Diapause in the Boll Weevil (Coleoptera: Curculionidae): Life-Stage Sensitivity to Environmental Cues

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Ann. Entomol. Soc. Am. 92(3): 396–402 (1999)

ABSTRACT This study examines the diapause response in naturally occurring boll weevils under field and simulated field environments of north Mississippi. Squares containing early-stage weevils were collected in July, August, and September and subsamples from each group were installed into similar dynamic environments in the laboratory. In this manner, some weevils experienced uninterrupted photoperiods and temperatures between the field and laboratory (controls), and others experienced a shift forward in time or backward in time between the field and laboratory (treated). Results indicate selective sensitivity among individuals to diapause-inducing or averting daylengths and temperatures during early life stages independent of later stages and during late stages (including adults) independent of earlier stages. For example, it appears that some individuals are sensitive primarily during the early or late life stages, and depending on the environmental cues received at these times, they may or may not develop the diapause phenotype as adults. However, the rates of gain or loss in the acquisition of diapause depend on the intensity and duration of the token stimuli during part or all of the life cycle. If the proper cues are sustained throughout the life cycle, then the expression of diapause in the population will be maximized. Alteration in cues at any time will increase or decrease the percentage of weevils in diapause, with the relative effect related to the intensity and duration of the original stimuli. Once they receive a threshold to diapause-inducing stimuli, populations appear to be more responsive to environmental change. These results may explain some of the variability observed in diapause among studies.

KEY WORDS *Anthonomus grandis grandis*, diapause, cotton, model

DIAPAUSE IN INSECTS is a neurohormonally mediated, dynamic state of low metabolism, reduced morphogenesis, increased resistance to environmental extremes, and altered behavioral activity (Tauber et al. 1986). Animals move into, through, and out of diapause in a series of interdependent steps. Prediapause is initiated when a life stage(s) perceives environmental cues (token stimuli) that warn of impending adverse conditions. The ensuing changes enable the animal to reach the diapausing stage in the proper condition and at the correct time and habitat. Diapause induction follows with the development and intensification of specific traits associated with dormancy per se. These traits include suppressed growth, development, reproduction, metabolism, behavior, and altered resistance to environmental extremes (e.g., increased cold, heat, or drought tolerance).

The changes that precede and accompany the diapausing state collectively represent the diapause syndrome (Tauber et al. 1986). Each characteristic associated with diapause is expressed at a specific time and develops at a specific rate under the direction of external and internal factors. Thus, the cues controlling the acquisition and full expression of the syndrome are both complex and dynamic. For example, successful induction and intensification may not occur if specific conditions do not develop at the proper time. In fact, the occurrence (or nonoccurrence) of certain environmental cues may alter or even reverse the induction process. The effectiveness of the diapause-inducing and intensifying stimuli and the sensitivity of the stage(s) perceiving the stimuli may even influence the duration of diapause development (Tauber et al. 1986).

For these reasons, it is important to know what environmental cues regulate diapause and how these cues interact with life stages in eliciting the full diapause response. This knowledge provides the foundation for conducting and interpreting research on diapause maintenance and postdiapause transition—the remaining phases of diapause. The current research on the boll weevil, *Anthonomus grandis grandis* Boheman, was undertaken with these concepts in mind.

Past research on boll weevil diapause sought to identify the primary token stimuli responsible for its initiation, and although this research generally identifies photoperiod, temperature, and host/diet as influencing factors, the exact influence of these variables on individual weevil life stages is poorly understood (see Wagner and Villavaso 1999). One reason for this situation is the lack of consistent and rigorous experimental design. For example, few tests have evaluated the response of several life stages to potential stimuli over a range of like conditions. Investigators used

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different methods to assess diapause on different weevil strains, making it difficult to evaluate and compare results within and among studies. These problems aside, research to identify the duration of sensitivity in the weevil to potential token stimuli is limited, perhaps because of a lack of understanding of its relevance.

Successful diapause induction depends on specific conditions occurring at the proper time, and any variation in these conditions may alter or reverse the induction process (Tauber et al. 1986). The effectiveness of the stimuli and the sensitivity of the stage(s) perceiving the stimuli may influence the depth and, thus, the duration of diapause. If the boll weevil responds to multiple environmental cues over its life cycle, as suggested by the literature (Wagner and Villavaso 1999), then the application of artificial (unnatural) procedures to study diapause would contribute to (help explain) the variable responses observed within and among studies.

Believing that the regulation of prediapause and diapause induction in the boll weevil is complex and dynamic, and that the use of techniques applied in the past will not advance our understanding of what happens in the field, we developed alternative methods to study diapause under simulated field conditions. Whereas past studies typically have been conducted using artificial conditions known to adversely affect the incidence of diapause in populations (e.g., using laboratory colony weevils reared on artificial diets under static environments), the current study evaluates diapause in wild weevils from Mississippi held under field and simulated field photoperiods and temperatures. Specifically, we evaluated the combined effects of these independent variables on early immature, late immature, and adult stages. The effect of high temperature was also evaluated on adults reared and held under diapause-inducing conditions. This study was conducted to better define the duration of sensitivity in wild weevils to diapause-inducing cues.

Materials and Methods

Experimental Procedures. Boll weevils originated from populations oviposited in cotton flower buds (squares) from commercial fields in Union County, MS, during July through September 1989, 1990, and 1992–1994. Fields were within 8 km of each other. To obtain a high percentage of early life stages among weevils, only green infested squares were removed from plants before flaring. Subsamples indicated that most weevils were eggs, 1st, and early 2nd instars at the time of collection, with fewer older larvae and no pupae.

Infested squares were brought to the laboratory immediately after collection and divided among clear plastic boxes (27 by 40 by 10 cm) that served as rearing containers. Squares were placed on hardware cloth supported by damp sponges 4 cm above the bottom of the boxes. Screened holes at the ends of the containers allowed ventilation. High humidity was maintained to prevent square drying.

Rearing containers were placed in environmental cabinets within which the temperature and lights were computer controlled using instructions described by Wagner and Villavaso (1999). Immature and adult boll weevils were held under simulated field temperatures and photoperiods of north Mississippi. Environments varied within and among days, incremented from different starting dates, depending on the objective of each test, described below.

Sensitivity of Early Versus Late Life Stages to Environmental Cues. To examine the sensitivity of early (occurring in the field) and late (occurring in the laboratory) life stages to diapause-inducing or -averting environments, infested squares were collected in July (early season), August (midseason), and September (late season), and subsamples from each collection date were placed in cabinets mimicking July, August, and September environments. In this manner, some weevils experienced uninterrupted photoperiods and temperatures between the field and laboratory (controls; from Wagner and Villavaso [1999]; Table 1), and others experienced a shift forward in time or backward in time between the field and laboratory (treated).

Treated weevils that were moved forward in time experienced conditions hypothesized to be more favorable to diapause induction than the controls held in the earlier environments. These weevils were collected in July 1989 and 1990 (JD 208 and 212) and were moved 20 and 40 d later than the controls (Table 1). Other weevils were collected in July 1992 (JD 213) and were advanced 33 d. Treated weevils that were moved backward in time experienced conditions hypothesized to be less favorable to diapause induction than the controls held in the later environments. These weevils were collected in September 1989 (JD 249) and were moved 20 and 40 d earlier than the controls, or they were collected in September 1992 (JD 255) and were moved 20 and 60 d earlier. Finally, treated weevils from August 1989 and 1990 (JD 230 and 229) were moved 20 d earlier and 20 d later than the controls.

Adult Sensitivity to Environmental Cues. Tests were conducted to examine adult sensitivity to diapause-inducing or -averting environments, independent of other life stages. For example, early stage weevils in squares were collected in July 1994 (JD 200) and reared under dynamic photoperiods and temperatures from that date. Adults were subsampled on emergence, and a treatment group was moved to a cabinet set 40 d later than the controls experiencing an uninterrupted environment.

In another test, adults were exposed to above-normal temperatures to examine whether this treatment would suppress diapause in weevils that were reared under a late, diapause-inducing environment. Immatures were collected in September 1993 (JD 263), reared under dynamic photoperiods and temperatures from that date, subsampled on emergence, and a treatment group was moved to a cabinet with temperatures set 60 d earlier than the controls. Both control and

Table 1. Percentage of prediapausing male and female boll weevils collected in the field as immatures in squares on different Julian dates and held in cabinets under dynamic photoperiods and temperatures from different starting dates until dissected

Year	Collect JD	Start JD	Adult diet	Adult age[a]	Males				Females			
					N	*n*	Cabinet mean emergence JD	%	*N*	*n*	Cabinet mean emergence JD	%
					Immatures moved forward in time							
89	208	228	S	18–21	60	60	240.4	55.0	39	39	240.1	28.2
89	208	248	S	18–21	61	60	262.2	73.3	73	73	262.1	35.6
89	230	250	S	18–22	124	124	264.4	83.1	130	130	264.5	70.8
90	212	232	S	19–23	147	147	244.4	69.4	190	187	244.2	49.7
90	212	252	S	19–25	167	167	266.7	88.6	178	177	266.8	84.2
90	229	249	S	19–21	51	51	265.2	94.1	35	35	265.4	97.1
92	213	246	S	19–20	117	116	261.2	75.9	114	113	261.2	41.6
					Immatures moved backward in time							
89	230	210	S	14–15	86	83	221.7	47.0	101	100	221.4	25.0
89	249	229	S	18–22	130	130	242.8	84.6	125	124	242.5	75.8
89	249	209	S	13–17	136	135	221.7	57.8	165	161	221.3	37.9
90	229	209	S	14–16	66	66	220.7	57.6	58	56	220.7	37.5
92	255	235	S	21–23	53	53	249.7	100.0	63	63	249.4	90.5
92	225	195	S	21–23	52	50	207.6	46.0	42	42	207.9	33.3
					Adults moved forward in time							
94	200	200	S	17–37	178	178	211.7[b]	48.9	162	161	211.7[b]	26.7
					Adults moved backward in time (temperature only)							
93	263	263	S	13–15	51	51	283.6[c]	90.2	48	47	283.8[c]	78.7
93	263	263	B	14–16	42	42	284.5[c]	92.9	46	46	284.4[c]	93.5

S, squares; B, bolls. *N*, indeterminate, reproductive, and diapausing adults. *n*, reproductive and diapausing adults used to calculate percentage diapause.

[a] Age at dissection.

[b] Light and temerature controls reset +40 d on emergence (e.g., to JD 252).

[c] Temperature control reset −60 d on emergence (e.g., to JD 224).

treatment groups were exposed to the same late-season photoperiods. Adults were fed squares or bolls.

Physiological Status of Weevils. Boll weevils were collected from rearing containers each day of the emergence period and placed in clear plastic containers (15 cm diameter by 6 cm deep) of 100 weevils or less. Containers were provisioned with fresh, debracted, pristine squares daily in excess of feeding demand. Some weevils were held as individual mating pairs in clear plastic cubes (2.5 by 2.5 cm) and fed 1 square or small boll per day. The physiological status of adults was determined by dissection 13–37 d after emergence. Adults were classified as indeterminate, reproductive, or prediapausing as described by Wagner and Villavaso (1999).

Analytical Procedures. Mean emergence dates of weevils were calculated for groups sorted by year, collection date, beginning laboratory date, adult diet, and sex (SAS Institute 1989). Frequency counts were obtained for indeterminate, reproductive, and prediapausing weevils in each group. The proportions of reproductive and prediapausing adults were calculated after excluding indeterminate weevils. Percentages of prediapausing males and females in each treatment group were plotted (dependent variable) at their respective mean emergence dates (independent variable) and compared with control data found in Wagner and Villavaso (1999). Treatment effects were also compared with the expected seasonal trends of diapause among males and females described by the logistic equations from Wagner and Villavaso (1999):

$$F(x_m) = 98.71/[1 + \exp(0.0865[230.1 - x])] \quad [1]$$

$$F(x_f) = 98.73/[1 + \exp(0.1023[242.5 - x])], \quad [2]$$

where $F(x_m)$ and $F(x_f)$ = percentages of prediapausing males and females, respectively, emerging on Julian date x. The 1st parameter of the equations represents the upper asymptote of the curves, the 2nd the slope, and the 3rd the Julian date at which 50% of the emerging animals are prediapausing.

Results and Discussion

Diapause is a multifaceted response of insects to token stimuli—environmental cues that are, in themselves, not favorable or unfavorable to the insect but which forecast adverse seasonal changes (Tauber et al. 1986). This response requires a period of receptivity to these cues that initiates changes in the animal in preparation for dormancy (prediapausing phase) and a period of suppressed morphogenesis, metabolism, behavior, and resistance to environmental extremes that commits the animal to diapause (diapause induction phase). Because the boll weevil overwinters as an adult, it potentially has considerable time during development to perceive these cues and prepare for diapause. Understanding the early sequence of events leading up to diapause is important to subsequent studies on diapause maintenance and termination.

Sensitivity of Early Versus Late Life Stages. Boll weevils that initiated development in July and were

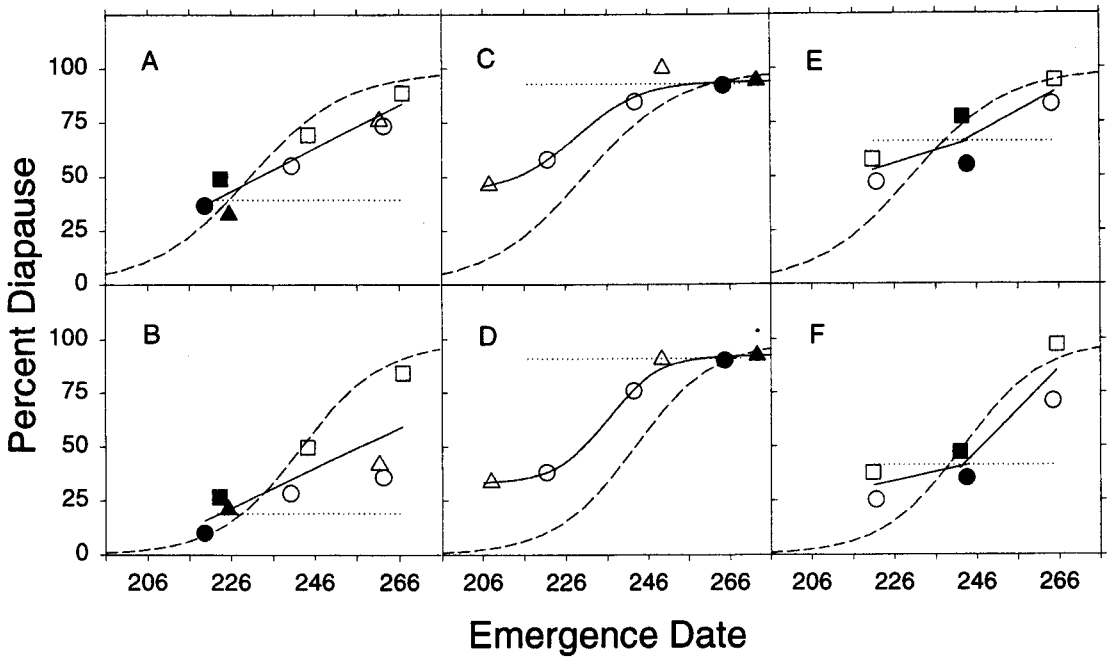

Fig. 1. Percentages of male (top row) and female (bottom) boll weevils in prediapause on the Julian date of emergence from insects collected in the field in squares and held under uninterrupted natural photoperiods and temperatures in the laboratory until dissected as adults (controls; solid data from Wagner and Villavaso [1999]) or subsampled on collection and moved (A and B) immatures forward in time, (C and D) backward in time, and (E and F) forward and backward in time (treated; open data). Circles depict data from 1989, squares 1990, and triangles 1992. Solid lines depict regressions fitted to control and treated data; dashed lines regression equations 1 and 2 to control data over entire season; and dotted lines mean diapause of controls.

subsequently transferred to August and September environments had higher percentages of diapause than weevils that remained in the earlier environments throughout their life cycle (Fig. 1 A and B, open versus closed data, respectively). The percentage of prediapausing adults increased linearly with the time of emergence among the control and treatment groups (solid lines). Imposing diapause-inducing conditions on later life stages had similar effects on males and females, as illustrated by the similar slopes of the regression lines: $Y = 0.992x - 181$ for males and $Y = 0.928x - 188$ for females. Although percent diapause was greater in treated than control weevils (mean controls = 39.4% for males and 19.2% for females, dotted lines, Fig. 1 A and B), it was less than that predicted by equations 1 and 2 (dashed lines, representing the expected seasonal trends of diapause in control weevils held under uninterrupted environments throughout their life cycle, from Wagner and Villavaso [1999]).

In a similar fashion, boll weevils that initiated development in August and were transferred to September environments had higher percentages of diapause than control weevils that remained in the midseason environment throughout their life cycle (Fig. 1 E and F, late open versus closed data). Although percent diapause in treated weevils was slightly lower than that predicted by equations 1 and 2 (compare the solid lines right of the closed data with the corresponding portions of the dashed lines), the rates of increase were similar in the 2 groups.

Boll weevils that initiated development in September and were subsequently transferred to August and July environments generally had lower percentages of diapause than the control weevils that remained in the later environments throughout their life cycle (Fig. 1 C and D, open versus closed data). The percentage of prediapausing adults decreased in a nonlinear fashion with the time of emergence among the control and treated groups (solid lines), given by the following equations:

$$F(x_{\text{males}}) = 42.72 + 51.22/[1 + \exp(0.1276[228.6 - x])] \quad [3]$$

$$F(x_{\text{females}}) = 32.62 + 59.84/[1 + \exp(0.1589[236.0 - x])]. \quad [4]$$

The shapes of these trends were similar to the seasonal trends observed among control weevils only, given by equations 1 and 2 (dashed lines). For example, the incidence of diapause was not affected by small negative displacements in time (solid versus dotted lines), but diapause decreased in weevils moved farther back in time, eventually leveling off in adults with the greatest displacement. Imposing diapause-averting condi-

tions on later life stages had a similar effect on males and females. Although percent diapause was less in treated weevils than controls (mean controls = 93.0% for males and 91.1% for females, dotted lines, Fig. 1 C and D), it was greater than that predicted by equations 1 and 2 (dashed lines).

Weevils that initiated development during August and were subsequently transferred to July environments had lower percentages of diapause than control weevils that remained in the midseason environments throughout their life cycle (Fig. 1 E and F, early open versus closed data). The rates of decrease in diapause among these treated weevils were less than those predicted by equations 1 and 2 (compare the solid line to the left of the closed data and the corresponding portion of the dashed line).

These tests provided evidence of the sensitivity of stages to diapause-inducing stimuli and, indirectly, of the stimuli themselves. Moving immature weevils forward in time allowed later life stages to experience diapause-inducing photoperiods and temperatures, which increased the percentage of weevils in diapause in spite of the diapause-averting cues received earlier in life (Fig. 1 A, B, E, and F). Moving weevils backward in time allowed later life stages to experience diapause-averting photoperiods and temperatures, which decreased the percentage of weevils in diapause in spite of the diapause-inducing cues received earlier in life (Fig. 1 C, D, E, and F). These changes were not the result of dietary factors because all weevils within tests (e.g., collected at the same time) were fed from the same group of squares, originating during the early, mid, or late season. These results do not exclude the possibility of a dietary effect on diapause, which can be further examined by taking advantage of the design of the experiment.

If the environmental cues responsible for diapause induction include a dietary factor, then it is reasonable to assume this factor would become more important as the season progresses. Weevils developing early in the season should experience host/diet conditions more favorable to reproduction than diapause, whereas the incidence of these states in a population should reverse as the host deteriorates seasonally. This study provided an opportunity to test this hypothesis, although only indirectly, by comparing the response of weevils held under contrasting field and laboratory environments. For example, weevils moved from a late field environment to an earlier laboratory environment and fed late-season squares should have higher diapause than weevils moved from a contrasting early field, later laboratory environment and fed early-season squares. Evidence supporting this hypothesis could not be found by comparing the 3 contrasting combinations in this study (Fig. 2; Table 1). In all cases, weevils from a later field/earlier laboratory environment had similar or lower diapause then those from the complementary later laboratory/earlier field environment.

Adult Sensitivity. Sensitivity of adult boll weevils to diapause-inducing stimuli was examined by collecting infested squares in mid-July (JD 200), rearing the

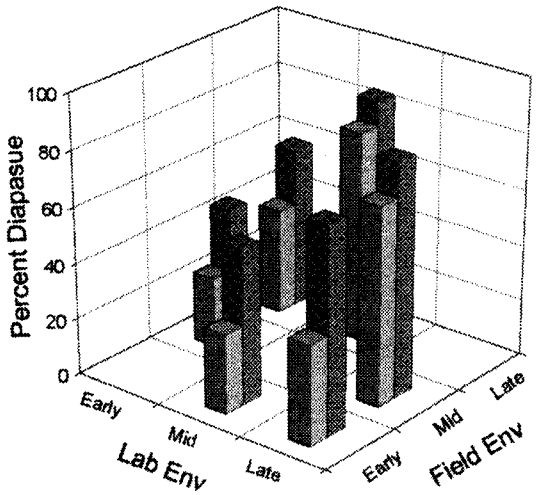

Fig. 2. Comparison of prediapause in treated male (dark) and female (light) boll weevils from early field/mid-laboratory environments with those from mid-field/early laboratory environments, early field/late laboratory with late field/early laboratory, and mid-field/late laboratory with late field/mid-laboratory (1989 data only, see Table 1 for data from other years).

insects in a dynamic environment from that starting date, and on eclosion, transferring a portion of adults to a cabinet simulating photoperiods and temperatures 40 d later than the controls. The percentage of weevils acquiring diapause increased from 17.5–48.9% (2.8 times) in males and 5.8–26.7% (4.6 times) in females (Fig. 3 A and B, solid versus open diamonds, respectively). These increases equated to daily rates of 0.77 and 0.51% in males and females, respectively (slopes of the solid lines), which indicate sensitivity of some adults to diapause-inducing stimuli independent of prior exposure.

It is not known how long boll weevils remain sensitive to diapause-inducing stimuli as adults, although it is reasonable to hypothesize that sensitivity diminishes during the early adult life because of the time required to perceive the cues and acquire the diapausing characteristics.

Effects of High Temperatures on Diapause Suppression in Adults. Weather in the mid-South is variable, and patterns of above and below normal temperatures are common throughout the year. If temperature influences diapause, especially during the adult stage as suggested by Earle and Newsom (1964), Lloyd et al. (1967), and Cobb and Bass (1968), then seasonal patterns may account for some of the variability observed in the process (see Wagner and Villavaso 1999). To examine the effects of above-normal temperatures on diapause, a portion of adults emerging from a late-season environment were transferred to a cabinet simulating temperatures 60 d earlier and much warmer than the controls (see Fig. 3 in Wagner and Villavaso [1999] for seasonal temperatures). Because weevils are capable of initiating dia-

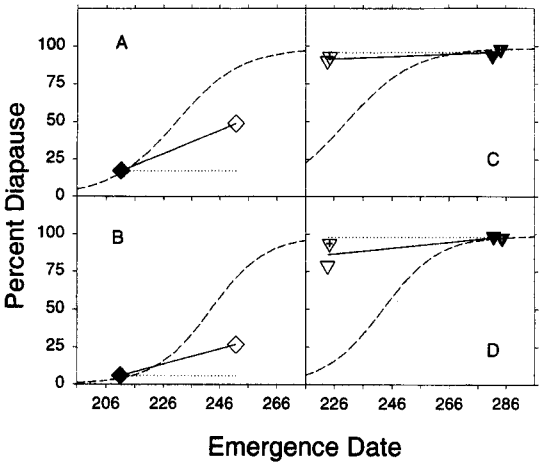

Fig. 3. Percentages of male (top row) and female (bottom) boll weevils in prediapause on the Julian date of emergence from insects collected in the field in squares and held under uninterrupted natural photoperiods and temperatures in the laboratory until dissected as adults (controls; solid data from Wagner and Villavaso [1999]) or subsampled on emergence and moved adults (A and B) 40 d forward in time changing lights and temperature and (C and D) 60 d backward in time changing temperature only (treated; open data). Diamonds depict data from 1994 and triangles 1993 (boll-fed adults, +). Solid lines depict regressions fitted to control and treated data; dashed lines regression equations 1 and 2 to controls over entire season; and dotted lines mean diapause of controls.

pause during the hotter months (Wagner and Villavaso 1999), we hypothesized that high temperatures would not markedly suppress diapause in adults reared under diapause-inducing environments.

On average, boll weevils in the treatment groups acquired diapause at similar rates to the controls (Fig. 3 C and D, open versus solid triangles), with an increase in temperatures resulting in a decrease in diapause of only 0.07 and 0.20% per day for males and females, respectively (slopes of the solid lines). The impact of high temperatures on males fed squares or bolls and females fed bolls was very similar—4–5% decrease in diapause over the 60-d period. The impact was greater on females fed squares—20% decrease over the period. Others have shown some high-temperature inhibition of diapause during the adult stage (Earle and Newsom 1964, Lloyd et al. 1967), but it is difficult to interpret these results given the differences in experimental techniques.

Summary and Conclusions. Results indicate that both early and late life stages are sensitive to dynamic photoperiods and temperatures; that individuals remain sensitive to these cues for different durations; and that the cues have a cumulative effect on diapause induction over part or all of the life cycle. Thus, some portion of the population will initiate diapause if the proper cues are perceived at the proper time regardless of the preceding or subsequent conditions, but to elicit a full diapause response in a population, reinforcement of the cues is required throughout the life cycle. Individuals also have different thresholds of sensitivity to these environmental stimuli (Wagner and Villavaso 1999).

Apparently it is easier to promote diapause than it is to halt it. For example, some weevils not only have the ability to initiate diapause during late development in the absence of early cues, but strong diapause-inducing signals perceived late have the potential to compensate for weak signals perceived early (note the linear response of the solid lines in Fig. 1 A and B, Fig. 3 A and B). In addition, the relative strength of the stimuli received early plays a role in determining the magnitude of the ensuing diapause response. This observation is illustrated by the change in slopes between the solid and dashed lines in Fig. 1 A and B relative to E and F. Percent diapause among treated females receiving weak signals early in life and stronger signals later in life increased at about half the rate as the modelled controls (e.g., difference in the slopes of the solid and dashed lines, Fig. 1B), whereas the rate of increase among treated females receiving stronger signals early was about equal to that of the controls (Fig. 1F). Similar findings were observed in males, except the early rate among treated males was about two-thirds that of the controls (Fig. 1A) as opposed to half the rate for females (Fig. 1B). Males are more sensitive than females to diapause-inducing stimuli throughout most of the season (Wagner and Villavaso 1999), explaining their greater response to like stimuli. These results suggest that the early life stages perceive a threshold to dynamic photoperiods and temperatures. As diapause-inducing signals intensify seasonally and the threshold is reached, additional stronger stimuli (see paragraph below) will initiate diapause at rates similar to those seen in insects receiving the stronger signals throughout their life (e.g., the controls). Because treated weevils in Fig. 1 E and F responded like the controls, we postulate that the threshold to photoperiod occurs no later than their collection date (i.e., ≈JD 230 corresponding to ≈13.3 h of daylight). The threshold for males probably occurs earlier than for females.

Boll weevils receiving diapause-inducing stimuli early in life and diapause-averting stimuli later in life do not produce the same responses as those receiving the opposite stimuli early versus late. For example, strong signals perceived early do not totally compensate for weak signals perceived late (note the lower asymptote of the solid lines, Fig. 1 C and D). At least 43% of the treated males (equation 3) and 33% of the treated females (equation 4) subjected to diapause-inducing conditions early retained a diapause status regardless of ensuing changes (Fig. 1 C and D). If these combined adaptations extend to other diapause-inducing stimuli that are not necessarily fixed seasonally (e.g., those attributed to the host plant), then the boll weevil should be able to alter its diapause response to changing environmental conditions that unfold during development. This adaptation would provide the species with flexibility to allocate portions of its population to reproduction or diapause as condi-

tions dictate and may help explain some of the variation observed in the diapause response (see Wagner and Villavaso 1999).

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Received for publication 8 June 1998; accepted 5 February 1999.