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Research

Life-History Parameters of *Striacosta albicosta* (Lepidoptera: Noctuidae) Under Laboratory Conditions

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Abstract

Striacosta albicosta (Smith) is a key pest of maize and dry beans in North America. It has expanded its distribution from the western Great Plains of the United States to the Great Lakes region in the United States and Canada. There has been limited research on the baseline biological aspects of this insect under controlled conditions. The objective of this study was to detail the biological parameters of *S. albicosta* feeding on an artificial diet under laboratory conditions. Overall survival from neonate to adult at 26.6 ± 1°C was 36.72% and the total developmental time was approximately 110 d. Survival of the egg, larval, prepupal, and pupal stages were 75.71, 98.50, 51.78, and 95.10%, respectively. Average duration of the egg, larval, prepupal, and pupal stages was 4.64, 28.20, 41.50, and 25.91 d, respectively. During the larval stage, 92.50% of larvae developed through seven instars and the remaining through six instars. Larvae that developed through six and seven instars exhibited a mean growth ratio of 1.60 and 1.47, respectively; however, there was no difference in pupal weight. Eggs laid by field-mated moths showed a fertility of 75.71%, compared with 4.18% from laboratory-reared moths. These data suggest that *S. albicosta* develop primarily through seven instars and the most vulnerable developmental stage is the prepupa. Laboratory conditions strongly affected fertility success. Information presented here greatly expands our understanding of *S. albicosta* biology, which can be used to improve the efficiency of laboratory bioassays and management techniques for this critical crop pest.

Key words: western bean cutworm, annual crop pest, artificial diet, development, life cycle

The western bean cutworm, *Striacosta albicosta* (Smith), is a univoltine owlet moth found in the United States, Canada, Mexico, and Colombia (Lafontaine 2004, Sánchez-Peña et al. 2016). In the Midwestern United States, *S. albicosta* is recognized as an important pest of maize (*Zea mays* L.) and dry beans (*Phaseolus vulgaris* L.). Since 1999, *S. albicosta* has undergone a range expansion from the western Great Plains eastward in the U.S. Corn Belt and into Ontario, Canada (Smith et al. 2018). It is now a regionally critical pest and since 2018 is under consideration to be a primary pest of maize in the United States (Archibald et al. 2017, Smith et al. 2018, US EPA 2018).

The life cycle of *S. albicosta* has been partially described in a few scientific publications (Antonelli 1974, Michel et al. 2010, Dyer et al. 2013). Previously published work has also included field and laboratory observations directed toward specific stages of the pest and aiming to improve *S. albicosta* management in maize and beans (Hoerner 1948; Douglass et al. 1955, 1957; Hagen 1962; Antonelli 1974; Blickenstaff 1979; Seymour et al. 2010). However, a detailed description of the complete development of the pest is lacking and the data presented for specific life stages vary significantly among publications. Furthermore, there is also a lack of studies that examine egg production and oviposition by individual females. This gap in the literature may be due to a previous lack of interest in studying *S. albicosta*, until its recent range expansion into the central and eastern Corn Belt of North America (Smith et al. 2018). In addition, this may partially be due to the difficulty in the development of an effective artificial diet and establishment of successful laboratory colonies maintained over many generations (Dyer et al. 2013).

In maize, *S. albicosta* eggs are laid on the upper surfaces of leaves, with a preference for plants that are near, but not past, pollination (Blickenstaff 1979, Michel et al. 2010, Paula-Moraes et al. 2013). Several studies have reported the average number of eggs per egg mass, although these numbers are quite variable: 3–79 (Hoerner 1948), 5–255 (Douglass et al. 1955), up to 407 (Blickenstaff 1979), 84–627 with an average of 321 (Douglass et al. 1957), 21–195 with an average of 52 (Hagen 1962), 5–200 with an average of 50

(Seymour et al. 2010), up to 300 (Antonelli 1974), and 2–345 with an average of 85 eggs per mass (Paula-Moraes et al. 2013).

Newly hatched larvae feed on the chorion and then typically move to the tassel within the whorl to feed on developing tassel tissue and pollen (Hagen 1962, Paula-Moraes et al. 2012). When larvae reach later instars, they will move downward and concentrate in the ear zone and enter the ear tip or through the side of the ear to feed on developing kernels (Michel et al. 2010, Seymour et al. 2010, Paula-Moraes et al. 2012). There is also high variability in the *S. albicosta* literature for the duration of the larval period, with the number of instars reported as five or six. The most detailed study reporting *S. albicosta* larval development dates from 44 yr ago (Antonelli 1974), and few studies have since reported larval development. None have reported complete development and mortality by instar. Furthermore, there are significant differences in developmental days reported. Two publications report the complete development of *S. albicosta* through five instars: Seymour et al. (2010) report average development between 30 and 35 d, whereas Douglass et al. (1957) reported a 22-d developmental period. Three other publications report complete larval development through six instars, where the average developmental times were 56, 31, and 28 d (Antonelli 1974, Blickenstaff 1979, Dyer et al. 2013).

In late summer and early fall, mature larvae drop to the ground, burrow 7–25 cm below the surface, and become prepupae (Appel et al. 1993, Seymour et al. 2010), remaining in a quiescent state throughout the winter (Hoerner 1948, Douglass et al. 1957). The next year, the prepupae undergo metamorphosis and pupate; adults typically begin to emerge in late June and early July, and flights usually end by late August (Dorhout and Rice 2004, Rice 2006, Hanson et al. 2015). Mating behavior is not greatly affected by temperature and humidity, most likely related to it being a univoltine species that experiences a narrow range of environmental conditions during moth flight (Konopka and McNeil 2017).

In this study, we evaluated the biological parameters of *S. albicosta* development under laboratory conditions and compared the reproductive aspects of field-collected and laboratory-reared female moths. By reporting the detailed parameters of this species' biology under laboratory conditions, this knowledge can inform rearing methodology for toxicological bioassays, field infestations, and other efforts to advance recommendations for resistance management and integrated pest management. In addition, *S. albicosta* is vulnerable to chemical and transgenic control methods for only a restricted period of its life cycle; thus, understanding its developmental biology is essential for the development of effective management strategies.

Materials and Methods

Insects and Laboratory Conditions

Experiments were conducted under laboratory conditions at the Agroecosystems Entomology Laboratory located at the University of Nebraska–Lincoln's West Central Research and Extension Center in North Platte, NE. All biology studies were conducted using neonate larvae from field-collected egg masses, or egg masses laid by field-collected adults from black light traps placed on the outer edge of maize fields in 2017 near Grand Island, NE (40°54′43.10″N, 98°16′33.60″W). Light traps consisted of a wooden frame (1.17 × 1.20 × 2.20 m) covered with metal screening with a mercury vapor black light trap (modeled after an 'Ellisco style' trap, Troyer Enterprises, North Platte, NE) on the top attached to a funnel into the interior of the cage. Inside each cage, late vegetative stage pinto bean plants were available (*P. vulgaris*) for oviposition and shelter. Each morning during the moth flight, adults were collected from light traps, transferred to the laboratory, and placed into rearing cages (63.5 × 63.5 × 63.5 cm; Bug Dorm, MegaView Science Co., Ltd., Talchung, Taiwan) also containing late vegetative stage pinto bean plants for oviposition. Adult diet consisted of a 5% sucrose and 0.2% ascorbic acid solution provided in a 150 mm × 15 mm sponge inside a Petri dish. Egg masses laid on bean plants were collected daily, placed on moistened filter paper inside Petri dishes, and held at 26.6 ± 1°C, 70–80% relative humidity (RH), 16:8 (L:D) h photoperiod, and monitored daily for eclosion. The artificial diet used was from the Dyer et al. (2013) rearing manual, which consisted of Black Cutworm dry mix (Bio-Serv F9240B, Bio-Serv, Inc., Frenchtown, NJ) and General Lep dry mix (Bio-Serv F9772). Egg, larval, and pupal development were evaluated as described below. All experiments were performed in a rearing room (26.6 ± 1°C, 70–80% RH, and 16:8 (L:D) h with evaluations performed daily at 2:00 p.m. CDT.

Adult and Egg Stages

To evaluate reproductive parameters for laboratory-reared *S. albicosta*, insects collected from the field as described above were maintained in the laboratory from egg until adult eclosion, following Dyer et al. (2013). One male and one female moth that emerged on the same day were placed in pairs inside oviposition cages. Oviposition cages consisted of a 30 × 30 × 30 cm cage (Bug Dorm, MegaView Science Co., Ltd., Talchung, Taiwan) containing late vegetative stage pinto bean plants for oviposition. Adult diet consisted of a 5% sucrose and 0.2% ascorbic acid solution provided in a 3.80 cm × 3.80 cm sponge inside a Petri dish. Cages were examined daily to record adult survival and to remove and count the number of eggs in each egg mass. Each 1-d-old egg mass was individually placed in a Petri dish (10 cm diameter, 1.5 cm height) lined with filter paper moistened with distilled water and observed daily until hatching. Dead females were dissected to determine the number of spermatophores and to count any unlaid eggs retained. Total fecundity (the sum of eggs laid and eggs retained in the body) and fertility (total number of eggs hatched) of 45 pairs were evaluated. The viability and embryonic period of 4,971 eggs (from 248 egg masses) was measured.

To compare the reproductive parameters of laboratory-reared insects with field-collected females, egg masses were obtained from 26 field-collected females. Adult females were collected from light traps in North Platte, NE (41°05′7.43″N, 100°46′24. 85″W) and transferred to the laboratory and placed into oviposition cages. Only one female was placed inside each oviposition cage. Moths and eggs were monitored as described above for the laboratory-reared insects. Fecundity and fertility of field-collected females were evaluated. The viability and embryonic period of 5,636 eggs (from 91 egg masses) were evaluated. Dead females were dissected to determine the number of spermatophores and to count any unlaid eggs retained.

Larval Stage

In this study, we divided the larval stage into two periods: 1) 'active larval period' where insects were active and feeding and 2) 'inactive larval period' (or prepupal period). This period is characterized by the interruption of feeding, a decrease in size due to loss of body water, fading of coloration, and behavior of the construction of the prepupal chamber using body fluids and humidity to cement organic materials available in the container.

Active Larval Period

The larval development study was conducted using 200 neonates 24 h after hatching. Neonates were selected from 10 different egg masses hatched on the same day and were individually placed in plastic containers (300 ml volume, 10 cm diameter, 15 cm height; ULINE, Wisconsin). To maintain humidity, holes were made in the lids, and a small wad of cotton (~1 cm in diameter) moistened with distilled water was added to each container. The diet and moist cotton were replaced daily. Daily observations were made to verify the survival and development of the larvae by collection of the molted head capsules. Head capsule width provides a more accurate and repeatable estimate of larval growth than weighing the mass of each larva (Dyar 1890). The head capsules were individually stored and labeled, by larva, in microcentrifuge tubes. The head capsules were measured (millimeter) with a micrometer under a microscope. The mean growth ratio was calculated by dividing the mean head capsule width of each instar by the mean head capsule width of the previous instar.

Inactive Larval Period (Prepupal Period)

When larvae reached the prepupal period, they were transferred into clean transparent plastic containers (300 ml volume, 10 cm diameter, 15 cm) containing a mixture of autoclaved sand (QUIKRETE Premium Play Sand, # 1113) and 10 ml of distilled water to provide a proper environment for metamorphosis. Daily observations were made to verify survival and to record pupal metamorphosis.

Pupal Stage

Pupae were kept in the same container and conditions as in the prepupal period. Pupae were monitored daily to record the emergence of adults and maintain moisture of the sand by adding 10 ml of distilled water as needed. On the second day after pupation, when the cuticle was hardened, each insect was weighed using a semianalytical balance (precision of 0.01 g) and sex determination was performed following Queiroz-Santos et al. (2018). Considering that precise sex determination is only possible during the pupal stage, the identity of each larva was preserved throughout the study. Therefore, it was possible to track the development of each *S. albicosta* from hatching until adult emergence, including the sex.

Data Analysis

Biological parameters, such as duration, size, and weight of each developmental stage, were analyzed using descriptive statistics with the calculation of means and SD. The sex ratio was calculated by the number of females divided by the number of females plus number of males. When appropriate, means of sexes were compared using Student's *t*-test assuming unequal variances, at a significance level of 5% ($\alpha = 0.05$).

Results

Entire Life Cycle

The overall survival of *S. albicosta* (from neonate to adult) reared in controlled and constant conditions was 36.72%, and the total developmental time was 110.10 d (Table 1).

Adult and Egg Stages

Laboratory-Reared Adults

The longevity of *S. albicosta* adults represents 9% of the complete developmental time. From the 45 laboratory-reared pairs, 18 (40.0%) did not mate, 13 (28.9%) mated one time, 11 (24.4%) mated two times, 2 (4.4%) mated three times, and 1 couple (2.2%) mated six times. Thus, on average females mated 1.74 times. The longevity of individuals that mated was significantly longer than individuals that did not mate ($t = 2.62$; df = 88; $P = 0.010$; Table 2). For both mated ($t = 2.70$; df = 52; $P = 0.009$) and unmated ($t = 2.03$; df = 34; $P = 0.033$) pairs, the longevity of females was significantly longer than males. There was no significant difference in the number of egg masses laid between mated and unmated moths (Table 2).

Unmated females had a numerically lower mean number of laid eggs and numerically higher mean number of retained eggs (although not statistically significant) compared with mated females (Table 2). The total fecundity (sum of laid and retained eggs) was not different between mated and unmated females ($t = 0.93$; df = 88; $P = 0.3546$). From the 4,971 eggs laid by laboratory-reared females, only 208 hatched, resulting in fertility (percentage hatching) of 4.18%.

Field-Collected Adults

With regard to the females collected in the field ($n = 26$), only 1 (3.9%) was not mated, 14 (53.9%) mated once, 8 (30.8%) mated twice, and 3 (11.5%) mated three times in the field before they were collected. On average, females mated 1.50 times. The observed mean fecundity was 218.44 ± 223.60 (SD) eggs per female (range: 0–917 eggs) and 6.71 ± 6.31 egg masses laid per female. From the 5,636 eggs obtained, 4,267 hatched, corresponding to an overall fertility of 75.71%.

Eggs

The embryonic period represented 4% of the total life cycle, with a mean duration of 4.63 ± 0.78 (SD) d (range: 2–7 d), with the majority (96.54%) ranging from 4 to 5 d (4.64 ± 0.48; Table 1).

Larval Stage

The total larval developmental time (including the active and inactive/prepupal periods) accounted for 64% of the entire *S. albicosta* life cycle. The mean duration of total larval development for larvae

Table 1. Survival and duration of *Striacosta albicosta* developmental stages reared on artificial diet under laboratory conditions (26.6 ± 1°C)

Stage	*N*, initial–final	Survival (%)	Mean ± SD Duration (d)	Range of duration (d)
Eggs	5,636–4,267	75.71	4.64 ± 0.48	4–5
Larvae	200–197	98.50	28.20 ± 3.93	21–36
Prepupae	197–102	51.78	41.50 ± 9.32	19–70
Pupae	102–97	95.10	25.91 ± 7.62	12–51
Adults (couples)	45	—	9.80 ± 5.22	3–28
Total	—	36.72	110.10	—

Table 2. Biological parameters of unmated and mated *Striacosta albicosta* females reared on artificial diet under laboratory conditions (26.6 ± 1°C)

		Unmated (n = 18)		Mated (n = 27)		
Sex	Biological parameter	Mean (± SD)	Range	Mean (± SD)	Range	P value[a]
Both	Longevity (d)	8.00 ± 4.80	3–20	10.85 ± 5.23	3–15	0.010
Female	Longevity (d)	9.56 ± 4.50	3–20	12.67 ± 5.49	3–28	0.044
	Egg masses	3.41 ± 6.29	0–21	6.71 ± 6.31	0–20	0.096
	Laid eggs	58.94 ± 121.41	0–460	144.81 ± 162.81	0–553	0.063
	Retained eggs	152.11 ± 114.44	0–460	119.48 ± 108.57	0–406	0.339
	Total fecundity	211.06 ± 154.83	0–548	264.30 ± 159.64	0–568	0.355
	Spermatophores	0	0	1.74 ± 1.06	0–6	—
	Fertility	0.00%	—	4.18%	—	
Male	Longevity (d)	6.44 ± 4.69	3–15	9.04 ± 4.33	4–19	0.043

[a]Statistical comparisons between unmated and mated moths for each parameter using a Student's t-test, considering different variances, at 5% level of significance.

Table 3. Mean and SD of larval and pupal duration, in days, of *Striacosta albicosta* during each instar, including the larvae which developed through six and seven instars, reared on artificial diet under laboratory conditions (26.6 ± 1°C)

Developmental stage	Six instars	Seven instars	P value[a]
	(n = 10)	(n = 74)	
Instar I	4.20 ± 1.14	4.46 ± 1.17	0.172
Instar II	3.70 ± 1.16	3.39 ± 0.81	0.191
Instar III	3.50 ± 1.27	3.18 ± 0.92	0.133
Instar IV	3.10 ± 0.57	3.37 ± 0.97	0.773
Instar V	4.40 ± 1.71	4.08 ± 1.30	0.743
Instar VI	6.10 ± 1.85	5.60 ± 1.78	0.617
Instar VII	—	4.53 ± 2.13	
Active larval stage	24.64 ± 2.50	28.61 ± 3.31	<0.0001
Inactive larval period (prepupae)	38.20 ± 11.19	42.89 ± 9.06	0.018
Total larval period (active + inactive)	63.20 ± 12.59	71.50 ± 9.36	0.005
Pupal	24.40 ± 9.91	25.63 ± 7.54	0.641
Total (larval + pupal)	87.60 ± 10.16	97.14 ± 10.90	0.011

[a]Comparisons of instar developmental time using a Student's t-test, considering different variances, at 5% level of significance.

developing through six instars was 63.20 ± 12.59 (SD) d, which was significantly shorter (t = 3.63; df = 86; P = 0.005) than the mean duration for larvae developing through seven instars: 71.50 ± 9.36 (SD) d (Table 3).

Active Larval Period

Survival for the active larval stage was high (98.50%), with only three deaths among the 200 neonates observed (Table 1). The active larval period represented 26% of the total life cycle. The majority of the larvae developed through seven instars (92.5%) and the rest through six instars. The active larval period lasted on average 24.64 ± 2.50 (SD) d for larvae developing through six instars and 28.61 ± 3.31 for larvae developing through seven instars, which was significantly longer (t = 2.62; df = 82; P = 0.011; Table 3, Fig. 1A).

After the third instar, there was a significant difference in head capsule size between larvae that developed through six versus seven instars (Table 4). The mean width of the head capsule ranged from 0.37 ± 0.04 mm in the first instar to 3.68 ± 0.14 mm in the final instar for larvae that developed through seven instars, and 0.36 ± 0.13 mm in the first instar to 3.59 ± 1.36 mm in the final instar for larvae that developed through six instars. Head capsule width was significantly larger for larvae developing through six instars compared with those developing through seven instars during the third through sixth instars (Table 4). The growth ratio was greater for larvae developing through six instars (1.60) than larvae developing through seven instars (1.47; Table 4, Fig. 2). For development through both six and seven instars, a high coefficient of determination (R^2) was observed, especially for those that went through seven instars, following the geometric progression described by Dyar (1890; Fig. 2).

Inactive Larval Period (Prepupal Period)

The prepupal period was marked by low survival, as 51.78% of larvae died during this period, with variation in duration between individuals ranging from 19 to 70 d (Table 1, Fig. 1B). The duration of this period was also the longest (37.7%) in relation to the total life cycle of the species in the laboratory. Larvae developing through six instars had longer prepupal duration compared to larvae developing through seven instars (t = 2.41; df = 86; P = 0.018; Table 3).

Pupal Stage

Under laboratory conditions, *S. albicosta* spent about a quarter of its life cycle (23.60%) as a pupa. Pupal survival was high (95.10%) and duration (mean 24.40 ± 9.91 [SD] d) was highly variable, ranging from 12 to 51 d (Table 1, Fig. 1C). The pupal duration for larvae that developed through six instars was not significantly different from larvae that developed through seven instars. (t = 0.50; df = 82; P = 0.641).

The average pupal weight of *S. albicosta* was 358.04 ± 51.67 mg with a large range (202–538 mg). There was no significant difference in pupal weight between females (356.29 ± 53.27 mg) and males (359.00 ± 50.66 mg; t = 0.06519; df = 123; P = 0.948). Similarly, no significant differences were observed between females (331.40 ± 101.69 mg) and males (372.20 ± 94.20 mg) that developed through six instars (t = 0.658; df = 9; P = 0.529) or females (358.27 ± 48.43 mg) and males (358.82 ± 45.95 mg) that developed through seven instars (t = 0.065; df = 123; P = 0.948). The sex ratio determined from 70 females and 69 males was 0.504, which does not differ significantly from a 1:1 ratio (χ^2 = 0.007; df = 1; P = 0.90).

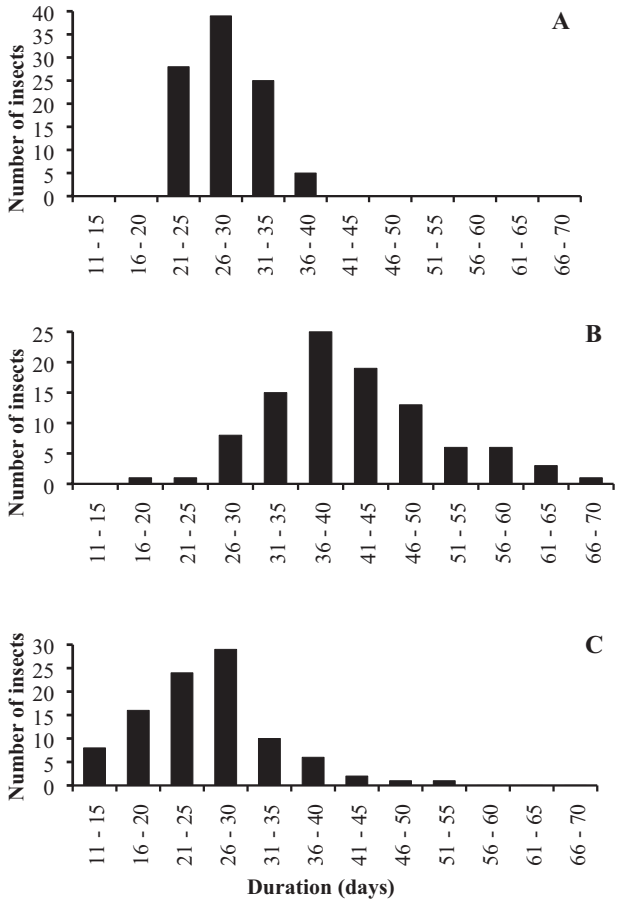

Fig. 1. Number of *Striacosta albicosta* that completed each stage or period, reared successfully until adult (n = 97) for 5-d intervals: (A) active feeding larvae; (B) prepupae—inactive feeding larvae; and (C) pupae. Larvae reared on artificial diet under controlled conditions.

Discussion

Our results indicate that the duration of the *S. albicosta* incubation period is short, ranging from 4 to 5 d for the majority of the eggs (Table 1), similar to that observed by Hagen (1962) and shorter when compared with Douglass et al. (1957) and Hoerner (1948), who reported 7 d on average under similar conditions. The average incubation period of *S. albicosta* reported here is also shorter when compared with other noctuid species that also present long diapause, such as *Agrotis malefida* Guenée (Lepidoptera: Noctuidae) at 7.93 d (Specht et al. 2013) and *Feltia submontana* Köhler (Lepidoptera: Noctuidae) at 7.09 d (Dias et al. 2019), whereas species that do not diapause present shorter incubation time, such as *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) at 3.3 d (Bento et al. 2007). Reporting an accurate egg incubation period is crucial for integrated pest management strategies. First, this period should be used in recommending the appropriate frequency of field scouting so that eggs are not laid and hatched in between scouting events, leading to underestimation of infestation and possibly exceeding of the economic threshold. An understanding of egg incubation period is also important for correctly timing insecticide applications to target early-instar *S. albicosta* larvae prior to entering the ear.

The longevity of *S. albicosta* moths reported in this study (8.00 ± 4.80 d; Table 1) is similar to that reported by Dyer et al. (2013) and Farhan (2013). Other authors also reported differences in longevity between male and female moths (Blickenstaff 1979, Farhan 2013), showing that females live longer than males, as we also observed in this study.

The fact that the number of eggs laid by females that had mated at least once is higher than those laid by unmated (Table 2) females agrees with previous reports that fecundity of noctuids is associated with mating status of females, albeit such eggs are not viable (Montezano et al. 2013, 2014, 2016). Our results from laboratory-reared moths indicate a substantial reproductive incompatibility under these conditions, where 40% of the pairs did not mate. This percentage is much higher than that found among field-collected females, where only one unmated individual was observed, representing less than 4% of the total insects collected. In addition to the high number of females from the laboratory that did not mate, we also observed very low fertility (4%) among females that had mated, which was significantly lower than the 76% fertility observed for field-collected females. Several factors may be associated with low fertility for laboratory-reared moths, including the effect of

Table 4. Head capsule widths of *Striacosta albicosta* larvae, at each instar and respective growth ratios

	Both sexes six instars (n = 8)			Both sexes seven instars (n = 28)			
Instar	Mean (mm) ± SD	GR	Range	Mean (mm) ± SD	GR	Range	P value[a]
I	0.36 ± 0.13	—	0.3–0.4	0.37 ± 0.04	—	0.3–0.4	0.598
II	0.57 ± 0.22	1.58	0.5–0.8	0.55 ± 0.05	1.49	0.5–0.6	0.578
III	1.20 ± 0.45	2.11	1.1–1.3	0.87 ± 0.05	1.58	0.8–0.9	0.001
IV	1.80 ± 0.68	1.51	1.6–1.9	1.34 ± 0.13	1.54	1.1–1.5	0.001
V	2.60 ± 0.98	1.44	2.5–2.8	2.00 ± 0.13	1.49	1.7–2.2	0.001
VI	3.59 ± 1.36	1.38	3.5–3.7	2.81 ± 0.13	1.41	2.5–3	0.001
VII	—	—	—	3.68 ± 0.14	1.31	3.5–4	0.047
Mean		1.60			1.47		

Insects reared on artificial diet under laboratory conditions (26.6 ± 1°C). GR (growth ratio).

[a]Comparisons of head capsule widths using a Student's t-test, considering different variances, at 5% level of significance.

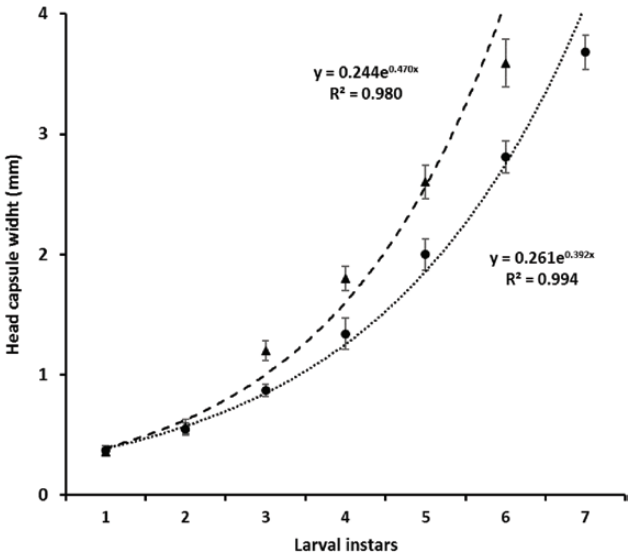

Fig. 2. Size of *Striacosta albicosta* head capsules with individuals that developed throughout six (n = 8, triangles and dashed line) and seven (n = 28, circles and dotted line) larval instars. Larvae reared on artificial diet, under controlled conditions.

laboratory conditions, which are very different from those experienced in nature, especially during adult flight periods. In the laboratory, moths are maintained in cages that restrict flight space, which may have interfered with mating behavior, as previously shown for other Noctuidae (Luo et al. 1999). It is known that flight can enhance reproduction and the capacity for mating in some noctuids; Luo et al. (1999) showed that there is a strong positive correlation between distance flown and total fecundity for *Mythimna separata* Walker (Lepidoptera: Noctuidae) moths.

Another important observation from our study is the high fertility of field-collected females, almost twice that reported in previous studies (Hoerner 1948, Hagen 1962, Difonzo 2009, Paula-Moraes et al. 2012). Although fertility of 76% is high compared with previously published literature for *S. albicosta*, this is fairly low when compared with other cutworm species, such as *A. ipsilon* at 93% (Bento et al. 2007), *A. malefida* at 97% (Specht et al. 2013), *Spodoptera dolichos* (Fabricius) (Lepidoptera: Noctuidae) at 98% (Montezano et al. 2016), and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) at 97% (Montezano et al. 2019). The relatively low fertility presented by *S. albicosta*, especially among laboratory-reared adults, may once again be attributed to the laboratory conditions that were less ideal compared with field conditions. Another explanation for the low fertility presented by laboratory-reared insects might be the effect of male age on mating status, which has been shown to be highly important for *S. albicosta* (Farhan 2013). Studies showed that sexually mature females mated with 2- or 8-d-old males were significantly less successful than those mated with 4- or 6-d-old individuals (Farhan 2013). Because our laboratory-reared egg masses came from a male–female pair of the same age, this might have decreased fertility and consequently successful fecundity. Field-mated moths had on average 1.50 spermatophores per female, whereas laboratory-reared moths had on average 1.75. However, the viability of laboratory eggs was only 4.75%. Our results show that the problem of viable eggs is not related to the lack of mating under laboratory conditions and might be related to environmental factors related to moth flight and diapause conditions because these are the most difficult aspects to reproduce under controlled conditions and have been proven to significantly affect hormone production and fertility success in other noctuids (Luo et al. 1999, Ureña et al. 2016, Reynolds et al. 2019).

Our results show that under laboratory conditions, *S. albicosta* spent 26% of their life cycle in the active larval period. This is the most critical stage for agricultural losses, when larvae will be feeding and causing economic damage. The active larval period is the interval with the most similarity between laboratory and field conditions, and may explain why our results (an average of 25 and 28 d for larvae completing six and seven instars, respectively) are similar to field data from Difonzo (2009; 28 d), Blickenstaff (1979; 31 d) and Seymour et al. (2010; 31 d). However, our results differ from other reports under field conditions: 22 d (Douglass et al. 1957) and 56 d (Antonelli 1974). These differences are most likely related to abiotic conditions such as the weather, as well as host plants also associated with thermic exigencies also shown for other Noctuidae.

The majority of published studies describe *S. albicosta* developing through six instars. However, in the present study under laboratory conditions, the collection and measurement of all head capsules allowed us to determine with precision that 92.50% of the larvae developed through seven instars, and just 7.50% developed through six instars (Table 3). Blickenstaff (1979), Dyer et al. (2013), and Difonzo (2010) reported larvae developing through six instars, although it is not clear if the prepupal stage was taken into account. Our results also differ from Seymour et al. (2010) and Douglass et al. (1957), who reported only five instars. Larval development in Noctuidae commonly includes six or seven instars; however, several factors can influence the number of instars (Esperk et al. 2007). The most common factors influencing instar number include temperature, photoperiod, food quantity and quality, humidity, injury, inheritance, and sex. Typically, instar number tends to increase under adverse conditions. Because our studies were conducted under controlled laboratory conditions, these results do not agree with the compensation scenario hypothesis that additional instars are inserted under poor conditions when larvae fail to reach a species-specific threshold-size with the 'normal' instar number (Nijhouth 1975).

As demonstrated for several Noctuidae species, head capsule size, especially at the end of development, can vary greatly depending on diet quality and environmental conditions (Parra et al. 1977, Mattana and Foerster 1988, Goudis 2014). The mean width of the final larval head capsule (Table 4) demonstrated that *S. albicosta* larvae developing through seven instars are larger than those developing through six instars at the completion of the larval stage. Our results for head capsule width in the sixth instar was similar to larvae reared using the same methods (3.49 ± 0.38 mm; Dyer et al. 2013). Goudis (2014) reared *S. albicosta* on different cultivars of dry beans and the last larval head capsule matches our results for seventh instar (3.10 ± 0.17). However, in the study by Goudis (2014), the instar number was not taken into account. Our results also differ considerably from Antonelli (1974) and Paula-Moraes et al. (2012) who reported 5.0- to 5.7-mm head capsule for sixth-instar larvae and 1.70 mm between third and fourth instars. This disparity may be a result of differences in rearing methodology, or most importantly, the time point at which measurements were taken (Dyer et al. 2013). Measures made in this study were taken after each molt when head capsules were unattached from the body. In contrast, other studies, with the exception of Dyer et al. (2013), do not indicate the precise timing of head capsule measurement; thus, differences in measurements might have resulted from such differences in time and precision.

The prepupal period corresponds to the time when larvae cease feeding (Hanson et al. 2013), enter a period of diapause, and later

prepare for metamorphosis to the pupal stage. Although in this study the prepupal period accounted for 38% of the total life cycle, it is expected that under natural conditions this period will be much longer, representing the complete phase of overwintering. This stage was also observed in our study to have high variability in duration, with the difference between the shortest and longest individuals being 51 d. Given our results showing 19 d as the minimum duration for the prepupal period, we can assume that all larvae passed through diapause, as the majority of Noctuidae that do not go through diapause present a maximum of 4- to 5-d prepupal development (e.g., Shorey et al. 1962, Liu et al. 2004, Montezano et al. 2016). The large variation found between individuals probably relates to the difficulty that the insect has in responding to laboratory conditions, which include higher temperatures than the insect has adapted to in the field. In this study, high mortality (51%) during the prepupal stage suggested that this is the most critical for the development of *S. albicosta*. Other experiments have shown even higher mortality of the prepupal stage: from 72% in the laboratory to 90% under field conditions (Blickenstaff 1979, Smith et al. 2018). Further studies of the prepupal stage under field conditions during the overwintering period are needed to better understand this critical life stage.

Our results demonstrated that under laboratory conditions, it was possible to reduce the complete *S. albicosta* life cycle to at least one-third of the cycle observed under natural conditions (Table 1). The limitations to further decrease this time, by decreasing the diapause period are most likely because under field conditions the prepupal period (inactive larval period) will go through a mandatory diapause and overwinter under low temperatures, frequently below zero (Hanson et al. 2015). In the laboratory, only adult, egg, and active larval periods represent the approximated field conditions of *S. albicosta*. The biological plasticity of reducing the developmental time under controlled conditions was also reported for other univoltine noctuid cutworms such as *A. malefida* (Specht et al. 2013) and *F. submontana* (Dias et al. 2019).

Pupal survival was relatively high when compared with the prepupal period (Table 1). Similar to the prepupal period, there was considerable variation in the number of days that individuals required to complete development. The duration of the pupal stage (Table 1) indicates that in addition to prepupal diapause, *S. albicosta* may also exhibit pupal diapause, which is found in other owlet moths (Specht et al. 2013, Reynolds et al. 2019). These results indicate that further studies should be conducted to elucidate the abiotic and biotic factors associated with the initiation and termination of *S. albicosta* prepupal and possibly pupal diapause. Understanding hormonal production and changes during such an important stage (Reynolds et al. 2019) can help us to better understand factors associated with prepupal development and adult emergence, which are still uncertain in the different regions where the pest occurs.

The most detailed study reporting *S. albicosta* larval development dates from Antonelli (1974), and since then, only a few studies have reported larval development (Michel et al. 2010, Seymour et al. 2010, Dyer et al. 2013) with none of these studies reporting complete development and mortality by stage. It was also not clear if the prepupal period was accounted for during such observations. Furthermore, there are significant differences in development time reported in the previous studies, even under similar rearing conditions, making it difficult to compare results for *S. albicosta* life-history parameters. Due to the proven occurrence of different numbers of larval instars demonstrated in this study, it is recommended that in future studies measuring the effects of chemicals and other toxins related to *S. albicosta* management, it is crucial that larval instars are evaluated as described in this study to provide consistent results.

All the above-mentioned aspects for the development of *S. albicosta* explain, in part, the difficulties of maintaining a successful *S. albicosta* laboratory colony. The low viability of laboratory-reared *S. albicosta* is very common and one of the major challenges in conducting research with this pest. The first attempt toward developing a *S. albicosta* rearing system yielded between 0.8 and 19.6% success for the first generation, and the second generation did not produce any viable eggs (Antonelli 1974). Doyle (1994) experienced a similar lack of success with only 3.6% of the eggs developing to adults and 0% of the second-generation adults laying viable eggs. In this study, we found that the main challenge for the development of *S. albicosta* populations in the laboratory was related primarily to the species' univoltine behavior and the mandatory prepupal diapause. This diapause, even under laboratory conditions, significantly interferes with the development of immature and adults, reflecting on the viability of the next generation (Reynolds et al. 2019). We therefore suggest the importance of additional research to determine the biotic and abiotic factors associated with the initiation, and especially the termination, of prepupal diapause (Hanson et al. 2015). Clarification of these factors should significantly increase the success of laboratory and mass rearing of this insect, and allow more precise standardized experimental trials. This knowledge will also be fundamental for inferences in the field, especially the association of the influence of edaphoclimatic factors on the emergence of *S. albicosta* adults, and also their entire life cycle on host plants.

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