Reproductive and Survival Responses of Overwintered Boll Weevils (Coleoptera: Curculionidae) to Diet[1]

C.P.-C. Suh[2], D.W. Spurgeon[3], and B.J. Reardon[4]

USDA, ARS, Insect Control and Cotton Disease Research Unit, 2771 F&B Road, College Station, Texas 77845 USA

Abstract   The boll weevil, *Anthonomus grandis grandis* Boheman (Coleoptera: Curculionidae), is a major pest of cotton (*Gossypium* spp.) that overwinters in an adult diapause. Diapause is primarily induced by adult diet, but late-season cotton, postharvest regrowth, and volunteer cotton also support reproduction, especially in the subtropics and tropics where conditions permit cotton fruiting during the fallow season. When cotton plants escape crop destruction efforts they may produce fruit and become heavily infested by overwintered weevils. The ecological implications of these plants to survival of overwintered weevils have not been studied. We examined the physiological and survival responses of trap-captured overwintered weevils to starvation and to square (reproduction-promoting) and boll (diapause-inducing) diets. Few newly captured overwintered weevils exhibited fat body hypertrophy or gonadal characters of diapause. Square feeding rapidly induced a high level of reproductive development in both weevil sexes but little fat accumulation. Compared with the square diet, a boll diet promoted more gradual reproductive development in female weevils, but also stimulated in both weevil sexes the development of hypertrophied fat bodies similar to those associated with diapause. Although diapause was not reinduced by the boll diet, resulting accumulations of fat allowed substantially greater host-free longevity compared with overwintered weevils that were not fed. The contributions of diapause and fallow-season reproduction to boll weevil overwintering survival are commonly recognized. Findings of this study identify an additional mechanism by which overwintered boll weevils may utilize fallow-season cotton to enhance survival, and reinforce the importance of eliminating cotton during the fallow season.

Key Words   *Anthonomus grandis grandis*, boll weevil, overwintering, diapause

The boll weevil, *Anthonomus grandis grandis* Boheman (Coleoptera: Curculionidae), is a major pest of cotton (*Gossypium* spp.) in the western hemisphere. In temperate zones the boll weevil overwinters primarily as an adult in reproductive diapause (Brazzel and Newsom 1959). Photoperiod, temperature, larval or adult diets, or some combination of these factors have been proposed as the cues inducing diapause (Beckham 1962, Brazzel and Hightower 1960, Cobb and Bass 1968, Earle and Newsom 1964, Hilliard and Keeley 1984, Lloyd et al. 1967), but

supporting evidence has been inconsistent among and often within studies. Recent work indicates that adult diet is the primary cue responsible for the diapause response (Spurgeon and Raulston 2006; Spurgeon and Suh 2017a, 2018; Spurgeon et al. 2018a, 2018b).

Although the boll weevil in the subtropics is known to diapause (Graham et al. 1979, Spurgeon 2008, Spurgeon and Raulston 2006, Spurgeon et al. 2003, Summy et al. 1993), reproduction on regrowth and volunteer cotton also occurs as long as fruiting plants are available (Summy et al. 1988). However, similar observations were common in temperate regions before the advent of modern harvest methods, when cotton plants often produced fruit in the field until they were killed by freezing temperatures (Hinds and Yothers 1909, Isley 1932, Mally 1901, Reinhard 1943, Sanderson 1907). One important difference between the temperate and subtropical or tropical regions is the likelihood of cotton plant death from freezing temperatures. Plant death from low temperatures usually occurs in temperate climates; whereas, in the subtropics and tropics, cotton plants often survive and fruit during the noncotton fallow season.

With concerted efforts to eliminate cotton plants during the fallow season, as occurs in eradication programs, regrowth or volunteer plants tend to be sparsely distributed or isolated. Individual plants often escape detection by overwintering weevils through much of the fallow season, but once discovered, they tend to be heavily infested (D.W.S. pers. obs.). This scenario (relatively few numbers of squares or bolls with most of them injured or infested) can result in a feeding environment similar to those used to induce diapause in the laboratory (Spurgeon and Raulston 2006, Spurgeon and Suh 2018). The physiological responses of overwintered weevils to this feeding environment, and associated survival benefits, have not been investigated. We examined physiological responses (fat body and reproductive development) of overwintered boll weevils to diets known to promote reproduction or diapause and assessed the contribution of a diapause-inducing diet to subsequent host-free longevity.

Materials and Methods

Overwintered adult boll weevils were captured in Southeastern Eradication Foundation pheromone traps (Technical Precision Plastics, Mebane, NC) baited with a standard 10-mg lure (Scentry Biologicals, Billings, MT) near College Station, TX. The traps were monitored daily from late April through late May, before squaring cotton was generally available. Weevils captured each day were examined for dead or moribund individuals, which were discarded, and remaining weevils were separated by sex using the method of Sappington and Spurgeon (2000). Weevils of known sex were then assigned to feeding treatments. When the numbers of captured weevils were low, weevils were held within environmental chambers (model I30BLL, Percival Scientific, Perry, IA) at 18.3 $\pm$ 0.5°C under a 13:11 (L:D) h photoperiod until sufficient numbers were available for assignment to a treatment. This temperature was used because it is sufficiently low to extend survival but not so low as to induce chilling injury (Spurgeon and Suh 2018, Spurgeon et al. 2018b).

Physiological response to diet. The experiment included six feeding treatments and an unfed treatment (control group) of newly captured weevils to

serve as a baseline for comparison. Totals of 60 females and 58 males comprised the baseline control group and were accumulated as assignment of weevils to other treatments progressed. The six feeding treatments represented combinations of food type (square or boll) and feeding duration (3, 6, or 12 d). Weevils assigned to the boll feeding treatment were held in mixed-sex groups of 30 weevils (15 males and 15 females) within 473-ml cardboard cartons with screened lids. One carton of weevils was assigned to each feeding period duration. Weevils in each carton were provided three bolls (20- to 25-mm diameter; replaced three times weekly) and water in a plastic cup fitted with a lid and a cotton wick. The boll diet is known to induce diapause (Spurgeon and Suh 2018, Spurgeon et al. 2018a) and was intended to determine whether the weevils could acquire the morphological characters of diapause after emergence from overwintering. Weevils assigned to the square feeding treatment (12–15 males and 13–15 females in each experimental repetition of each feeding duration) were held individually within 100 × 15-mm petri plates. The weevil in each plate was provided a single square (6- to 9-mm-diameter bud) with intact bracteoles and a short section of water-saturated cotton wick. Squares were replaced daily. The square diet is known to promote reproductive development (Spurgeon and Raulston 2006) and was intended to indicate the temporal pattern of reproductive development associated with colonization of squaring cotton. Irrespective of the assigned feeding treatment, the weevils were held within an environmental chamber at 29.4 ± 0.5°C with a photoperiod of 13:11 (L:D) h until they were examined by dissection. The experiment was conducted a total of five times over 2 yr.

Physiological response to the diet treatments was assessed by dissection under water in a paraffin-lined petri plate as described by Spurgeon et al. (2003). Fat bodies were classified as hypertrophied if they were white, in distinct globules, and obscured most or all of the other internal organs, and not hypertrophied if they appeared otherwise. Female reproductive status was based on the presence (reproductive) or absence (nonreproductive) of oocytes with visible accumulations of yolk. When vitellogenic oocytes or eggs were present, they were inspected for oosorption that was indicated by flocculation of the yolk (Spurgeon et al. 2003). In males, testes that were small and opaque with fat were classed as nonreproductive (Spurgeon et al. 2003). Testes without an opaque fatty sheath were classed as reproductive irrespective of their size. Weevils exhibiting a hypertrophied fat body and nonreproductive gonads were classed as diapausing.

All analyses and summarizations were computed using SAS (SAS Institute 2012). Physiological status of baseline boll weevils determined immediately after capture was examined separately from weevils assigned to feeding treatments. This separation was necessary to allow the use of effects models for the fed weevils. For weevils representing the baseline group, fat body condition (hypertrophied or not hypertrophied), reproductive status, and diapause status were examined for association with weevil sex in contingency tables, where weevil sex formed table rows, status of the examined character formed columns, and repetition of the experiment formed strata which are analogous to blocks (Stokes et al. 2012). Occurrence of oosorption also was examined for captured females in the baseline group. In each analysis where marginal totals were sufficient, statistical associations were examined using the Mantel–Haenszel row mean scores statistic (Q_{SMH}; Stokes et al. 2012). In some tables, expected values were <5 for every cell

within a column, so the cell counts were too small to yield meaningful analyses. In those cases, Agresti–Coull 95% confidence intervals were calculated in lieu of formal statistical testing. When the responses of the weevils were completely uniform (a column marginal total = 0), results are reported without statistical analysis.

Within the feeding experiment, responses to some treatment combinations (e.g., either sex fed squares) were nearly or completely uniform, which resulted in problems with separation and infinite likelihoods in the intended analyses. Therefore, the models we used varied with the physiological parameter that was examined. The probability of fat body hypertrophy was examined for boll-fed weevils in a generalized linear mixed model using a binomial distribution. A conditional model with fixed effects of weevil sex, days of feeding, and their interaction was computed using Laplace estimation. Experimental repetition nested within year [repetition(year)] was a random effect. Events/trials syntax was used so that residual error would be the error term for testing the effects of weevil sex and the sex × feeding duration interaction. The random term of days fed × repetition(-year) was included as the error term for testing the effects of feeding duration (3, 6, or 12 d). Pair-wise comparisons among more than two means were adjusted for multiplicity using the SIMULATE option. Occurrence of hypertrophied fat body in square-fed weevils was not examined statistically because of complete (female) or nearly complete uniform responses (males).

The probability of reproductive development and probability of diapause were examined separately for females fed bolls because some nonreproductive females lacked a hypertrophied fat body and, therefore, could not be classified as diapausing. Both analyses used a conditional model with a binomial distribution and events/trials syntax. The sole fixed effect was feeding duration, and repetition(year) was a random effect. Incidence of reproductive development or diapause for other combinations of weevil sex and diet were examined or summarized without formal analysis, as described for the baseline group. The probability of oosorption was examined only for reproductive females that were fed bolls (oosorption does not occur in nonreproductive females). The statistical model was exactly the same as for analyses of reproductive development and diapause. Oosorption in females fed squares was infrequent, and this response was summarized with binomial proportions and associated confidence intervals.

Results from contingency table analyses are presented as proportions (± 95% CL). Results from generalized mixed models are presented as probabilities (± SE).

Host-free longevity. During the second year of study, weevils were allocated to experiments examining the influences of fat body hypertrophy on subsequent host-free survival. Overwintered weevils were obtained from pheromone traps as previously described, separated by sex, and assigned to groups that were either unfed, or that were fed before the survival period. Weevils that were unfed (single-sex groups of 25 weevils, three cohorts of each sex) were placed in 20 × 20 × 20-cm screened acrylic survival cages with a water source and a refuge of crumpled craft paper (30 × 40 cm). Each single-sex cohort was contained in a separate cage. Survival cages were held within environmental chambers at 23.9 ± 0.5°C with a 13:11 (L:D) h photoperiod. Survival was monitored weekly until all weevils were dead. Weevils that were fed were initially held in single-sex cohorts of 25 weevils within the 473-ml cardboard cartons. Weevils in each carton were provided a water
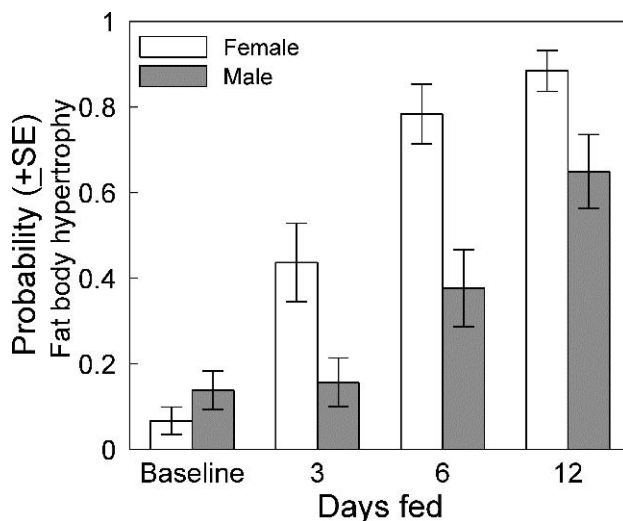
Fig. 1. Mean probability of fat body hypertrophy for overwintered boll weevil adults immediately after capture in pheromone traps (Baseline), and after feeding on cotton bolls at 29.4 ± 0.5°C under a 13:11 (L:D) h photoperiod for 3, 6, or 12 d. Error bars for the baseline are 95% CL; error bars corresponding to feeding durations are SE.

source and two bolls (20- to 25-mm diameter). Bolls were replaced thrice weekly for 14 d. At the end of the feeding period, each cohort (21–24 males; 23–25 females) was placed in a survival cage and monitored as described for the unfed weevils. Survival functions of fed and unfed weevils, stratified by weevil sex and cohort, were compared using the log-rank statistic of PROC LIFETEST.

Results

Physiological response to diet. The incidence of hypertrophied fat bodies in the baseline group (newly captured, unfed weevils) was generally low and similar between weevil sexes ($Q_{SMH} = 1.92$, df $= 1$, $P = 0.17$; "Baseline" in Fig. 1). When the weevils were fed bolls, the probability of fat body hypertrophy tended to increase with duration of feeding ($F = 12.90$; df $= 2, 8$; $P < 0.01$; Fig. 1). The negligible weevil sex × feeding duration interaction ($F = 0.27$; df $= 2, 12$; $P = 0.76$) suggested the temporal increase in the incidence of fat accumulation occurred in both sexes, although the probability of fat body hypertrophy was higher for females compared with males ($F = 41.08$; df $= 1, 12$; $P < 0.01$; Fig. 1). In contrast, of the 413 weevils fed squares (206 females, 207 males), only one male exhibited fat body hypertrophy.

Analyses indicated an association between weevil sex and reproductive status for the unfed trap baseline weevils ($Q_{SMH} = 72.88$, df $= 1$, $P < 0.01$). The proportion of newly captured females that was classed as reproductive was 0.217 (0.130–0.338; Fig. 2a), whereas the proportion of males classed as reproductive was 0.983 (0.900–1.000). However, these distinctions are misleading because the proportion
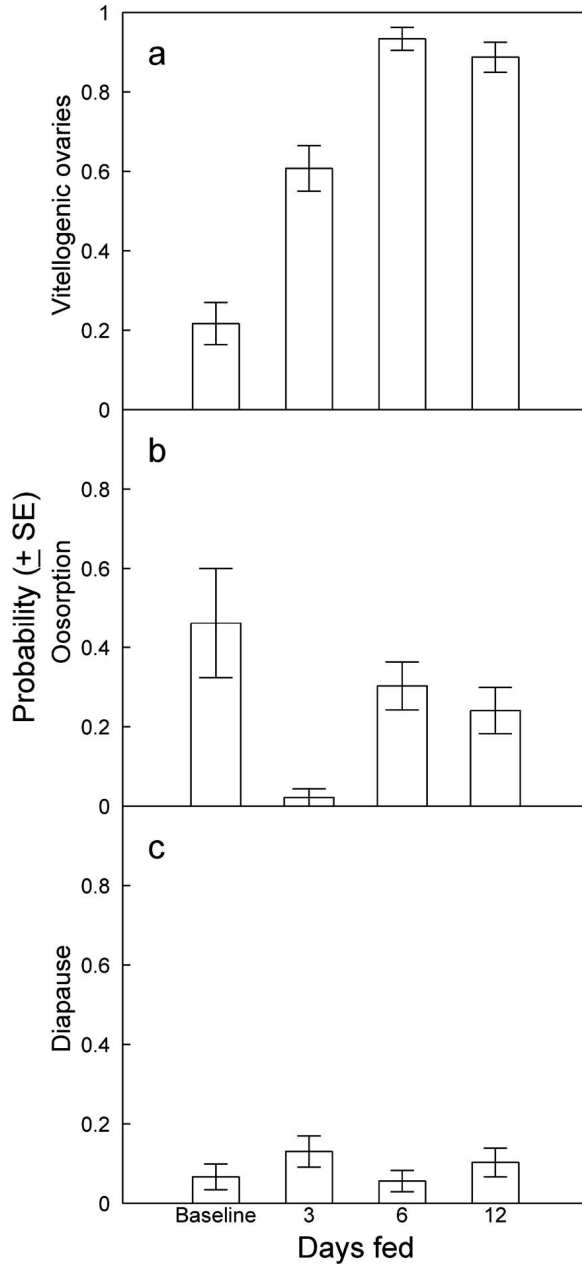
Fig. 2. Physiological characters of overwintered female boll weevil adults immediately after capture in pheromone traps (Baseline), and after feeding on cotton bolls at 29.4 ± 0.5°C under a 13:11 (L:D) h photoperiod for 3, 6, or 12 d. Physiological characters were presence of (a) vitellogenic ovaries, (b) oosorption, and (c) diapause (hypertrophied fat body and lack of vitellogenic oocytes). Error bars for the baseline are 95% CL; error bars corresponding to feeding durations are SE.

of males classed as reproductive was influenced by the low incidence of fat body hypertrophy, and fat body hypertrophy is associated with the opaque condition of the testes of nonreproductive males (Spurgeon et al. 2003). In comparison, females without vitellogenic oocytes were classed as nonreproductive irrespective of fat body condition.

When the weevils were fed squares, most of the females (0.958, 0.878–0.990) exhibited developing ovaries after 3 d, and all females were reproductive after feeding on squares for ≥6 d. All males that fed on squares were reproductive irrespective of the feeding period duration. When the weevils were fed bolls, all but one male (0.986, 0.918–1.000) were reproductive after 3 d, and all males were reproductive after feeding for ≥6 d. When females were fed bolls the incidence of vitellogenic ovaries tended to increase with the duration of feeding ($F = 12.48$; df = 2, 8; $P < 0.01$; Fig. 2a). The probability of reproductive females was lower at 3 d compared with 6 (adjusted-$P < 0.01$) or 12 d (adjusted-$P = 0.015$) but was not different between 6 and 12 d (adjusted-$P = 0.61$).

A small proportion of females in the baseline group exhibited oosorption (0.100, 0.043–0.205), but only 13 of 60 (21.7%) females were reproductive. Therefore, oosorption was common among the reproductive females (0.463, 0.232–0.709; Fig. 2b). When females were fed squares, only two weevils exhibited oosorption—one at 6 d (0.014, 0.000–0.084) and one at 12 d (0.015, 0.000–0.090). When females were fed bolls, the incidence of oosorption was initially low (3 d) but appeared higher when feeding durations were ≥6 d (Fig. 2b). However, these differences were not statistically significant ($F = 4.04$; df = 2, 8; $P = 0.06$).

Based on dissections of weevils in the baseline group, the proportion of females classed as diapausing at the time of their capture was 0.067 (0.022–0.164; Fig. 2c), and only a single newly captured male (0.017, 0.000–0.100) was classed as diapausing. No females or males were classed as diapausing after any duration of square feeding, and only one male fed bolls (0.014, 0–0.082; 3 d) was classed as diapausing. Although 20 of the 217 female weevils fed bolls were classed as diapausing, the incidence of diapause was similar to the incidence of diapause in the baseline group of females, and did not change with increased feeding duration ($F = 1.15$; df = 2, 8; $P = 0.37$; Fig. 2c). The respective patterns of incidence of reproductive development (Fig. 2a) and diapause (Fig. 2c) for females fed bolls appeared inconsistent because the incidence of reproductive development tended to increase with feeding duration, whereas the incidence of diapause remained static. This apparent discrepancy was caused by the relatively high incidence of females (26.2%) that exhibited neither fat body hypertrophy nor ovary development after feeding on bolls for 3 d. The incidence of lean, nonreproductive females diminished to about 1% by 6 d of boll feeding.

Host-free longevity. The log-rank test indicated a difference between the respective survival functions of the baseline group (newly captured, unfed weevils) and weevils that were fed bolls before starvation ($\chi^2 = 129.96$, df = 1, $P < 0.01$; Fig. 3). In general, weevils initially provided bolls for 14 d tended to survive without food for 2–3 weeks longer than those in the baseline group which were starved immediately after capture in traps. The maximum longevity of fed weevils was more than 6 weeks compared with 3 weeks for unfed weevils. Including the feeding period, the fed weevils tended to survive 4–8 weeks longer than those denied food.
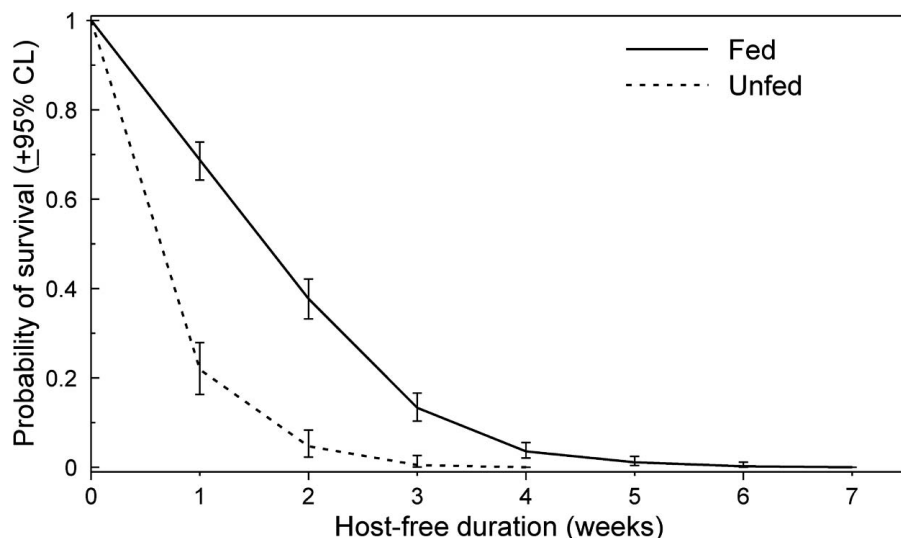
Fig. 3. Survival functions (probability of survival ± 95% CL) at 23.9 ± 0.5°C with a 13:11 (L:D) h photoperiod for trap-captured boll weevil adults held without food (unfed), or held without food after feeding on bolls (fed) for 14 d at 29.4 ± 0.5°C with a 13:11 (L:D) h photoperiod.

Discussion

The newly captured overwintered weevils were characterized by relatively low incidences of fat body hypertrophy, ovary development, and diapause, and a relatively high incidence of oosorption within the few females that were reproductive. Although only a small proportion of newly captured female boll weevils exhibited ovary development, we had anticipated a complete absence of reproductive development in these weevils. Ovary development has been reported for weevils feeding on nonfruiting cotton or vegetative cotton structures (Brazzel and Newsom 1959; Cole and Adkisson 1981, 1982; Esquivel et al. 2004; Grossman 1928; Vanderzant and Davich 1958). Further, nearly half of the newly captured females that were reproductive also exhibited oosorption, which appears rapidly in response to starvation (Spurgeon and Suh 2017b). Considering that seedling cotton was available in the field when the weevils were trapped, it seems likely that the overwintered females that were classed as reproductive at the time of capture had recently fed on seedling cotton plants.

Responses of the overwintered weevils that were fed after capture depended on the assigned diet. For overwintered weevils fed squares, the incidence of fat body hypertrophy, diapause, and oosorption decreased rapidly, but the incidence of developed ovaries increased. In comparison, when the weevils were fed bolls the incidence of reproductive development increased more slowly (females), the incidence of diapause was decreased (males) or was unchanged (females), and the incidence of oosorption varied but remained substantial. Although oosorption

occurs rapidly in response to starvation (Spurgeon and Suh 2017b), it also occurs in response to an inadequate or nonpreferred diet (Spurgeon et al. 2003, Vanderzant et al. 1959). Most importantly, the incidence of fat body hypertrophy was increased in both weevil sexes fed the boll diet. This increase in fat content provides the best explanation for the ecologically relevant increase in host-free survival observed for boll-fed weevils compared with unfed overwintered weevils.

Although overwintered weevils fed the boll diet accumulated fat in a manner similar to diapausing weevils, the high incidence of reproductive development indicates that we did not reinduce diapause. In addition, the host-free longevity for boll-fed overwintered weevils was considerably less than that observed for weevils recently induced into diapause (Spurgeon 2008; Spurgeon and Suh 2017a, 2018; Spurgeon et al. 2008, 2018b). Suh and Spurgeon (2006) previously demonstrated enhanced survival of overwintering boll weevils fed vegetative-stage regrowth cotton early in the fallow season. In the tropics or subtropics where maturing volunteer or regrowth cotton might be encountered late in the fallow season, the increased longevity permitted by boll feeding could play an important role in extending overwinter survival until squaring cotton becomes available. These results should be informative to management or eradication programs because they provide a mechanism by which fallow-season cotton might improve boll weevil overwinter survival, in addition to the traditionally recognized mechanisms of diapause induction or reproduction.

Acknowledgments

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