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Temperature Influences on Diapause Induction and Survival in the Boll Weevil (Coleoptera: Curculionidae)

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Abstract

The boll weevil, *Anthonomus grandis grandis* Boheman (Coleoptera: Curculionidae), has been the most important pest of cotton (*Gossypium* spp.) wherever it occurs. Although eradication programs in the United States have reduced the range of this pest, the weevil remains an intractable problem in subtropical Texas, Mexico, and much of South America. A key to managing the weevil in the subtropics and tropics might lie in better understanding its diapause and overwintering survival in regions characterized by relatively high late-season temperatures. We examined the temporal patterns of acquisition of diapause characters at 18.3, 23.9, and 29.4°C, and the effects of temperature during the diapause-induction period on subsequent host-free survival at 23.9°C. Occurrence of the diapause characters generally increased with weevil age at all temperatures but appeared more rapidly at higher temperatures. Acquisition of the diapause characters tended to occur slightly earlier in female weevils compared with the male weevils. Despite the slower development of diapause characters at lower temperatures, when adult weevils were fed under low temperatures, subsequent host-free survival was enhanced. These results are consistent with reports of increased weevil survival with delayed entry into overwintering. Our findings also suggest that the potential host-free survival facilitated by diapause occurring in subtropical or tropical production regions may be reduced compared with dormancy developing in southern temperate regions. This reduced survival potential emphasizes the importance of a maximized host-free season and suggests that the late-season diapause spray intervals should be short enough to ensure that the number of dormant weevils developing in late-season cotton is minimized.

Key words: diapause, dormancy, temperature, cotton, weevil

Historically, the boll weevil (*Anthonomus grandis grandis* Boheman) (Coleoptera: Curculionidae) has been the most serious pest of cotton (*Gossypium* spp.) wherever it occurs. Immense investments in organized eradication programs have reduced the range of this pest in the U.S. cotton to the southernmost cotton production regions of Texas. However, intractable populations in the Lower Rio Grande Valley of Texas and Mexico have been resilient and represent sources of reinfestation of adjacent, eradicated production regions (TBWEP 2016). In addition, the boll weevil remains a key pest across much of the cotton-producing areas of South America (Scataglini et al. 2006) despite intensive investigation into its management. A key factor facilitating the ecological success of the boll weevil has been its ability to survive for extended periods in the absence of the cotton host.

Whether the adult dormancy enabling extended host-free survival by the boll weevil is best characterized as a diapause or a quiescence has been questioned. Guerra et al. (1982) classified the dormancy as a quiescence based on the rapid resumption of oviposition by field-collected weevils maintained under laboratory conditions. However, the history of weevils collected by Guerra et al. (1982) was unknown, and diapause status was assessed only on the basis of a fat body observed through the abdominal cuticle. Spurgeon et al. (2003) found that this method of assessing diapause was inadequate. In addition, Andrewartha (1952) stated that diapause and quiescence can be difficult to distinguish. Denlinger (1986) acknowledged the many definitions of diapause but distinguished it from an immediate response to adverse conditions (quiescence). Denlinger (1986) also used the term dormancy to encompass both diapause and quiescence. Because information on the maintenance and termination of the boll weevil dormancy sufficient to distinguish it as a diapause or a quiescence is not currently available and the dormancy has been

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historically considered a diapause, we use the terms diapause and dormancy interchangeably.

Irrespective of the nature of the boll weevil dormancy, its ability to survive the fallow season was well documented even before Brazzel and Newsom (1959) reported the existence of adult diapause in the weevil. However, many of these reports of overwinter survival originated from an era before the adoption of mechanized harvest, chemical crop termination, and determinate cultivars (Fenton and Dunnam 1927; Gaines 1935, 1959; Hinds and Yothers 1909). During this earlier era, cotton stalks often bearing new fruiting structures were present in the field until a killing freeze (Smith 1921). From these studies, it was apparent that overwintering survival was influenced by climate, which varied with geographical area (Sanderson 1907, Hinds and Yothers 1909) and wintertime temperatures (Gaines 1935, 1953, 1959; Bondy and Rainwater 1942), but also by the timing when weevils entered overwintering habitat (Hinds and Yothers 1909, Bondy and Rainwater 1942, Reinhard 1943). Under modern production practices, late-season boll weevils can be denied continuous access to the cotton host by mechanized harvest and thorough crop destruction. The timeliness of these activities is widely regarded as an important factor influencing boll weevil overwintering survival, especially considering the observation that newly emerged weevils denied the opportunity to feed before entering overwintering quarters have limited survival potential (Mitchell et al. 1966). Time of entry into overwintering habitat (Parajulee et al. 1996, Sterling 1971, Taft et al. 1973), habitat quality (Hopkins et al. 1972, Brown and Phillips 1989, Carroll et al. 1993, Parajulee et al. 1997), and extent and duration of low winter temperatures (Pfrimmer and Merkl 1981, Price et al. 1985, Slosser and Fuchs 1991) are still regarded as important determinants of overwintering survival. Whereas these reports provide valuable insights into the dynamics of boll weevil overwintering in temperate production regions, their relevance to subtropical and tropical regions is less obvious.

Rummel and Summy (1997) contrasted the overwintering ecology of the boll weevil between temperate and subtropical regions. Based on their synthesis of the literature, they concluded the nature of adult diapause in the subtropical weevil was poorly understood, although extended host-free survival in the subtropics was clearly demonstrated. A subsequent survival study failed to detect differences in host-free survival between boll weevils from the Lower Rio Grande Valley and weevils from northern Texas when diapause was induced by manipulating the diet of the adult (Spurgeon et al. 2008). In addition, Spurgeon and Raulston (2006) conducted extensive studies with both southern temperate and subtropical weevils and failed to demonstrate any effect of photoperiod on diapause induction in either population. In the studies of Spurgeon and Raulston (2006), adult diet was the primary determinant of diapause, although temperature during the adult stage influenced the weevil age at which diapause status could be reliably assessed by dissection. These collective reports suggest that apparent differences in the diapause response of temperate and subtropical boll weevils may be caused by regional differences in temperatures during phases of the cotton production season; specifically, late-season temperatures during those periods when diapause would be induced. Although numerous studies have examined aspects of the diapause response under different temperatures or at different adult ages (Lambremont 1961, Earle and Newsom 1964, Betz and Lambremont 1967, Harris et al. 1969, Tingle and Lloyd 1969, Cole and Adkisson 1983, Wagner and Villavaso 1999), none of these studies were designed to examine the individual or interactive effects of temperature or adult age on the perceived diapause response nor to associate observed levels of diapause with subsequent host-free survival. In most cases, lack of standardized methods or systematic control of both temperature and weevil age at the time of diapause assessment likely led to confounding of these effects (Spurgeon and Raulston 2006).

Because temperature conditions during the late-season diapause induction period vary considerably among temperate, subtropical, and tropical cotton production regions, it seems beneficial to understand the implications of these differences on diapause induction. Our objective was to examine the influence of temperature during the induction period on incidence of diapause of the boll weevil and to assess the effects of these temperatures on subsequent host-free survival.

Materials and Methods

Our objectives were addressed in two separate experiments; one in which we examined the time course of appearance of the morphological characters of diapause at different temperatures, and the other in which we examined the consequences of different temperatures during diapause induction on subsequent host-free survival at a constant temperature. In both studies, experimental weevils were obtained as larvae by collecting oviposition-punctured flower buds (squares) from cotton plants in Central Texas. Collected squares were held in acrylic cages within an environmental chamber maintained at about 29°C with a 13:11 (L:D) h photoperiod. Squares were examined periodically for the presence of pupae, which were harvested daily. Pupae were held in the same environmental chamber as the squares in groups of 40–50 on a layer of moistened vermiculite within a 15 × 100 mm Petri plate. Pupae were examined daily for adult eclosion, and newly eclosed adults were separated by sex using the tergal notch method (Sappington and Spurgeon 2000). In both experiments, adult weevils were confined as single-sex groups in 473-cm^3 cardboard cartons. Each carton was closed with a wire-screened lid and contained water provided in a 29.5-ml plastic cup with a cotton wick protruding through the cup lid. Adult weevils were fed unblemished cotton bolls, 20–25 mm in diameter, and with bracteoles removed.

In both experiments, morphological characters of diapause were assessed by dissection of weevils pinned under water in a paraffin-lined dish. Morphological criteria to distinguish diapause were those reported by Spurgeon et al. (2003). Briefly, fat bodies were considered hypertrophied if they were white, in large globules, and mostly obscured the other organs. Fat bodies not fitting this description were considered not hypertrophied irrespective of their abundance. The fat bodies characterized as hypertrophied are associated with the presence of a hexamerin storage protein in the hemolymph which is indicative of diapause (Lewis et al. 2002). In males, the testes were considered indicative of diapause if they were atrophied (small and opaque with fat). In females, the ovaries were considered indicative of reproductive if they exhibited vitellogenic oocytes, eggs, or follicular relics that may indicate prior oviposition (Grodowitz and Brewer 1987). Individual weevils were classed as diapausing only if they possessed both the hypertrophied fat body and atrophied testes (males) or nonreproductive ovaries (females).

Acquisition of Diapause Characters

The experiment was conducted to determine the time course over which male and female boll weevils display the morphological characters of diapause at different temperatures. Development of the diapause characters was examined at three temperatures (18.3, 23.9, and 29.4°C ± 1°C) under a photoperiod of 13:11 (L:D) h. These temperatures were arbitrarily selected to represent a range broadly representative of temperatures during the preharvest and harvest periods from temperate to subtropical production regions. Within each temperature, weevils were examined by dissection at five ages. Studies of temperature dependence of reproductive development (Spurgeon and

Raulston 1998) indicated development rate was approximately twice as rapid at 29.4°C compared with 18.3°C, and the rate at 23.9°C was intermediate to these temperatures. Therefore, ages at dissection differed among temperatures to ensure that adequate time was provided for display of the reproductive (or diapause) characters by the last age of assessment. Ages at dissection were 2, 4, 6, 8, and 10 d at 29.4°C; 3, 6, 9, 12, and 15 d at 23.9°C; and 4, 8, 12, 16, and 20 d at 18.3°C. Each repetition of the experiment included a single-sex cohort (carton) of 15 weevils for each combination of temperature and age at dissection (15 cohorts of each sex, a total of 450 weevils). Each carton was provided a single boll for feeding, and the boll was replaced thrice weekly. Therefore, the carton of weevils was the experimental unit. The experiment was conducted three times, each repetition representing a different collection of weevils.

All analyses were conducted using SAS software (SAS Institute 2012). The diapause response was assessed by conditional, generalized linear mixed models using the binomial distribution with events/trials syntax and estimated by adaptive quadrature (PROC GLIMMIX). Because the ages at dissection differed among temperatures, the responses at each temperature were analyzed separately. In each analysis, fixed effects were weevil sex, age at dissection, and their interaction, and the random effect was repetition of the experiment. The events/trials syntax eliminated the need to include a random interaction term to serve as the error for tests of fixed effects. For some combinations of sex, age, and temperature, no diapausing weevils were observed. The nonresponse resulted in quasi-complete separation and either unreasonable variance estimates or nonconvergence because of an infinite likelihood. In those cases, the number of 'events' was rescaled from 0 to 0.5 to allow model convergence. This rescaling does not change model estimates for treatment combinations with at least one nonzero response. For treatment combinations with nonresponses, reported results reflect lack of response instead of the rescaled response. Where the sex × age interaction was non-negligible, simple effects of each factor were examined. Type-I experiment-wise error was controlled by a multiplicity adjustment (the SIMULATE option of LSMEANS) where comparisons in responses were made among ages. Estimated mean probabilities were obtained on the data scale by the ILINK option.

Host-Free Survival After Feeding at Different Temperatures

Because we had no means of determining appropriate feeding periods to obtain weevils in the same diapause state at the different temperatures, we used the same feeding period duration (14 d) at each of 18.3, 23.9, and 29.4°C (± 1°C). This feeding period duration ensured a high incidence of diapause at each of the studied temperatures. During both feeding and survival periods, the weevils were exposed to a photoperiod of 13:11 (L:D) h. A complete replication of the experiment consisted of two single-sex cohorts (one of females, one of males) of 40 weevils each confined within respective cardboard cartons as previously described (one cohort of each sex at each temperature; a total of 240 weevils). Each carton of weevils was provisioned with three unblemished and debracted bolls (20–25 mm diameter) that were replaced thrice weekly. At the end of the 14-d feeding period, 25 weevils were randomly selected from each carton for survival assessments. Weevils that were not selected for survival assessments were dissected as previously described to estimate the proportion of weevils attaining diapause. Each weevil selected for the survival study was painted on the right elytron using a nontoxic paint pen (Speedball Painters, Hunt Manufacturing, Statesville, NC) and then numbered sequentially using a technical pen (Pigma Micron 005, Sakura Color Products, Osaka, Japan). The groups of numbered weevils were each placed within respective acrylic survival cages that were ventilated by aluminum window screening. Each cage contained a refuge of crumpled craft paper (30.5 × 45 cm) and water within a plastic snap-cap vial. The water was made accessible by penetrating the vial lid with a cotton wick. Survival cages were maintained within an environmental chamber at 23.9 ± 1°C and 70 to 80% RH. Cages were examined weekly to record mortality until no live weevils remained. The experiment was conducted three times, each time with weevils from a different field collection (a total of 720 weevils, 450 of which were used to determine survival functions).

The incidence of diapause was compared among temperature treatments using a conditional, generalized linear mixed model with Laplace estimation (PROC GLIMMIX), a binomial distribution, and events/trials syntax. Fixed effects were weevil sex, feeding temperature, and their interaction. Repetition of the experiment was a random effect. Estimates of the probability of diapause were obtained on the data scale using the ILINK option.

Survival functions were compared among feeding period temperatures and weevil sexes using the LIFETEST procedure. In each analysis, repetition of the experiment and either sex (for tests of temperature) or temperature (for the test of sex) were stratification variables. Statistical differences among the functions were evaluated using the Wilcoxon statistic, and comparisons of functions among temperatures controlled Type-I experiment-wise error with an adjustment for multiplicity (the SIMULATE option).

Results

Acquisition of Diapause Characters

No diapausing weevils were observed at 4 d of adulthood at 18.3° or 2 d of adulthood at 29.4°C. In addition, no male weevils displayed the characters of diapause at 8 d at 18.3°, 3 d at 23.9°, or 4 d at 29.4°C (Fig. 1).

Examination of the age-dependent pattern of diapause occurrence at 18.3°C indicated a significant sex × age interaction (Table 1) so the main effect tests of sex and age at dissection were not interpretable. Simple effect tests of sex within weevil ages indicated that the probability of diapause was higher for females compared with males at 12 d and higher for males compared with females at 20 d, but there were no differences at 4, 8, or 16 d of adulthood (Table 2; Fig. 1a). Multiple comparisons (adjusted $P < 0.05$) of the probability of diapause among ages within weevil sex indicated differences for both females and males (Table 2). Multiple comparisons for females at different ages indicated no difference in the incidence of diapause at 4 or 8 d of age. The incidence of diapause at 4 or 8 d of age was lower compared with ages ≥ 12 d (Fig. 1a). There were no differences in the probabilities of diapause for females that were 12–16 d of age. The pattern of appearance of diapause characters in males was similar to that in females except for a shift to later ages. The probability of diapause in males was not different among ages from 4 to 12 d, whereas the incidences of diapause at these ages were lower than at ages of 16 or 20 d (Fig. 1a). The probability of diapause in males did not differ between adult ages of 16 or 20 d.

Analyses of diapause occurrence at 23.9°C indicated a significant effect of weevil age (Table 1), but sex was not significant. Interpretation of the main effects was not straightforward because of the significant sex × age interaction (Table 1). Simple effect tests indicated a significant age effect within both sexes (Table 2). For females, the probability of diapause at 3 d of adult age was not distinguishable from that at 6 d but was lower for other ages (Fig. 1b). The probability of diapause at 6 d was lower compared with either 9 or 15 d but was not different from that at 12 d once adjustments were made for multiplicity. The incidences of diapause at ages of
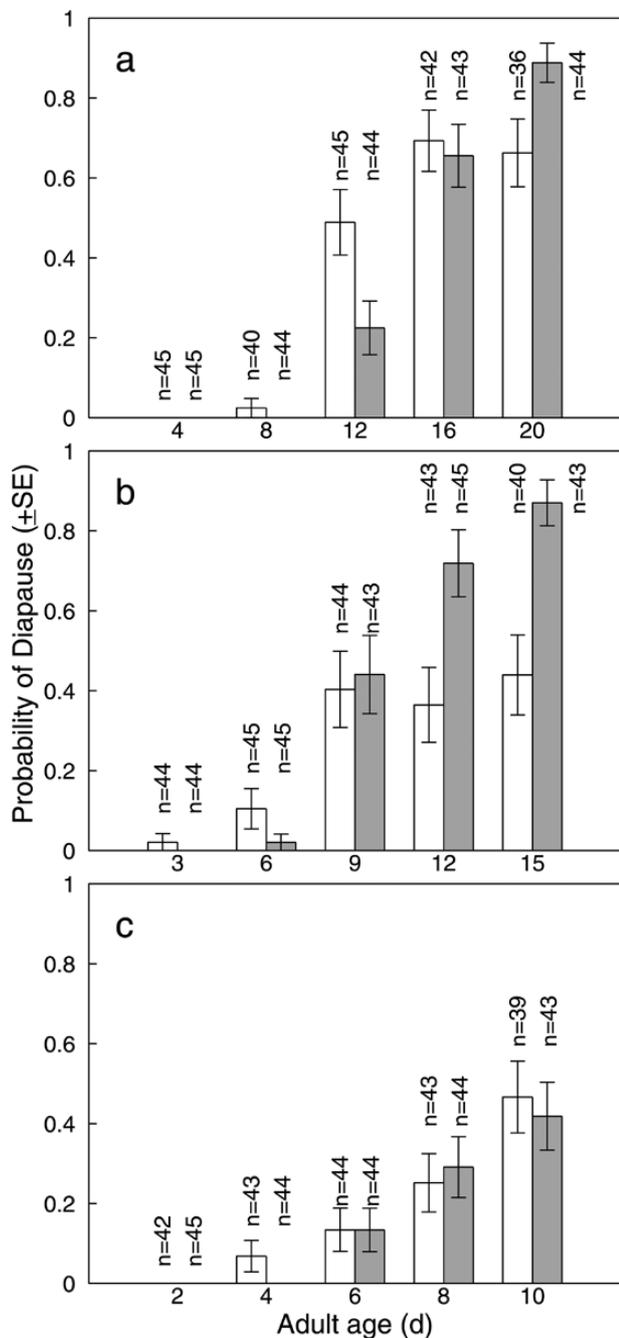
Fig. 1. Temporal patterns in the probability of diapause in boll weevil females (white bars) and males (gray bars) fed cotton bolls as adults at 18.3 (a), 23.9 (b), or 29.4°C (c).

9–15 d were not different (Fig. 1b). For males, the lowest probability of diapause occurred at ages of 3 and 6 d, which was lower compared with later ages. The probability of diapause was lower after 9 d compared with 15 d, but these incidences were not different compared with 12 d after adjustment for multiplicity (Fig. 1b). The probability of diapause was higher for males than for females after 12 and 15 d (Table 2; Fig. 1b), but no differences between weevil sexes were demonstrated at earlier ages.

For weevils fed at 29.4°C, the analyses indicated no sex × age interaction and no difference between sexes in the probability of diapause (Table 1). However, the incidence of diapause increased with weevil age (Table 1, Fig. 1c). Multiple comparisons (adjusted $P < 0.05$) indicated that the probability of diapause was not different among ages from 2 to 6 d but was lower at these ages compared with 10 d (Fig. 1c). The probability of diapause at 8 d was not different from that at either 6 or 10 d of adult age after adjustments for multiplicity.

Host-Free Survival After Feeding at Different Temperatures

Statistically similar levels of diapause were observed for both sexes and at all temperatures after the 14-d feeding period (Table 3; Fig. 2). Furthermore, the sex × temperature interaction appeared negligible (Table 3). Therefore, differences in subsequent survival functions should not have been greatly influenced by differences in the incidence of diapause corresponding to the temperature during the induction period.

Analyses controlling for weevil sex and experimental repetition indicated differences in survival functions corresponding to temperature during the 14-d feeding period (Table 4). Comparisons among survival functions corresponding to feeding period temperature indicated similar survival for weevils fed at 18.3 or 23.9°C, which was greater compared with weevils fed at 29.4°C (Table 4; Fig. 3a). Comparisons of survival between weevil sexes, controlling for feeding temperature and experimental repetition, indicated greater survival for male weevils compared with females (Table 4; Fig. 3b).

Discussion

Diapause assessments by serial dissections indicated generally increasing probability of diapause with increased age under all feeding temperature treatments. At 18.3°C, the incidence of diapause continued to increase until about 12 d of adult age for females and until 16 d for males. At 23.9°C, the occurrence of morphological characters of diapause ceased to increase after 9 d for females and about 12 d for males. The slight delay in the pattern of increasing diapause incidence for males, compared with females, may be explained by the fact that in addition to developing a

Table 1. Tests of model effects of the probability of diapause for adult boll weevils fed cotton bolls for different durations at three different temperatures

Model effect	18.3°C			23.9°C			29.4°C		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
Sex	0.03	1, 18	0.857	1.67	1, 18	0.212	0.20	1, 18	0.657
Age[a]	24.89	4, 18	<0.001	17.09	4, 18	<0.001	12.26	4, 18	<0.001
Sex × age	2.95	4, 18	0.049	3.77	4, 18	0.021	0.22	4, 18	0.927

The analysis used a conditional mixed model with a binomial distribution.
[a]Ages were 4, 8, 12, 16, and 20 d at 18.3°C; 3, 6, 9, 12, and 15 d at 23.9°C; and 2, 4, 6, 8, and 10 d at 29.4°C.

Table 2. Simple effect tests of the sex × age interaction from analysis of the probability of diapause for adult boll weevils fed cotton bolls for different durations at two different temperatures

| Simple effect	18.3°C				23.9°C			
	Age	F	df	P	Age	F	df	P
Sex within age	4	0.00	1, 18	1.000	3	0.10	1, 18	0.753
	8	0.06	1, 18	0.804	6	2.36	1, 18	0.142
	12	6.46	1, 18	0.020	9	0.12	1, 18	0.736
	16	0.14	1, 18	0.718	12	10.28	1, 18	0.005
	20	5.49	1, 18	0.031	15	15.00	1, 18	0.001
	Sex	18.3°C				23.9°C		
Age within sex	Female	9.72	4, 18	<0.001		5.46	4, 18	0.005
	Male	16.55	4, 18	<0.001		13.84	4, 18	<0.001

The analysis used a conditional mixed model with a binomial distribution.

Table 3. Tests of model effects of the probability of diapause for adult boll weevils fed cotton bolls for 14 d at three different temperatures

Model effect	F	df	P
Sex	0.43	1, 10	0.526
Temperature[a]	1.69	2, 10	0.233
Sex × temperature	0.22	2, 10	0.803

The analysis used a conditional mixed model with a binomial distribution.
[a]Temperatures were 18.3, 23.9, and 29.4°C.
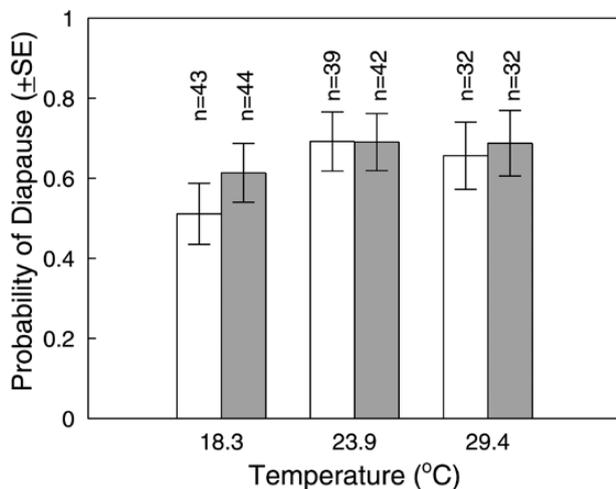
Fig. 2. Probability of diapause for boll weevil adult females (white bars) and males (gray bars) fed cotton bolls for 14 d at 18.3, 23.9, or 29.4°C.

Table 4. Kaplan-Meier tests and multiple comparisons among host-free survival functions of adult boll weevil sexes fed cotton bolls for 14 d at different temperatures

| Model effect or comparison	Wilcoxon χ^2	df	P
Sex	6.620	1	0.010
Feeding temperature	24.839	2	<0.001
18.3 versus 23.9°C[a]	0.887	1	0.606
18.3 versus 29.4°C[a]	13.633	1	0.001
23.9 versus 29.4°C[a]	21.636	1	<0.001

Temperature during the host-free survival period was 23.9 ± 1°C.
[a]Multiple comparisons among survival functions corresponding to feeding temperatures of 18.3, 23.9, and 29.4°C are adjusted for multiplicity using the SIMULATE option of SAS.

hypertrophied fat body, males must develop to the point of testicular atrophy to be classified as diapausing; females must simply fail to initiate development of the ovaries. Differences between sexes in the temporal patterns of diapause occurrence at 29.4°C were not observed. The more rapid development at this higher temperature may have obscured differences between the sexes compared with the lower temperatures. It is also possible that an additional age increment may have been needed to permit maximal expression of diapause at 29.4°C. Regardless, temperature dependence of the appearance of the diapause characters was roughly similar to that expected based on the temperature dependence of reproductive development (Spurgeon and Raulston 1998). The results also illustrate a substantial influence of age at dissection on perceived incidence of diapause, which was predicted by Spurgeon and Raulston (1998) and has served as a basis for their criticism of some earlier diapause studies.

The higher host-free survival rates of males compared with females are difficult to interpret unambiguously, especially considering that several previous studies using either vegetative stage cotton as food (Esquivel et al. 2004, Suh and Spurgeon 2006) or observations of survival under ambient conditions (Westbrook et al. 2003, Spurgeon 2008) did not report similar differences. Regardless, differences observed in this study occurred early in the host-free survival period. Considering that the dissections indicated a substantial proportion of the weevils were not in diapause, the higher male survival we observed may have been caused by a comparatively higher cost of egg production for nondiapausing female weevils compared with testis or accessory gland development for nondiapausing males. In all combinations of weevil sex and feeding temperature, there appeared an inflection point early during the survival period. These points (29.4°C, week 3–4; 18.3 and 23.9°C, week 6) may indicate a division in survival potential of reproductive versus diapausing weevils because each survival cohort was a mixture of reproductive and diapausing adults. This observation suggests explicit examination of internal morphology as a predictor of host-free survival may provide additional useful insights into boll weevil overwintering ecology.

The host-free survival of weevils fed at comparatively lower temperatures (18.3 and 23.9°C) tended to be greater compared with that of weevils fed at the highest temperature (29.4°C) even in the absence of substantial differences in the respective incidences of diapause. This improved survival may indicate that fat is more effectively accumulated at the lower temperatures because of reduced baseline metabolic rates, compared with higher temperatures. These observations were consistent with those of Spurgeon (2008) regarding survival patterns of cohorts of weevils fed and held under
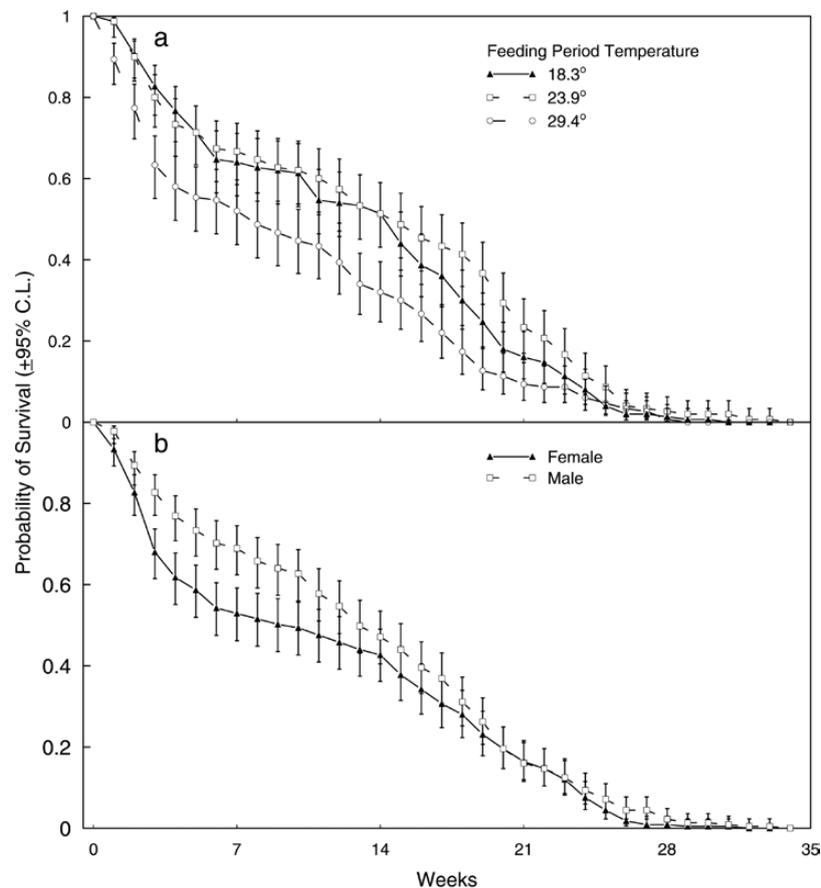
Fig. 3. Host-free survival of boll weevil adults at 23.9°C after feeding on cotton bolls for 14 d at 18.3, 23.9, or 29.4°C (a), and survival of female and male weevils controlling for feeding temperature (b).

ambient conditions. Spurgeon (2008) was able to explain differences among survival functions of most weevil cohorts on the basis of temperature during the host-free period, except for the latest cohorts which experienced markedly cooler temperatures during the feeding period. Numerous other reports have indicated an association between increased overwintering survival of the weevil and late entry into overwintering quarters (Hinds and Yothers 1909, Gaines 1935, Reinhard 1943, Taft et al. 1973, Rummel and Carroll 1983, Parajulee et al. 1996). Although survival of weevils late to enter overwintering habitat may be enhanced by generally lower temperatures during the survival period, our results suggest that lower temperatures during the feeding period preceding diapause may also enhance weevil overwintering survival.

The lower survival in association with feeding at higher temperatures observed in this study, combined with reduced post-feeding survival with increased temperature (Spurgeon 2002, 2008), suggest limited host-free survival potential of the boll weevil in subtropical and tropical regions. These observations accentuate the importance of thorough crop destruction and maximization of the host-free period to boll weevil management and eradication. The ecological rigors of overwinter survival under tropical or subtropical conditions may also increase the importance of reproductive or feeding hosts other than cultivated cotton in perpetuating weevil populations. Finally, enhanced survival of weevils entering dormancy when temperatures are relatively low cautions against substantially widened late-season spray intervals directed at diapausing weevils. In all, our findings contribute to a more complete understanding of the factors influencing boll weevil overwintering survival that may facilitate refinement of late-season control and eradication tactics.

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