to bugs reared under long-day conditions, suggesting that a low-intensity diapause may have been induced. Yeargan and Barney (1996) also found little sensitivity of adult *N. americanoferus* and *N. roseipennis* to photoperiod, as did Volkovich et al. (1992) in adult *P. maculiventris*. Substantial adult sensitivity to photoperiod for diapause induction has been observed among various phytophagous and some predaceous Heteropterans (e.g., Hodek 1979, Numata 1987, Musolin and Saulich 1999). In contrast, Ito and Nakata (1998) found that the adult of *Orius sauteri* (Poppius) and *Orius minutus* (L.) were not sensitive to photoperiod for diapause induction.

Short photoperiod served not only to induce diapause in *O. insidiosus*, but also to maintain it, as has been reported for many other insect species (Tauber et al. 1986). Diapausing females transferred from short photoperiod to long photoperiod at various ages (after exposure of various durations to short photoperiod) initiated oviposition at similar intervals after transfer to long-day conditions. This observation corresponds with van den Meiracker's (1994) suggestion that ovi-

position by diapausing female *O. insidiosus* would resume rapidly after transfer to long-day conditions. A similar result was obtained for the coreid bug *Anasa tristis* (De Geer) transferred from outdoors to constant long-day photoperiod in the laboratory throughout the winter (Nechols 1988), indicating that long photoperiod quickly terminated diapause.

Females held under short-day conditions as adults had protracted preoviposition periods, but oviposition was ultimately initiated by nearly all individuals regardless of duration of the exposure to short photoperiod. These results indicate that diapause development was occurring during the period that females were held under short-day conditions. The role of short photoperiod in maintaining diapause is further demonstrated by comparing preoviposition periods of diapausing females transferred from short to long photoperiods, as noted above. There were no significant differences in posttransfer preoviposition periods, again indicating that long photoperiod could rapidly contribute to diapause termination. However, the longer females were held under short-day conditions, the shorter the preoviposition period (after transfer) became (Table 1), although this difference was not significant. This suggests that diapause development was occurring during the prolonged exposure to short photoperiod.

Knowledge of photosensitive stages is valuable for timing the release of beneficial arthropods. The release of *O. insidiosus* nymphs in systems experiencing short photoperiods (e.g., greenhouses lacking supplementary lighting in the autumn or winter of the Temperate Zone) may fail to provide adequate biological control because of the induction of diapause among the predators. Release of adults would be a better approach because of the reduced incidence of diapause in bugs exposed to short photoperiod only during the adult stage, although the risk of some diapause induction remains.

Our results also have important implications for rearing programs. Diapause can provide a means for storing reared beneficial arthropods during periods of low demand, or for stockpiling beneficial insects for sale of large numbers (Tiitanen 1988, Tauber et al. 1993). Predaceous arthropods that diapause can be stored, in a state of diapause, for significantly longer periods and with considerably less negative impact (e.g., reduced mortality) than is the case when non-diapausing predators are simply held at low temperatures (Tiitanen 1988, Tauber et al. 1993). Understanding the timing of photosensitive stages and the conditions requisite for diapause induction, maintenance, and termination permits more efficient use of diapause in storing commercially produced predators.

Photoperiodic sensitivity of *O. insidiosus* for diapause induction appears to occur in the late nymphal instars (the fourth and fifth, with the fifth more sensitive) and in at least the early period of the adult stage. Further, adult females remain sensitive to photoperiod for diapause maintenance, and terminate diapause rather rapidly when transferred from short photoperiod to long photoperiod. Short photoperiod thus

serves to maintain diapause in this species. It should be pointed out that although our results indicate sensitivity of photoperiod in particular life stages, the extent of the photoperiodic response may be affected by changing photoperiod, in contrast with the constant photoperiods used in these experiments (Tauber et al. 1986).

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