

# Circadian rhythms of feeding, oviposition, and emergence of the boll weevil (*Coleoptera: Curculionidae*)

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**Abstract** Circadian rhythm of feeding, oviposition, and emergence of boll weevil adults were determined at five different photophases (24, 14, 12, 10, and 0 hours) and a constant 27°C temperature, 65% RH in the laboratory. Squares from Petri dishes, where they were exposed to boll weevil females, were removed and examined for feeding and oviposition punctures every 4 hours during daylight (0700–1900 h) and every 12 h at night (1900–0700 h) over eight consecutive days. Cohorts of randomly selected egg-punctured squares were sampled from ovipositing females at 0700, 1100, 1500, and 1900 during 24 hours and under different photophase treatments, and maintained in Petri dishes at 27 ± 1°C, 65% RH. Dishes were observed twice daily (1900 and 0700 h) for adults emerging at day or night. Circadian rhythm of oviposition was not affected by the length of the photophase. The boll weevil has round-the-clock circadian rhythm of oviposition, with a daytime preference. We observed that 82.4%–86.0% of the boll weevil eggs were deposited between 0700 and 1900 h, and 14.0%–17.6% between 1900 and 0700 h during a 24-h period. Feeding of boll weevil females in photoperiods 24:0 h (complete light) and 0:24 h (complete darkness) did not significantly change between 0700–1900 h versus 1900–0700 h, while the daily cycle of light and darkness in other photoperiods significantly increased the feeding punctures from 0700–1900 compared with 1900–0700 h. The circadian rhythm of emergence depended significantly on the time of oviposition and the length of the photophase. Investigation of boll weevil circadian rhythm provides a better understanding of boll weevil ecology and reveals potential weak links for improving control technologies targeting their reproductive strategies.

**Key words** *Anthonomus grandis*, emergence, circadian rhythm, oviposition, photophase  
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## Introduction

The boll weevil, *Anthonomus grandis grandis* (Boheman), is a key pest of cotton in non-eradication areas of the USA, Mexico, and South America. Female weevils oviposit eggs in cotton squares (flower buds) and young bolls, where

legless white grubs develop through three instars and a pupal stage within the fruit. The adult emerges inside the fruit and chews its way out. The complete life-cycle requires 15–20 days. Both adult and immature weevils damage cotton. Adults cause damage via feeding and oviposition punctures on fruiting structures, while the grubs feed within the fruit. When bracts of damaged squares open, which is referred to as flaring, damaged squares are usually aborted by the plant and drop to the ground.

The activity rhythms of many insects are governed by abiotic factors, but light is the basic factor that sets the

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timing of the activity phase in nearly every case (Harker, 1961; Edwards, 1964; Tshernyshev, 1996). The daily cycle of light and darkness is the main environmental cue organisms use to synchronize circadian rhythms to the 24-h day. A circadian rhythm of activity is a major characteristic of insects affecting their ecology (Neville, 1967; Pittendrigh, 1972; Roberts, 1965, 1974; Beck, 1980; Tshernyshev, 1984), and it is important to correctly select the optimal photoperiod for their maintenance. The time of peak activity is determined by physiological processes that trigger behavioral reactions in insects. The objectives of this study were to determine the effects of photoperiod on circadian rhythms of: (i) feeding; (ii) oviposition; and (iii) emergence of boll weevil adults.

## Materials and methods

### *Boll weevil culture and cotton squares*

All boll weevils for these experiments were reared under similar conditions in the laboratory from field-collected infested squares. Approximately 1 000 infested squares were collected from the ground in cotton fields in the Lower Rio Grande Valley of Texas during May–June 2003. Squares were carefully dissected, and those containing live third instars were reclosed and held within screen cages in an environmental chamber at  $27 \pm 1^\circ\text{C}$ , 65% RH, and a photoperiod of 13:11 (L:D) h. Temperature and humidity were monitored by a Fisher-brand Traceable Relative Humidity Meter with temperature readout (Fisher Cat. No. 11-661-12, Friendswood, TX). After completion of larval development, five pupae were harvested from squares and placed in 9-cm diameter Petri dishes containing a shallow layer of moist vermiculite. Pupae were examined daily until adult eclosion. On the day of eclosion, adults were sexed as described by Sappington and Spurgeon (2000), weighed on an analytical balance, and males were marked with red paint on the right elytron. Only adults weighing between 10–15 mg on the day of the eclosion were used in the study. Mating was facilitated by a 5-day conditioning period under the same environmental conditions used for rearing adults. During this period, mixed-sex groups of 20 weevils (10 males and 10 females) were held in 15-cm diameter Petri dishes. Each dish was ventilated by a 4-cm diameter circular screened hole in the lid. Each dish contained a cotton wick saturated with water, and weevils were provided with five uninfested, greenhouse-grown squares (7–10 mm diameter at the widest part of the flower bud with intact bracteoles) daily. We assumed all females were mated by the end of the conditioning period.

### *Experimental conditions*

Five different photoperiods were used [10:14; 12:12; 14:10; 24:0; and 0:24 (L:D) h] and all photophases were initiated at 0700. Temperature in all cases was maintained at  $27 \pm 1^\circ\text{C}$  and relative humidity at about 65%. Homogeneous groups of 10 weevil females were entrained to each of the five photoperiods for 5 days prior to studies.

### *Circadian rhythm of feeding and oviposition.*

Females were individually placed in Petri dishes (150 mm  $\times$  15 mm) with a 4-cm circular screened (nylon) window on the top. Five uninfested squares were exposed to boll weevil females at 0700, 1100, 1500, and 1900 h during the 24-h period. For feeding and oviposition, five groups of 10 females were held in environmental chambers programmed for the five different photoperiods as described above. Squares were removed and examined for feeding and oviposition punctures every 4 hours from 0700 to 1900 and 12 hours from 1900 to 0700 for 8 consecutive days. Unsealed punctures were considered as feeding punctures. Oviposition punctures were distinguished by a frass plug and/or a waxy substance either closing the puncture or present on the periphery of the puncture. Everett and Ray (1962) reported a correlation between the numbers of such sealed punctures and the numbers of eggs that the weevils deposited. We used the numbers of sealed punctures as a relative estimate of egg numbers.

### *Circadian rhythm of emergence*

Distinct cohorts of randomly selected egg-punctured squares were periodically obtained from each of those exposed to boll weevil females at different hours of the day and under different photoperiods. To avoid underestimating the production of adults due to larval cannibalism, only squares containing a single egg-puncture were selected. The number of egg-punctured squares in each cohort varied based on their availability (Table 1). Each cohort was held in a 150 mm  $\times$  15 mm plastic Petri dish vented as previously described. Cohorts of squares were maintained under the same environmental conditions as the adults for oviposition. Beginning on day 10 and continuing until day 25 after oviposition, plates were observed twice daily (0700 and 1900) for adults that had emerged in the day or night-time. After day 25, squares were opened to determine if live weevils remained. In addition to emergence, we estimated the sex ratio of the adult progeny and their development time. The median of the emergence distribution was calculated as described by Scheffler (1980).

**Table 1** Total number of cohorts/egg-punctured squares sampled for determination of circadian rhythm of emergence.

Time squares exposed (h)		Photoperiod (L:D)				
		24:0	14:10	12:12	10:14	0:24
0700–1100	No. (L/D)	8/47	8/63	7/76	8/40	4/10
1100–1500	No. (L/D)	7/39	9/69	9/78	9/53	5/8
1500–1900	No. (L/D)	7/30	8/63	8/56	8/36	5/14
1900–0700	No. (L/D)	6/48	7/34	6/39	6/37	5/13

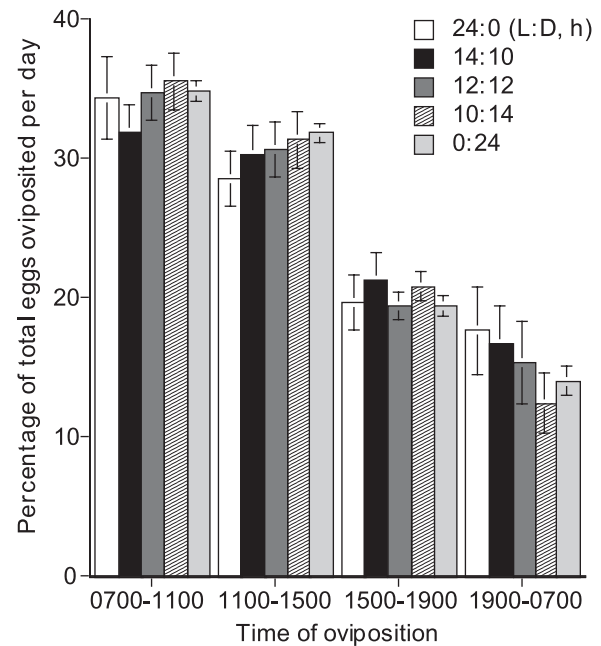
### Statistical analyses

Data were analyzed using analysis of variance (ANOVA), and means were separated by Tukey's honestly significant difference (HSD) ( $\alpha = 0.05$ ) test (Wilkinson *et al.*, 1992). Percentage data were transformed using the arcsine-square root method (Sokal & Rohlf, 1994). Relationships between time of oviposition and eggs oviposited during a given period under different photophases were described by a simple linear regression calculated using PROC GLM (SAS Institute, 1999).

## Results

### Circadian rhythm of oviposition and feeding

Circadian rhythms of oviposition were not affected by photoperiod. The range of boll weevil eggs deposited between 0700–1100 h from the total during a 24-h period was from 31.8% to 34.8% in all photoperiods used ( $F = 0.9$ ;  $df = 4,35$ ;  $P = 0.474$ ); 28.5%–31.8% for 1100–1500 h ( $F = 0.8$ ;  $df = 4,35$ ;  $P = 0.518$ ); 19.4%–21.2% for 1500–1900 h ( $F = 0.2$ ;  $df = 4,35$ ;  $P = 0.919$ ); and 14.0%–17.6% for 1900–0700 h ( $F = 1.3$ ,  $df = 4,35$ ;  $P = 0.279$ ) (Fig. 1). The linear regression indicated a significant relationship between percentage of daily eggs oviposited and the time of day when squares were exposed to the females, independent of photophase treatments (Table 2). According to Tshernyshev's (1984) classification of insect types of circadian rhythm

**Fig. 1** Circadian rhythm of oviposition at different photoperiods.

activity, the boll weevil exhibits round-the-clock circadian rhythm of oviposition, mainly in the daytime. But photoperiod significantly affected the total number of eggs oviposited per female per day:  $6.8 \pm 0.5$ ,  $6.6 \pm 0.3$ , and  $7.2 \pm 0.4$  eggs per female per day at 24-, 14-, and 12-h photophases, respectively, compared with  $4.2 \pm 0.4$  eggs per female per day at 10-h photophase, and  $2.3 \pm 0.5$  eggs per female per day at 0-h photophase ( $F = 15.4$ ;  $df = 4,45$ ;  $P = 0.001$ ).

Feeding of boll weevil females in photoperiods 24:0 h (complete light) and 0:24 h (complete darkness) did not significantly change between 0700–1900 versus 1900–0700 hours, while the daily cycle of light and darkness in other photoperiods significantly increased the feeding punctures from 0700–1900 compared with 1900–0700 h (Table 3, in the columns related to these time periods). The range of percent of boll weevil feeding punctures, from the total (100%) during a 24-h period, were not significantly different during the time when squares were exposed to weevil females: 0700–1100, 1100–1500, 1500–1900, and 1900–

**Table 2** Regression parameters relating percentage egg punctures (PEP) by boll weevil females per day and time when exposed to cotton squares (TSE) under different photoperiod (PhP).

Relation	Slope (SE)	$P_{\text{slope}}$	Intercept (SE)	$P_{\text{intercept}}$	$R^2$
PEP-TSE-PhP (24:0, h)	−5.90 (0.928)	0.024	39.75 (2.541)	0.004	95.3
PEP-TSE-PhP (14:0, h)	−5.44 (0.984)	0.031	38.60 (2.696)	0.005	93.9
PEP-TSE-PhP (12:12, h)	−6.94 (1.004)	0.020	42.35 (2.750)	0.040	96.0
PEP-TSE-PhP (10:14, h)	−6.78 (1.100)	0.025	41.35 (3.012)	0.005	95.0
PEP-TSE-PhP (0:24, h)	−7.48 (1.220)	0.026	43.70 (3.342)	0.006	94.9

**Table 3** Circadian rhythm of feeding by boll weevil females.

Time of square exposed, h	Feeding punctures by female at photoperiod (L:D)					Tukey's HSD test for means in denominator within a row
	24:0	14:10	12:12	10:14	0:24	
0700–1100	1.3 ± 0.3/ 19.7 ± 4.4 <sup>†</sup> A	1.2 ± 0.2/ 17.4 ± 2.8 A	0.9 ± 0.1/ 16.4 ± 2.7 A	1.2 ± 0.2/ 25.0 ± 4.8 A	0.4 ± 0.1/ 13.0 ± 3.5 A	$F = 0.4$ ; $df = 4,265$ ; $P = 0.775$
1100–1500	0.9 ± 0.2/ 13.6 ± 2.6 A	1.4 ± 0.2/ 21.7 ± 2.9 A	1.4 ± 0.2/ 25.4 ± 3.5 A	1.1 ± 0.2/ 22.9 ± 5.0 A	0.6 ± 0.1/ 19.4 ± 4.1 A	$F = 0.3$ ; $df = 4,241$ ; $P = 0.881$
1500–1900	1.1 ± 0.3/ 16.7 ± 4.8 A	1.3 ± 0.2/ 19.8 ± 2.9 A	1.4 ± 0.3/ 25.4 ± 5.5 A	1.0 ± 0.3/ 20.8 ± 6.7 A	0.6 ± 0.1/ 19.4 ± 3.6 A	$F = 1.6$ ; $df = 4,281$ ; $P = 0.162$
(1900–0700)/3	1.1 ± 0.2/ 16.7 ± 2.7 A	0.9 ± 0.1/ 14.0 ± 1.9 A	0.6 ± 0.1/ 10.9 ± 2.6 A	0.5 ± 0.1/ 10.4 ± 2.6 A	0.5 ± 0.1/ 16.1 ± 3.1 A	$F = 0.4$ ; $df = 4,250$ ; $P = 0.779$
Sum 1900–0700	3.3 ± 0.5 a	2.7 ± 0.3 b	1.8 ± 0.3 b	1.5 ± 0.4 b	1.5 ± 0.3 a	
Sum 0700–1900	3.3 ± 0.5 a	3.9 ± 0.3 a	3.7 ± 0.4 a	3.3 ± 0.4 a	1.6 ± 0.2 a	
Sum 24	6.6/100	6.6/100	5.5/100	4.8/100	3.1/100	
$P$ Sum 1900–0700 vs. Sum 0700–1900	$P = 0.941$	$P = 0.033$	$P = 0.008$	$P = 0.031$	$P = 0.465$	

<sup>†</sup>The numerator is mean ( $\pm$  SE) number of feeding punctures per female under time contact with squares; the denominator is percentage of feeding punctures per female under time contact with squares from total per day.

Means ( $\pm$  SE) within a column followed by the same lower case letter (related to time of square exposed to weevil females Sum 1900–0700 and Sum 0700–1900) and those within a row followed by the same capital letter (related to time of square exposed to weevil females: 0700–1100, 1100–1500, 1500–1900, and 1900–0700/3) are not significantly different (Tukey's HSD test).

0700/3 (data for the 12-h period, from 1900 to 0700, was divided into three to obtain the corresponding values for a fourth time of squares exposed period) in all photoperiods used (Table 3 in the rows related to time when squares were exposed to boll weevil females).

#### Circadian rhythm of emergence

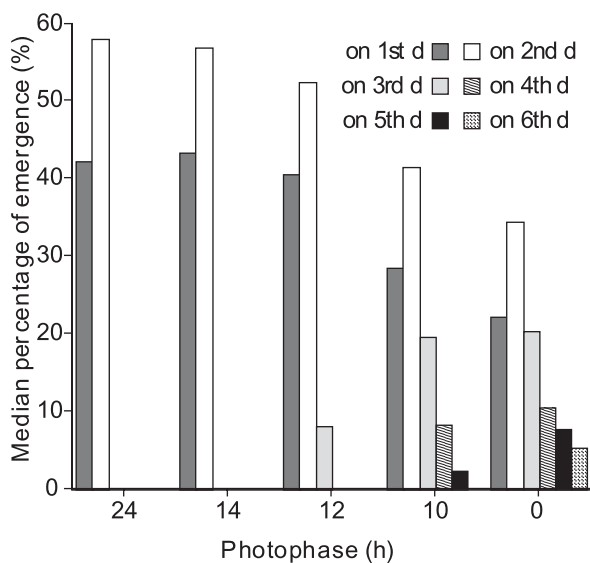
Emergence of boll weevils that developed from eggs

laid from 0700 to 1100 h was significantly higher in the day (0700–1900 h) under 24- ( $P = 0.034$ ), 14- ( $P = 0.033$ ), and 12-hour ( $P = 0.045$ ) photophases than in the night (1900–0700), while emergence at 10 and 0 hours of photophases did not differ significantly from day to night ( $P = 0.753$  and  $P = 0.712$ , respectively) (Table 4). Boll weevil emergence from eggs oviposited 1100–1500 h did not differ significantly at any photoperiods tested, except 0:24 h, where most emerged at night ( $P = 0.047$ ). For boll

**Table 4** Effects of photoperiod and time of oviposition on circadian rhythm of boll weevil female emergence (%).

Time of oviposition	Photoperiod (L:D, h)									
	24:0		14:10		12:12		10:14		0:24	
	0700–1900	1900–0700	0700–1900	1900–0700	0700–1900	1900–0700	0700–1900	1900–0700	0700–1900	1900–0700
0700–1100	65.7 a $P = 0.034$	34.3 b	71.9 a $P = 0.033$	28.1 b	64.0 a $P = 0.045$	36.0 b	54.6 a $P = 0.753$	45.4 a	41.7 a $P = 0.712$	58.3 a
1100–1500	59.0 a $P = 0.459$	41.0 a	53.5 a $P = 0.699$	46.5 a	48.1 a $P = 0.479$	51.9 a	55.7 a $P = 0.660$	44.3 a	36.7 b $P = 0.047$	63.3 a
1500–1900	30.4 b $P = 0.015$	69.6 a	61.8 a $P = 0.042$	38.2 b	28.5 b $P = 0.009$	71.5 a	63.3 a $P = 0.043$	36.7 b	45.0 a $P = 0.778$	55.0 a
(1900–0700)/3	53.3 a $P = 0.834$	46.7 a	64.6 a $P = 0.044$	35.4 b	71.0 a $P = 0.024$	29.0 b	23.8 b $P = 0.009$	76.4 a	46.7 a $P = 0.834$	53.3 a

Pair of means within a row under the same photoperiod and time of oviposition followed by the same letter are not significantly different.



**Fig. 2** Effects of different photophases on distribution of boll weevil emergence.

weevils developing from eggs oviposited from 1900–0700 h, emergence was significantly higher in the day time under 14- ( $P = 0.044$ ) and 12-h ( $P = 0.024$ ) photophases, while under short photophase (10 h) emergence was significantly higher at night ( $P = 0.009$ ). At photophases of 24 and 0 h, boll weevil emergence did not differ significantly between day and night (Table 4). The length of distribution of boll weevil emergence in days was positively correlated with the length of photophase and ranged from 2–3 d (24, 14, or 12 h) to 5–6 d at 10 h or 0 h (Fig. 2). The median of emergence was 42.1%, 43.2% and 40.5% at day 1; and 57.9%, 56.8%, and 52.4% on day 2 when boll weevils developed at 24-, 14-, and 12-h photophases, respectively; and 8.1% on the third day when boll weevils developed at 12-h photophase. Long-day photoperiod resulted in a compact distribution of emergence (Fig. 2). Total emergence was significantly higher under light and dark cycling (51.0% at 14:10; 49.4% at 12:12; and 48.8% at 10:14 h) than under constant light (37.8%) or constant darkness (18.8%) ( $F = 13.6$ ;  $df = 4, 128$ ;  $P = 0.001$ ).

## Discussion

In insects, the circadian system is responsible for imposing daily rhythmicity on a variety of processes, including locomotor activity, oviposition, hatching, pupation, and ability to return at the appropriate time to a food source that is available only at a particular time of the day. The circadian system functions as a biological clock, capable

of providing the individual with information on the time of day and the ability to measure lapses of time (Page, 2003). Daily light and darkness are the main environmental cues organisms use to synchronize circadian rhythms to the 24 hours of the day. The light-dark cycle not only has a synchronizing function but also a direct excitatory or inhibitory influence. Together these two effects determine, to a great extent, the time of day at which an animal is active (Aschoff, 1960). *Drosophila* spp. is the classic example of the influence of photophase on synchronization of emergence (Pittendrigh, 1967). Circadian rhythm of oviposition activity of several *Drosophila* spp. on highland populations in Argentina were early in the afternoon in the field (1400–1600 h) as opposed to populations from a much warmer lowland site, where flies were mainly active in the early evening prior to sunset (Dahlgaard *et al.*, 2001). In each cross between genetically different strains of *Drosophila melanogaster*, the oviposition curves of  $F_1$  and  $F_2$  were usually close to the midparent curve (Allemand & David, 1984). The circadian rhythms of oviposition and emergence, and photo- and gravity-tropism of egg-parasitoid *Trichogramma* spp. have been reported (Afonina *et al.*, 1985, 1986; Dakhiya *et al.*, 1985; and Greenberg, 1991). The highest oviposition of *Trichogramma evanescens* Westwood occurred during the afternoon and lasted until the evening. The oviposition stopped during the night and started again on the next day. The emergence of the parasitoid started at 0600 h. The maximum emergence of *T. evanescens* occurred from 0800 to 1000 h. Abrupt reduction of emergence was after 1400 h. The emergence stopped in the interval from 2200 to 0600 h. Greenberg *et al.* (1996) showed that *Catolaccus grandis* (Burks), an ectoparasitoid of boll weevil larvae, oviposited the highest number of eggs between 0700–1300 h (48.5%–78.0%). Most *C. grandis* emerged during 1900–0700 h (70.0%). The cabbage fly, *Delia brassicae* Bouche by Hawkes, and the flower flies, *Syrphidae* spp., have maximum oviposition at the end of the day (cited in Tshernyshev, 1984). Sharp drops in duration of daylight also stimulated oviposition by Pyralidae at dusk (Tshernyshev, 1984). He *et al.* (2004) reported that about 95% of *Aphidius ervi* Haliday, an important parasitoid of aphids, emerged during the photophase. Females attacked aphids in both light and dark conditions. The number of eggs laid and parasitism were significantly greater in the photophase than in scotophase. The peak oviposition time of *Anopheles gambiae* Giles, the African malaria mosquito, may be regulated by the light-dark cycle rather than oviposition habitat characteristics or feeding times (Sumba *et al.*, 2004). Butterflies emerge during the morning, but most moths emerge during the evening (Tshernyshev, 1984).



Flight of the weevil, *Phyllobius argentatus* L., was observed round-the-clock (Lewis & Taylor, 1965), while flight of the alfalfa weevil, *Hypera postica* Gyll., was limited to daylight time, although it significantly increased with decreasing illumination (Procopy & Gyrsco, 1965). The main factor regulating the circadian rhythms of Colorado potato beetle activity is light, not air temperature (Mindep, 1981). Adult boll weevils exhibited a daily rhythm in their susceptibility to standardized doses of the insecticide, methyl parathion (Cole & Adkisson, 1964). The mortality produced by the insecticide was intimately related to the time of day at which the toxicant was applied. The period of greatest resistance always occurred at dawn and recurred at 6-h intervals throughout the 24-h cycle. The greatest difference in response occurred under a photoperiod of 10:14 h, where the same dose of methyl parathion killed approximately 10% of the weevils treated at dawn but almost 90% of those treated only 3 h later (Cole & Adkisson, 1964). Rhythmic locomotor activity and daily susceptibility to deltamethrin were tested in the pine weevil, *Hylobius abietis* (L.). Under a long photoperiod, 18:6 h, a peak of locomotor activity occurred at the beginning of the dark phase, and the minimum occurred in the middle of the light phase (Pszczolkowski & Dobrowolski, 1999).

Circadian rhythms of boll weevil oviposition and emergence were unknown prior to this study. It is possible that the rhythms of boll weevil oviposition and emergence are endogenous because they were maintained during constant conditions of light and temperature and could not be induced by direct influence of any non-control factors. Presence of endogenic rhythm and its expression depended completely on insect genetics and did not disappear in relation to the environment of the parents. Circadian rhythm has been expressed as a result of influence on the forming embryo of the circadian rhythm of the maternal organism. Similarly the transmission of rhythm from maternal organism to the daughter was shown for the fly *Dacus (Strumela) tryoni* Frogg (Bateman, 1955). The heritability of the circadian rhythm trait is independent of the previous environment of the maternal organisms. *Drosophila* reacted to the light cycle of the current environment but this was not reflected on the rhythms of their progeny (Tshernyshev, 1984). Moreover, endogenic rhythms are more typical for insects of tropical or subtropical origin (Tshernyshev, 1984). The boll weevil is a tropical species which has expanded only recently into temperate regions. Investigation of the circadian rhythms of oviposition and emergence of boll weevils provides a better understanding of mechanisms controlling their ecology and for evaluating their reproductive strategies.

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