

Variation in Diapause Responses Between Geographic Populations of the Predator *Geocoris punctipes* (Heteroptera: Geocoridae)

JOHN R. RUBERSON,¹ KENNETH V. YEARGAN,² AND BLAKE L. NEWTON²

Ann. Entomol. Soc. Am. 94(1): 116-122 (2001)

ABSTRACT The effect of photoperiod on preimaginal development and diapause induction (for reproductive diapause) was evaluated for two geographic populations of the predator *Geocoris punctipes* (Say). One population was from Lexington, KY (N38° 04', W84° 29'), and the other from Tifton, GA (N31° 28', W83° 31'). Six photoperiods were used in the experiment (all at 24 ± 1°C): 10:14, 11:13, 12:12, 13:11, 14:10, and 15:9 (L:D) h. Photoperiod and population had significant effects on the developmental times of embryos and nymphs. However, the developmental differences had no apparent relationship with photoperiod, and those between populations were slight (<1 d). The incidence of diapause increased for both populations as photoperiod decreased, but at daylengths shorter than 14:10 (L:D) h, the frequency of diapause increased much more steeply in the Kentucky population than in the Georgia one. At its peak, the incidence of diapause in the Georgia population (40.9%; 10:14 [L:D] h) was about half that of the peak of the Kentucky population (81.8%; 12:12 [L:D] h). Also, the critical photoperiod for diapause induction was ≈1 h longer in the Kentucky population than in the Georgia population. The preoviposition period was notably affected by photoperiod, and this effect differed between populations. Short daylengths prolonged the preoviposition period in both populations, but the contraction of the preoviposition period in response to longer daylength was more pronounced in the Georgia population. The considerable difference in diapause incidence between the two populations may reflect the relative predictability of inclement conditions in the respective locations.

KEY WORDS *Geocoris punctipes*, photoperiod, reproductive diapause, preoviposition period, life history

THE BIGEYED BUG *Geocoris punctipes* (Say) is an abundant predator in several prominent cropping systems in the United States (e.g., Whitcomb and Bell 1964, Pfannenstiel and Yeargan 1998, Yeargan 1998). Both nymphs and adults of *G. punctipes* are active and aggressive predators that attack a wide variety of pests in cotton, soybean, and other crops (Waddill and Shepard 1974, Ables et al. 1978, Crocker and Whitcomb 1980, Kerns and Gaylor 1993, Medal et al. 1997). In addition, this predator is prone to remain in a habitat, even with few prey, because of its ability to derive nutrients from plants (Stoner 1970, Naranjo and Stimac 1985). Its penetration into important agroecosystems, impact on relevant pest species, and retention in these systems despite low prey populations make *G. punctipes* an attractive focus for developing biological control efforts in ephemeral, row-crop agriculture.

Despite its apparent importance and high visibility in several crops, little is known about the overwintering biology of *G. punctipes*. Dynamics of *G. punctipes* populations during the warm growing season have been well-documented for a variety of crops, but activity during the cool and cold seasons of the year

remain unexplored. Bugg et al. (1991) reported that *G. punctipes* was active in cool-season cover crops (various legumes and rye) in early May in south Georgia, and adults are active quite early in the spring in this region (J.R.R., unpublished data). However, the activities of the bug from midfall until early spring are an important aspect of the predator's biology that must be elucidated to devise crop systems that provide perennial resources to conserve key natural enemies.

The means by which *G. punctipes* passes the winter in temperate regions is unknown. Numerous heteropteran species overwinter as adults in a state of diapause (Ruberson et al. 1998, Musolin and Saulich 1999), and this appears to be the case for at least some *Geocoris* spp. Adults of *Geocoris pallens* Stål in southern California cease reproduction after mid-July and apparently enter an aestival diapause (Staten 1970). Smith (1923) also believed that *G. bullatus* (Say) passes the winter in the adult stage in Idaho (but see Tamaki and Weeks [1972] who found eggs of this species during the winter in south-central Washington). It is possible that *G. punctipes* also overwinters in adult diapause. However, *G. punctipes* has a substantial geographical distribution, which includes much of the southern two-thirds of the United States (Readio and Sweet 1982); therefore, a variety of overwintering responses may occur. Variability among geographical populations in overwintering responses has been reported for

¹ Department of Entomology, University of Georgia, P.O. Box 748, Tifton, GA 31793.

² Department of Entomology, University of Kentucky, Lexington, KY.

other widely distributed insect species (Danilevsky 1965, Tauber et al. 1986).

The objectives of our research were first to determine whether *G. punctipes* from two widely separated geographic populations enter a photoperiodically induced diapause and second to characterize the induction of diapause of these two populations of *G. punctipes* in relation to different photoperiods. This information will provide insight into the overwintering ecology of this species as well as indicate the extent of geographic variability in the diapause syndrome within the species.

Materials and Methods

Acquisition and Maintenance of Predators. Adult *G. punctipes* were collected from various habitats at two locations: Kentucky (Lexington, Fayette County; N 38° 04', W 84° 29') and Georgia (Tifton, Tift County; N 31° 28', W 83° 31'). Bugs collected from these two locations represent populations from the northern (Lexington, KY) and southern (Tifton, GA) portions of its range. Our experiments were duplicated simultaneously in our respective laboratories in Kentucky and Georgia. Approximately half of the bugs collected from the field at each location were shipped to the other laboratory so that both geographic populations were studied in both laboratories. In the laboratory, the bugs were held in male:female pairs (in 100 by 20-mm plastic petri plates) at 25 ± 1°C and a photoperiod of 14:10 (L:D) h. Each pair was provided with frozen eggs of the corn earworm, *Helicoverpa zea* (Boddie), for prey and water in a saturated cotton ball. In addition, a small piece of dry cotton batting was placed in each container as a substrate for oviposition. Oviposition substrates were examined daily for eggs; prey and water were replaced every other day. Eggs (in cotton substrate) were transferred to the experimental conditions (see below), and rearing was initiated in these conditions. All *G. punctipes* used in our experiments were the F₁ progeny of field-collected bugs.

Experimental Procedures. Bugs of both populations were reared under identical conditions in both laboratories. Six photoperiods were used in the study: 10:14, 11:13, 12:12, 13:11, 14:10, and 15:9 (L:D) h. This represents much of the range of photoperiods encountered by the two populations. In Tifton, GA, the photoperiod ranges from 10.2:13.8 (L:D) h at winter solstice to 13.8:10.2 (L:D) h at summer solstice (sunrise to sunset, with the addition of civil twilight). In Lexington, KY, the photoperiod ranges from 9.5:14.5 to 14.5:9.5 (L:D) h. The two locations also differ in their winter conditions. Winter temperatures in the Lexington, KY, area are considerably lower than those in southern Georgia, and autumn temperatures decline earlier and more steeply in Kentucky than in Georgia (Fig. 1).

The same rearing protocols were precisely followed at both locations, and all studies were conducted at 24 ± 1°C regardless of photoperiod. At least 100 eggs of *G. punctipes* from the field-collected adults of each

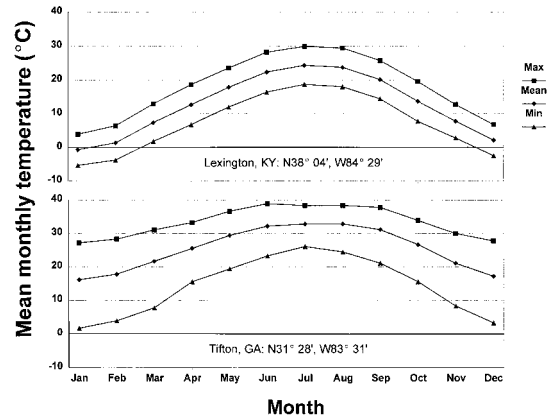


Fig. 1. Monthly temperatures (minimum, mean, and maximum temperatures) for Lexington, KY, and Tifton, GA. Average data for Lexington are from the period 1961–1990, whereas the low and high averages are for 1896–1996 (compiled by the U.S. National Weather Service, Lexington). The data for Tifton are from the period 1925–1998 (compiled by the Coastal Plain Experiment Station, University of Georgia).

geographic population were placed in each of the photoperiodic treatments at each location. The duration of development from oviposition to hatch was recorded. Upon eclosion from eggs, nymphs were transferred individually to petri plates, where they were held throughout their immature developmental period. Nymphs were provided with frozen corn earworm eggs, and water in a small cotton ball. Development of the nymphs was monitored, and the date of adult emergence recorded. After adult emergence, bugs were paired with counterparts from the same photoperiod treatment, and individual pairs were provided with *H. zea* eggs, water-saturated cotton balls, and pieces of dry cotton batting as oviposition substrates. Prey and saturated cotton balls were replaced every other day, and oviposition substrates were examined and replaced daily. Oviposition was monitored daily. Females that had failed to oviposit by 20 d postemergence were considered to be in diapause; a 20-d period represents a 2–3-fold increase over the preoviposition period (5–7 d) of reproductively active females at 24°C.

Females that died prematurely during the experiment or failed to oviposit by the 20th day after emergence were dissected to determine the condition of their ovaries. Males were not dissected. Females were considered to be in diapause if the reproductive system was reduced, with little or no development of ova (Ruberson et al. 1998). In contrast, females with developed ova were considered to be nondiapausing, as were any females that oviposited before the 20th day of their adult life. The percentage of females of each population in diapause was calculated for each photoperiodic treatment and by study location.

Statistical Analyses. Initially, developmental times were compared among photoperiods and between populations with study location (i.e., research laboratory) as a third variate. However, study location had

Table 1. Relationship between photoperiod and egg (oviposition to hatch) and nymphal (egg hatch to adult emergence) developmental times (in days) of two geographic populations (Georgia and Kentucky) of the predator *G. punctipes* reared at various photoperiods ($24 \pm 1^\circ\text{C}$; means \pm SE)

Photoperiod (L:D)	Georgia		Kentucky	
	Egg	Nymph	Egg	Nymph
10:14	12.9 \pm 1.20	30.0 \pm 1.86	12.6 \pm 1.08	29.4 \pm 2.30
<i>n</i>	144	94	181	94
11:13	12.6 \pm 0.71	34.4 \pm 2.76	12.4 \pm 0.64	33.6 \pm 2.41
<i>n</i>	250	128	197	110
12:12	11.2 \pm 0.87	29.8 \pm 2.09	10.9 \pm 0.71	29.3 \pm 1.77
<i>n</i>	126	101	200	90
13:11	11.6 \pm 0.73	31.9 \pm 1.52	12.3 \pm 0.77	31.1 \pm 1.60
<i>n</i>	233	136	197	107
14:10	13.0 \pm 0.76	34.3 \pm 2.72	12.2 \pm 0.90	34.8 \pm 2.34
<i>n</i>	199	100	169	113
15:9	10.7 \pm 0.79	30.3 \pm 2.75	11.3 \pm 0.55	30.5 \pm 2.75
<i>n</i>	232	118	131	112

no significant effect on developmental times or pre-oviposition periods; therefore, data from both research laboratories were pooled for analysis. Subsequently, the developmental times of embryos and nymphs and the preoviposition periods of nondiapausing females were examined using two-way analysis of variance (SAS Institute 1992). Where significant differences were observed, means were separated using the Waller–Duncan Bayesian *k* ratio with *k* set at 500. Additional pairwise comparisons between geographic populations within photoperiods were made using pooled *t*-tests (SAS Institute 1992). Comparisons of diapause incidence between populations within photoperiods were done using a *G* test (Sokal and Rohlf 1994).

Results

Preimaginal Development. The duration of embryonic development was significantly affected by photoperiod ($F = 354.71$; $df = 5, 2,247$; $P < 0.0001$) but not by population ($F = 0.26$; $df = 1, 2,247$; $P = 0.6077$), although there were significant interactions between photoperiod and population ($F = 48.94$; $df = 5, 2,247$; $P < 0.0001$; Table 1). The variation failed to follow any clear pattern in relation to photoperiod, and we suspect that it may simply represent an experimental artifact rather than a feature of the bugs' phenology.

Photoperiod ($F = 201.63$; $df = 5, 1,291$; $P < 0.0001$) and geographic population ($F = 7.12$; $df = 1, 1,291$; $P = 0.0077$) significantly affected nymphal developmental times (Table 1), and these two variables also interacted significantly ($F = 3.34$; $df = 5, 1,291$; $P = 0.0053$). However, as was the case with the eggs discussed above, there was no directional pattern of variation in relation to photoperiod for either population of *G. punctipes* (Table 1). Again, we consider this variation to be experimental artifact.

Reproduction. The incidence of diapause (i.e., failure to oviposit or produce mature ova within 20 d of adult emergence) differed significantly between the two populations at all daylengths shorter than 14 h (Fig. 2; Table 2). At the two long-day conditions (14:10 and 15:9 [L:D]), nearly 100% of the females from both

populations reproduced. However, the frequency of diapause was substantially less in the Georgia than in the Kentucky population at the shorter photoperiods. Diapause incidence in the Kentucky population increased rapidly from 14:10 to 12:12 (L:D) h, with an asymptote for diapause incidence slightly above 80%. In contrast, the diapause response curve for the Georgia population increased more gradually as photoperiod decreased from 14:10 to 11:13 (L:D) h, leveling at $\approx 40\%$. Thus, less than half of the Georgia bugs entered diapause at any photoperiod, whereas over 80% of the Kentucky bugs did so under short-day conditions, indicating a stronger diapause response in the Kentucky bugs.

The critical photoperiod for diapause induction (defined here as the point where diapause is induced in 50% of those inclined to diapause; Tauber et al. 1986) also differed between the two populations (Fig. 2). Although the critical photoperiod for the Georgia population was $\approx 12.4:11.6$ (L:D) h, it was $\approx 13.2:10.8$ (L:D) h for the Kentucky population. These photoperiods would be encountered on ≈ 20 August and 10 September for the Kentucky and Georgia populations, respectively (Fig. 3).

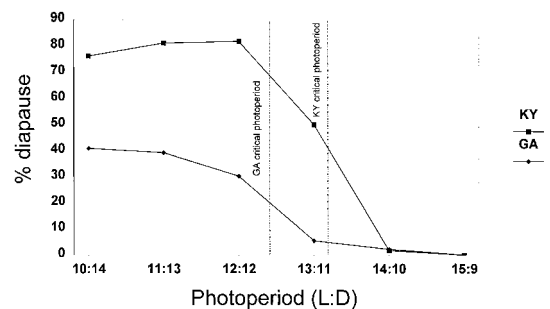


Fig. 2. Incidence of diapause in two geographic populations (GA, Georgia; KY, Kentucky) of *G. punctipes* in relation to photoperiod ($24 \pm 1^\circ\text{C}$; sample sizes presented in Table 2). Timing of the critical photoperiod (point where diapause is induced in 50% of those inclined to diapause) for the two populations is indicated by vertical dashed lines labeled with the appropriate population.

Table 2. Results from dissection of female *G. punctipes* from two geographical populations which had failed to oviposit by the 20th day after molting to the adult stage under various photoperiodic conditions ($24 \pm 1^\circ\text{C}$)

Photoperiod (L:D)	Georgia			Kentucky			Chi-square value ²	P ^b
	Reduced ovaries	Develop ova	% diapausing (n ^a)	Reduced ovaries	Developed ova	% diapausing (n ^a)		
10:14	20	1	40.9 (44)	32	0	76.2 (42)	51.20	<0.001
11:13	20	3	39.2 (51)	42	4	81.1 (53)	57.27	<0.001
12:12	12	0	30.2 (43)	37	3	81.8 (44)	60.55	<0.001
13:11	1	1	5.5 (55)	24	1	50.0 (50)	24.40	<0.001
14:10	NA ^c	NA	2.2 (46)	1	0	1.7 (58)	1.14	>0.10
15:9	NA	NA	0 (55)	NA	NA	0 (52)	0.00	1.00

Reduced ovarian development (reduced ovaries) is indicative of diapause, whereas the presence of mature or maturing ova (developed ova) indicates a reproductive, hence nondiapause, state.

^a Number of females dissected, including diapausing and nondiapausing bugs, and ovipositing females.

^b Values are for comparisons of % diapause between the two geographic populations.

^c NA represents treatments in which all females oviposited.

The duration of the preoviposition periods during the 20-d observation period after adult emergence (Table 3) was significantly affected by photoperiod ($F = 64.41$; $df = 5, 366$; $P < 0.0001$) and population ($F = 71.35$; $df = 1, 366$; $P < 0.0001$). There was also a significant interaction between photoperiod and population ($F = 8.71$; $df = 5, 366$; $P < 0.0001$). Frequency of females ovipositing changed with respect to photoperiod for both populations (Fig. 2). Further, dissections of females after termination of the experiment on day 20 revealed that nearly all of the females that had failed to oviposit by day 20 had very reduced ovaries, commensurate with the diapause syndrome (Table 2). Under longer daylengths, the variability of the preoviposition periods declined, and the mean duration shortened as well (Table 3; Fig. 4). Thus, longer daylengths promoted earlier and more synchronous oviposition. This variability indicates a graded response to photoperiod, which may be expressed as varying degrees of diapause intensity. There were significant differences in preoviposition periods between the two populations at 12:12, 13:11, 14:10, and 15:9 (L:D) h for the 20-d period over which

observations were made. No such differences were observed for the 10:14 or 11:13 (L:D) h treatments during this period. In all cases of significant differences, the preoviposition period for the Georgia population was shorter than that of the Kentucky population (Table 3). The effect of photoperiod on the preoviposition period was more pronounced for the Georgia bugs than for the Kentucky bugs (Fig. 4).

Discussion

Our results provide no evidence for preimaginal diapause in *G. punctipes* because there were no notable developmental effects of photoperiod on either embryonic or nymphal development. Photoperiodic effects on nymphal development have been reported in other studies of heteropteran predators (Ruberson et al. 1991, Tommasini and Nicoli 1996) and of phytophagous heteropterans (Musolin and Saulich 1997, 1999), and significant effects of photoperiod on preimaginal development were obtained in our study. But the lack of an obvious relationship with daylength suggests that these differences were experimental artifacts unrelated to the diapause syndrome.

It is clear from our results that there is a reproductive diapause in both geographic populations of *G.*

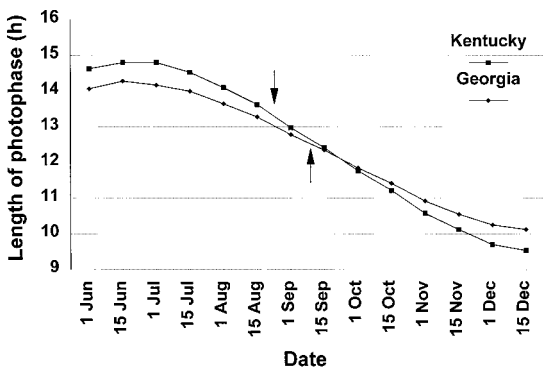


Fig. 3. Photoperiods occurring in the two locations of origin for the populations of *G. punctipes* studied (includes civil twilight; data from U.S. Naval Observatory). Arrow pointing down denotes the critical photoperiod for the Kentucky population, whereas the arrow pointing up indicates the critical photoperiod for the Georgia population ($24 \pm 1^\circ\text{C}$).

Table 3. Preoviposition periods (in days) for female *G. punctipes* from two geographical populations (Georgia and Kentucky) reared under various photoperiods ($24 \pm 1^\circ\text{C}$)

Photoperiod (L:D)	Population		P t, df
	Georgia	Kentucky	
10:14	12.3 ± 4.98	13.5 ± 3.89	0.5825
n	22	6	0.56, 26
11:13	13.2 ± 4.27	15.6 ± 2.51	0.2384
n	28	5	1.20, 31
12:12	8.9 ± 3.78	17.5 ± 2.65	<0.0001
n	32	4	4.38, 34
13:11	6.5 ± 2.37	11.8 ± 3.99	<0.0001
n	53	24	7.14, 75
14:10	6.7 ± 1.32	8.5 ± 2.21	<0.0001
n	44	57	4.95, 99
15:9	4.9 ± 0.97	6.0 ± 1.31	<0.0001
n	52	51	4.58, 101

Statistics are for pairwise comparisons of populations within photoperiods (pooled t-test).

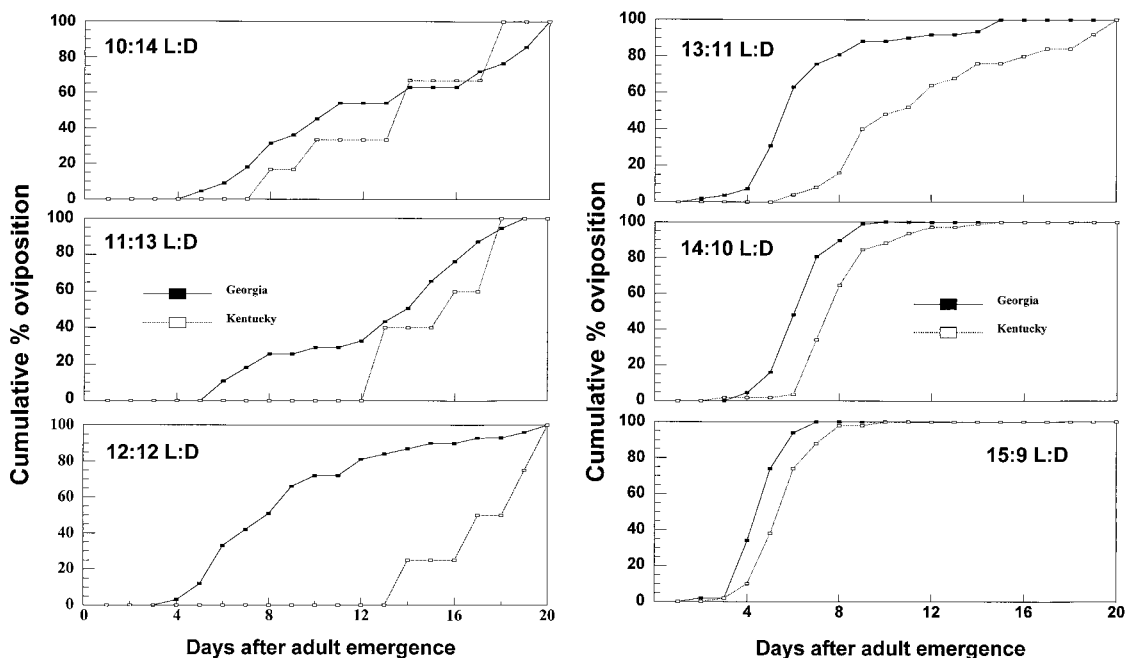


Fig. 4. Cumulative percentage of females initiating oviposition during the first 20 d of adult life in relation to age under different photoperiods ($24 \pm 1^\circ\text{C}$) for two geographic populations of *G. punctipes*. Sample sizes (i.e., total number of females that oviposited within 20 d) for each photoperiod (L:D) h were six (10:14), five (11:13), four (12:12), 24 (13:11), 57 (14:10), and 51 (15:9) for the Kentucky population and 22 (10:14), 28 (11:13), 32 (12:12), 53 (13:11), 44 (14:10), and 52 (15:9) for the Georgia population.

punctipes, although the incidence and intensity of response varied between the populations. Further, photoperiod had important effects on the incidence and expression of diapause in both populations.

Diapause incidence was strongly affected by photoperiod for both populations (Fig. 2), but the response was much more pronounced for the Kentucky than the Georgia population. The shape and magnitude of the response curve for the Kentucky population are comparable to the diapause response observed for *Nabis americoferus* Carayon and *Nabis roseipennis* Reuter populations also collected near Lexington, KY (Yeargan and Barney 1996). In contrast, the diapause response curve for the Georgia population increased more gradually as photoperiod decreased from 14:10 to 11:13 (L:D) h, leveling at $\approx 40\%$. Thus, less than half of the Georgia bugs entered diapause at any photoperiod, whereas $>80\%$ of the Kentucky bugs did so under short-day conditions.

The critical photoperiod for diapause induction for the Georgia population was $\approx 12.4:11.6$ (L:D) h and $\approx 13.2:10.8$ (L:D) h for the Kentucky population. It is important to note, however, that temperature often modifies photoperiodic responses in insects. Temperatures in south Georgia often exceed 25°C through much of September (Fig. 1), and high temperatures tend to discourage or delay the induction of autumnal diapause (Tauber et al. 1986). Thus, it is quite likely that diapause in the Georgia population in the field would actually occur somewhat later in the season. The difference in critical photoperiods between the

two populations at the temperature tested thus amounted to a 0.60 h increase per 5-degree increase in latitude, although the critical photoperiods for the respective populations are most likely modified in the field as noted above. Similar latitudinal variation has been observed for other insects (Danilevsky 1965, Tauber et al. 1986), but its expression in the field may be modified by environmental factors as well, such as local climatic and shelter conditions, and altitude.

The graded response in the incidence of diapause induction and in the length of the preoviposition period for both populations indicates a quantitative response to daylength, which has been reported in other insects that undergo a reproductive diapause as adults (Tauber and Tauber 1973, Kimura 1990). It should be noted that oviposition was only monitored for 20 d after adult emergence, so longer preoviposition periods were precluded by the experimental design. Nevertheless, within the 20-d observation period there were clear shifts in preoviposition period related to both photoperiod and population. Preoviposition periods were lengthened and more variable under short photoperiods than at 14:10 (L:D) h or 15:9 (L:D) h (Table 3; Fig. 4), demonstrating a quantitative response, at least for diapause induction. The lengthening of preoviposition periods also was more pronounced for the Kentucky population than for the Georgia population in the intermediate photoperiods (13:11 and 12:12 [L:D]) indicating a more intense diapause response in the Kentucky population in these photoperiods.

The difference in diapause frequency and intensity (as expressed by preoviposition periods) between the two populations likely reflects the different conditions under which the two populations exist. A comparison of the annual temperature patterns for the two locations demonstrates the different temperature regimes (Fig. 1). The temperatures in Lexington are more moderate year round than are those in Tifton. Also, the range of variability between mean monthly minimum and maximum temperatures remains rather constant throughout the year in Lexington (range, of ≈ 10 – 12°C). In contrast, the temperatures in Tifton are higher in the summer, and much more variable during the winter (minimum to maximum range of 23 – 25°C in December and January) than those in Lexington. Thus, for any given winter the temperatures in Tifton will be more difficult to predict than those in Lexington, with a reasonable possibility in any month of temperatures amenable to growth and activity. Under these conditions, it would be appropriate for a broad range of overwintering responses (from diapause to avoidance of diapause with reproduction) to be maintained in a population, whereas this range should be narrowed by the more predictable, less salubrious winter conditions in Lexington, that would frequently eliminate bugs that attempt to reproduce during the winter. These differences in predictability of winter conditions are reflected in the different responses of the two populations. Over half of the Tifton population failed to enter diapause (as defined by our preoviposition criteria), and those that failed to enter diapause under short photoperiods typically exhibited a range of preoviposition periods. Such a flexible life history would be adaptive in a highly variable environment that has a reasonable probability of being amenable to reproduction, as is the case in the Tifton area (Fig. 1). In contrast, the Lexington climate is more consistently adverse in the winter, and the bugs were much more likely to delay reproduction either through diapause or through delayed preoviposition periods, as would be expected under these conditions.

The results obtained here may be modified by more natural events, such as changing rather than static photoperiods and temperatures. Nevertheless, they demonstrate clear differences between the two populations of *G. punctipes* and clearly show the importance of photoperiod for the induction of reproductive diapause in this predator. Further, the presence of both diapausing and reproductive individuals in winter populations provides an opportunity to devise overwintering habitats suitable to both groups, which can serve as sources from which predators can colonize desired crop systems the following spring.

Acknowledgments

Our thanks to Maurice J. Tauber and Catherine A. Tauber (Cornell University), and Dmitry L. Musolin (Osaka City University) for their critical reviews and helpful comments. We also appreciate the assistance of Mindy Houle, Henry Price, Will Carroll, and Peggy Goodman (laboratory of J.R.R.) for their assistance with rearing. The investigation

reported here was conducted in connection with projects of the Georgia and Kentucky Experiment Stations (University of Kentucky paper #00-08-89).

References Cited

- Ables, J. R., S. L. Jones, and D. W. McCommas, Jr. 1978. Response of selected predator species to different densities of *Aphis gossypii* and *Heliothis virescens* eggs. *Environ. Entomol.* 7: 402–404.
- Bugg, R. L., F. L. Wäckers, K. E. Brunson, J. D. Dutcher, and S. C. Phatak. 1991. Cool-season cover crops relay intercropped with cantaloupe: influence on a generalist predator, *Geocoris punctipes* (Hemiptera: Lygaeidae). *J. Econ. Entomol.* 84: 408–416.
- Crocker, R. L., and W. H. Whitcomb. 1980. Feeding niches of the big-eyed bugs *Geocoris bullatus*, *G. punctipes*, and *G. uliginosus* (Hemiptera: Lygaeidae: Geocorinae). *Environ. Entomol.* 9: 508–513.
- Danilevsky (Danilevskii), A. S. 1965. Photoperiodism and seasonal development of insects. Oliver and Boyd, Edinburgh.
- Kerns, D. L., and M. J. Gaylor. 1993. Biotic control of cotton aphids (Homoptera: Aphididae) in cotton influenced by two insecticides. *J. Econ. Entomol.* 86: 1824–1834.
- Kimura, M. T. 1990. Quantitative response to photoperiod during reproductive diapause in the *Drosophila auraria* species-complex. *J. Insect Physiol.* 36: 147–152.
- Medal, J. C., A. J. Mueller, T. J. Kring, and E. E. Gbur, Jr. 1997. Predation of *Spissistilus festinus* (Homoptera: Membracidae) nymphs by hemipteran predators in the presence of alternative prey. *Florida Entomol.* 80: 451–456.
- Musolin, D. L., and A. Kh. Saulich. 1997. Photoperiodic control of nymphal growth in bugs (Heteroptera). *Entomol. Rev.* 77: 768–780.
- Musolin, D. L., and A. Kh. Saulich. 1999. Diversity of seasonal adaptations in terrestrial true bugs (Heteroptera) from the Temperate Zone. *Entomol. Sci.* 2: 623–639.
- Naranjo, S. E., and J. L. Stimac. 1985. Development, survival, and reproduction of *Geocoris punctipes* (Hemiptera: Lygaeidae): effects of plant feeding on soybean and associated weeds. *Environ. Entomol.* 14: 523–530.
- Pfannenstiel, R. S., and K. V. Yeargan. 1998. Association of predaceous Hemiptera with selected crops. *Environ. Entomol.* 27: 232–239.
- Radio, J., and M. H. Sweet. 1982. A review of the Geocorinae of the United States east of the 100th Meridian (Hemiptera: Lygaeidae). *Misc. Publ. Entomol. Soc. Am.* 12: 1–91.
- Ruberson, J. R., L. Bush, and T. J. Kring. 1991. Photoperiodic effect on diapause induction and development in the predator *Orius insidiosus* (Heteroptera: Anthracoridae). *Environ. Entomol.* 20: 786–789.
- Ruberson, J. R., T. J. Kring, and N. Elkassabany. 1998. Overwintering and the diapause syndrome of predatory Heteroptera, pp. 49–69. *In* M. Coll and J. R. Ruberson [eds.], *Predatory Heteroptera: their ecology and use in biological control*. Proceedings, Thomas Say Publications in Entomology Entomological Society of America, Lanham, MD.
- SAS Institute. 1992. SAS user's manual, Release 6.03, SAS Institute, Cary, NC.
- Smith, R. H. 1923. The clover aphid: biology, economic relationship and control. *Idaho Agric. Exp. Stn. Res. Bull.* 3.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*, 2nd ed. W. H. Freeman and Co., New York.

- Staten, R. T. 1970. The bionomics and entomophagous vector capabilities of *Geocoris punctipes* Say. Ph.D. dissertation, University of California, Riverside.
- Stoner, A. 1970. Plant feeding by a predacious insect, *Geocoris punctipes*. J. Econ. Entomol. 63: 1911–1915.
- Tamaki, G., and R. E. Weeks. 1972. Biology and ecology of two predators, *Geocoris pallens* Stål and *G. bullatus* (Say). USDA-ARS Tech. Bull. 1446.
- Tauber, M. J., and C. A. Tauber. 1973. Quantitative response to daylength during diapause in insects. Nature (Lond.) 244: 296–297.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. Seasonal adaptations of insects. Oxford University Press, New York.
- Tommasini, M. G., and G. Nicoli. 1996. Evaluation of *Orius* spp. as biological control agents of thrips pests. Further experiments on the existence of diapause in *Orius laevigatus*. IOBC/WPRS Bull. 19: 183–186.
- Waddill, V., and M. Shepard. 1974. Potential of *Geocoris punctipes* [Hemiptera: Lygaeidae] and *Nabis* spp. [Hemiptera: Nabidae] as predators of *Epilachna varivestis* [Coleoptera: Coccinellidae]. Entomophaga 19: 421–426.
- Whitcomb, W. H., and K. Bell. 1964. Predaceous insects, spiders, and mites of Arkansas cotton fields. Univ. Ark. Agric. Exp. Stn. Bull. 690.
- Yeagan, K. V. 1998. Predatory Heteroptera in North American agroecosystems: an overview, pp. 7–19. In M. Coll and J. R. Ruberson [eds.], Predatory Heteroptera: their ecology and use in biological control. Proceedings, Thomas Say Publication in Entomology. Entomological Society of America, Lanham, MD.
- Yeagan, K. V., and W. E. Barney. 1996. Photoperiodic induction of reproductive diapause in the predators *Nabis americanoferus* and *Nabis roseipennis* (Heteroptera: Nabidae). Ann. Entomol. Soc. Am. 89: 70–74.

Received for publication 31 May 2000; accepted 5 September 2000.
