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Biotic potential, fertility and life table of Spodoptera albula (Walker) (Lepidoptera: Noctuidae), under controlled conditions


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Biotic potential, fertility and life table of *Spodoptera albula* (Walker) (Lepidoptera: Noctuidae), under controlled conditions

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ABSTRACT

This study aimed to evaluate the biotic potential, life table parameters and fertility of *Spodoptera albula* (Walker, 1857) under controlled conditions (25 ± 1°C, 70 ± 10% RH and 14 hour photo phase). The longevity, pre, post and oviposition periods, fecundity and fertility of 13 couples were evaluated. The longevity of females (13.500 days) was significantly higher than those of males (11.154 days). The mean durations of the pre, post and oviposition periods were 2.615, 1.769 and 9.385 days, respectively. The mean fecundity was 1.417.69 eggs and mean fertility was 1.340.401 larvae, per female. On average, females copulated 1, 231 times. A strong positive correlation was observed between the number of copulations and fecundity \((r = 0.847, p <0.001)\), as well as a strong negative correlation between the number of copulations and the duration of the pre-oviposition period \((r = -0.762, p = 0.002)\), and longevity \((r = -0.788, p = 0.001)\). The biotic potential of *S. albula* was estimated at 8.768 x 10\(^2\) individuals / female / year. The net reproductive rate \((R_0)\) was 353,904 times per generation and the mean generation time \((T)\) was 37.187 days. The intrinsic rate of increase \((r_m)\) was 1,105, with a finite rate of increase \((\lambda)\) of 3,019.

Key words: armyworm, development, fecundity, reproduction, spermatophore.

INTRODUCTION

The genus *Spodoptera* Guenée, 1852 is cosmopolitan and includes many of the most important agricultural armyworm caterpillars (Pogue 2002). *S. albula* (Walker, 1857) has been recorded from Florida to Southern Texas, throughout the Caribbean, Central America, and from Venezuela south to Paraguay and Southern Brazil (Pogue 2002, Zenker et al. 2010), and Chile (Angulo et al. 2008). *S. albula* has been erroneously referred to as "*Spodoptera sunia* (Guenée, 1852)", which is currently recognized as *Neogalea sunia* (Guenée, 1852), representative of the subfamily Cuculliinae (Poole 1989).
The larvae of *S. albula* have been recorded as feeding on at least 55 species belonging to 29 plant families (Montezano et al. 2013). Generally the larvae move into crops from the invading plants found between the rows and/or along the edges (González-B 1966, Hallman 1979, Savoie 1988).

In many places, especially in Central America, *S. albula* makes it unfeasible to develop important crops such as tobacco (Stoyan and Machado 1970, Novo Padrino et al. 1984, 1985, Páez Gázquez and Novo Padrino 1987), cotton (Alcaraz Vieco 1962, González-B 1966), tomato (Gloria-B 1975), cabbage (Armstrong 1994), sesame, soybean (Hallman 1979, 1983), peanuts (Teixeira et al. 2001), sunflower (Pruett and Guamán 2001), papaya (Semillas del Caribe 2010) and even seedling production in forestry nurseries (Vázquez et al. 1999).

The importance of this species is increased by its tolerance to various chemical insecticides and to the *Bacillus thuringiensis* Cry1Ac gene (Zenner de Polanía et al. 2008, Amaya et al. 2009). Its importance, motivated studies on its biology (Stoyan and Machado 1970, Novo Padrino and Martínez Reyes 1985, La Rosa et al. 1992), its damage potential (Novo Padrino et al. 1984, 1985, Páez Gázquez and Novo Padrino 1987), and on the identification of pheromonal components for behavioral control (Bestmann et al. 1988, Dunkleblum et al. 1995).

This study complements the previous one on immature (Montezano et al. 2013) and aims to evaluate and describe the developmental biological parameters of *S. albula*, with special emphasis on its biotic potential and on its life table and fertility, under controlled conditions.

**MATERIALS AND METHODS**

All experiments were carried out in a climate controlled room (25 ± 1°C, 70 ± 10% RH and a 14 hour photo phase), with daily observations. Information on the origin of insects, rearing methodology and data on immature stages are described in detail by Montezano et al. (2013) and all procedures were carried out according to the international practices for animal use and care under the control of an internal committee of the Universidade de Caxias do Sul, Brazil.

Considering the previously described incompatibilities between biotypes of the fall armyworm, from different host plants or localities, during copulation (Murúa and Virla 2004, Sadek and Anderson 2007, Murúa et al. 2008), the insects used in the experiment belong to the first generation obtained from a female collected in the field (see Montezano et al. 2013). Adults were kept in pairs (n = 13) within cylindrical plastic containers, 10 cm in diameter and 15 cm high, with tops closed using plastic film, to which container long filter paper strips were attached, to stimulate oviposition. The bottom part of the container was closed with a Petri dish (10.5 cm diameter), and its bottom was lined using filter paper.

To avoid the effect of the pupal weight on the reproductive aspects (Tisdale and Sappington 2001), females from pupae weighing 0.19g (n = 6) and 0.20g (n = 7) and males from pupae weighing 0.17g (n = 7) and 0.18g (n = 6) were used. Similarly, to avoid the effects of adults age on their capacity to copulate (Kehat and Gordon 1975, Ellis and Steele, 1982, Rogers and Marti Jr 1994), the couples were formed with adults which emerged on the same date.

The food was composed of the diet described by Hoffmann-Campo et al. (1985) which consists of honey (10g), sorbic acid (1g), Methylparaben (1g), sucrose (60g), and distilled water (1000 ml). All components were dissolved in distilled water and the obtained solution was kept under refrigeration (7°C). Pilsen beer was added to the solution at a proportion of ¼, on a daily basis, and made available to the insects in a 5 cm in diameter Petri dish lined with cotton wool. Additionally, distilled water was provided for the hydration of the insects, in another 5 cm cotton lined Petri dish. We calculated the fecundity (number of eggs per female), the fertility
BIOTIC POTENTIAL, FERTILITY AND LIFE TABLE OF *S. albula*

(number of hatched larvae per female), the longevity and the duration of the pre-oviposition, post-oviposition and oviposition periods.

Containers were examined daily to record adult mortality and to remove and record eggs. The fecundity (number of eggs per female), longevity and duration of pre, post and oviposition periods were evaluated. Dead females were dissected to determine the number of spermatophores they received from males while copulating.

To estimate fertility, the viability of 16 egg clusters taken from four couples, including the first and last, totaling 4,454 eggs were evaluated. To this end, each egg cluster was individualized in a Petri dish, whose bottom was lined with filter paper moistened with distilled water, where it remained until the eclosion of the larvae. All the evaluated egg clusters were from couples whose females, after death, had two spermatophores in the bursa copulatrix, proving they had been fertilized during the experiment.

All biological parameters were analyzed using descriptive statistics with the calculation of means and standard deviations. The means were compared using a t-test assuming unequal variances, at a significance level of 95%. The fecundity, longevity of both sexes and the duration of pre, post and oviposition periods were correlated (Pearson Product Moment Correlation) with the number of matings of each couple.

After gathering the biological parameters, the Biotic Potential (BP) was calculated considering the resistance of the environment as being null, using the equation described in Silveira Neto et al. (1976), $BP = (sr * d)^n - er$, where: (sr) sex ratio is number of females divided by number of females plus number of males; (d) viable individuals per female consisting of the number of eggs per female (or fecundity) multiplied by total immature survival; (n) number of generations per year or 365 days divided by total lifespan and (er) environmental resistance, in this case considered as null.

The fertility life table was developed using data from the immature stages of *S. albula* provided by Montezano et al. (2013) and is presented graphically by plotting the probability of survival values at the midpoint of each interval, or survival ($lx$), and the total number of eggs per female per week, which became females, or specific fertility ($mx$).

Using the life table, the values of the different reproductive parameters of *S. albula* were calculated. The net reproductive rate ($Ro$), the ratio between the number of females in two successive generations; the mean generation time ($T$), the mean number of days from the birth of the parents to the birth of offspring; the daily intrinsic rate of increase ($rm$) and the daily finite rate of increase ($\lambda$), followed the formulas contained in Silveira Neto et al. (1976).

**RESULTS AND DISCUSSION**

In this study, the longevity of *S. albula* (Table I) was similar to that described by La Rosa et al. (1992) who reported 12.4 days at 25°C and 13.2 days at room temperature (average of 26.7°C). However, these values were higher than those described by Martin Zequeira (1982) (~10.8) at approximately 21°C and by Novo Padrino et al. (1985) who reported values of 10, 8 and 7 days at 19.60, 23.03 and 25.30°C, respectively.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
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<th>Range</th>
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<tr>
<td>Longevity (days)</td>
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<td>8-17</td>
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<td>Longevity (days)</td>
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<td>1-5</td>
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<tr>
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<tr>
<td>Oviposition (days)</td>
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<td>1.56</td>
<td>7-11</td>
</tr>
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<td>55.68</td>
<td>606-2298</td>
</tr>
<tr>
<td>Male</td>
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</tr>
<tr>
<td>Longevity (days)*</td>
<td>11.42</td>
<td>2.57</td>
<td>8-16</td>
</tr>
</tbody>
</table>

Comparison of male and female mean longevity using Student *t* test, considering different variances, at a 95% level of significance (*p < 0.05*).
Considering the Montezano et al. (2013) data, which indicates a mean duration of the immature stages as 31.52 days, the average longevity of *S. albula* corresponds to 28.32%, or more than one quarter of their life cycle. These results are similar to other studies involving *Spodoptera* (i.e., Mattana and Foerster 1988, Habib et al. 1983, Bavaresco et al. 2004, Busato et al. 2005). These results also indicate that the extended longevity of *S. albula*, like other species of the genus such as *S. dolichos* (Fabricius, 1794), *S. eridania* (Stoll, 1782), *S. exigua* (Hübner, 1808), *S. frugiperda* (J.E. Smith, 1797) and *S. ornithogalli* (Guenée, 1852) which have a great ability for dispersal and even migration (Ferguson et al. 1991), is related to its wide distribution within the American Continent, extending between the parallels 30° North and South (Pogue 2002, Angulo et al. 2008, Zenker et al. 2010).

On average each female had 1.23 copulations, noting that three (23.08%) did not copulate, four copulated only once (30.77%) and six copulated twice (46.15%). This mean value is within the range described for *S. frugiperda* by Murúa et al. (2008), who found very discordant values between different *S. frugiperda* populations in Argentina (0.78 to 2.32 spermatophores per female). Regarding the absence of copulation in some *S. albula* pairs, these same authors reported that in some *S. frugiperda* cohorts more than 20% of the females did not mate, while in other cohorts more than 20% of couples performed more than two copulations. Moreover, considering that Milano et al. (2008), using 25 *S. frugiperda* pairs per cage, obtained a mean of over three spermatophores per female with a maximum of six, at 25°C, it is expected that a greater number of *S. albula* individuals per cage also increases the number of copulations.

The longevity of *S. albula* females was significantly higher than males (Table I) and was negatively correlated with the number of matings (*r* = -0.788, *p* = 0.001) indicating that *S. albula*, similar to *S. littoralis* (Kehat and Gordon 1975, Ellis and Steele 1982), presents a prolonged longevity as a result of reduced and delayed mating. Rogers and Marti Jr (1997) determined that when there is only a single opportunity for mating, two days after the emergence was the optimum age for mating *S. exigua* females to achieve their maximum reproductive potential, but they lived the fewest number of days. Additionally, Hou and Sheng (1999) describe a reduction in longevity of *H. armigera* (Hübner, 1808) females which have multiple matings. These authors attribute these results to interactions between egg production and metabolism. Multiple matings further stimulate egg production and accelerate energy and material consumption, decreasing resources available for somatic maintenance.

With respect to the different longevity between sexes, in studies with representatives of *Spodoptera*, some authors found greater longevity of females [i.e. Santos et al. 1980 - *S. cosmioides* (Walker, 1858); Melo and Silva 1987, Garcia and Clavijo 1989, Santos et al. 2004 - *S. frugiperda*; Farahani et al. 2011 - *S. exigua*], others of males [i.e. Parra et al. 1977, Mattana and Foerster 1988 - *S. eridania*; Bavaresco et al. 2003 - *S. cosmioides*; Xue et al. 2010 - *S. exigua*] or some even found no statistical differences between sexes [i.e. Habib et al. 1983 - *S. cosmioides*, Botton et al. 1998 - *S. frugiperda*, Santos et al. 2005 - *S. eridania*]. Considering that the longevity of males, was hardly correlated with the number of matings (*r* = -0.112, *p* = 0.715), the results of this study allow us to infer that the greater longevity of females with respect to males is due to the reduced number of copulations.

A strong negative correlation between number of copulations and the pre-oviposition period (*r* = -0.762, *p* = 0.002) was observed, indicating that *S. albula* presents an extension of the pre-oviposition as a function of the reduced number and absence of mating, which is also reflected as prolonged longevity, similar to *S. littoralis* (Kehat and Gordon 1975, Ellis and Steele 1982), *S. exigua* (Rogers and Marti Jr 1997), *Helicoverpa armigera* (Hübner, 1808) (Hou and Sheng 1999) and *Trichoplusia ni* (Hübner, [1803]) (Ward and Landolt 1995).
However, there was no significant correlation between the number of copulations and oviposition period \((r = -0.300, p = 0.319)\) and post-oviposition period \((r = 0.216, p = 0.479)\). Nevertheless, the reduction of the oviposition period related to a larger number of copulations, as described by Hou and Sheng (1999), is certainly related to a higher reproductive activity in females which copulated more.

The relatively short pre-oviposition period (Table I) indicates that \(S.\ albula\) adults complete sexual maturity soon after emergence, as occurs with other \(Spodoptera\) representatives (i.e. Parra et al. 1977, Habib et al. 1983, Mattana and Foerster 1988, Tisdale and Sappington 2001). However, the onset of oviposition, at least in the first days after emergence, is conditioned on the occurrence of the first mating. This initial mating period should be near the second day after the emergence of both sexes, as described in Rogers and Marti Jr (1997) for \(S.\ exigua\).

The average fertility of \(S.\ albula\), with approximately 1,400 eggs per female (Table I) is relatively high when compared with the mean values indicated for the same species in other publications such as: 930 eggs by Alcaraz Vieco (1962); 548, 542 and 995 eggs under mean temperatures of 25, 30 and 26.7°C, by La Rosa et al. (1992); and between 800 to 1,400 eggs by Novo Padrino and Martinez Reyes (1985). Such variations are relatively common and reported in studies with \(S.\ cosmioides\) (i.e. Habib et al. 1983, Bavero et al. 2003, 2004), \(S.\ eridania\) (Parra et al. 1977, Mattana and Foerster 1988, Santos et al. 2005), \(S.\ exigua\) (i.e. Greenberg et al. 2001, Tisdale and Sappington 2001, Farahani et al. 2011), \(S.\ frugiperda\) (i.e. Santos et al. 2004, Barbosa et al. 2005, Barros et al. 2010) and \(S.\ litura\) (Fabricius, 1775) (Xue et al. 2010). However, the variations can be attributed to several factors such as the conditions of each experiment and the biotypes related to the different host or geographic regions (i.e. Giolo et al. 2002, Murúa and Vírla 2004, Sadek and Anderson 2007, Barbosa et al. 2008, Murúa et al. 2008). Nevertheless, the greater number of eggs obtained in this study indicates that the diet and methodology employed to rear the immatures (Montezano et al. 2013) and adults were suitable for the development of \(S.\ albula\) in laboratory.

Although high, fertility varied greatly between individuals (Table I), with a positive correlation \((r = 0.847, p < 0.001)\) between the number of eggs and number of copulations. The positive relationship between fecundity and number of copulations has been documented for \(S.\ exigua\) (Rogers and Marti Jr 1996), \(S.\ frugiperda\) (Snow et al. 1970, Rogers and Marti Jr 1994, Milano et al. 2008), \(S.\ littoralis\) (Ellis and Sleep 1982, Sadek and Anderson 2007), \(Spodoptera\) \(litura\) (Fabricius, 1797) (Chu and Yang 1991) and other noctuids such as \(H.\ armigera\) (Hou and Sheng 1999) and \(Trichoplusia\ ni\) (Hübner, [1803]) (Ward and Landolt 1995, Landolt 1997).

Our results, together with the various publications that present a positive relationship between fecundity and fertility, indicate that if somehow the number of copulations were anticipated and increased, by using multiple couples per cage (Milano et al. 2008), the fecundity of \(S.\ albula\) could be even greater.

The high egg viability (94.54%) is certainly related to the proven fertilization of females who had two spermatophores. This percentage agrees with the 94-98% reported by Novo Padrino and Martinez Reyes (1985) and generally refers to \(Spodoptera\) representatives in studies where multiple mating is known to enhance the reproductive capacity, including fertility (Kehat and Gordon 1975, Sadek 2001, Sadek and Anderson 2007, Milano et al. 2008, Milano et al. 2008).

The biotic potential of \(8.686 \times 10^{22}\) individuals per female per year, resulting from the equation
BP = (sr*d)ⁿ - er ∴ BP = (0,515 x 1,130.400)⁸.²⁹⁶ - 0, is obtained when we consider that: 141 female and 133 male immature reached the pupal stage, at a ratio of 0.515 (Montezano et al. 2013); on average each female oviposited 1,417.75 eggs and the overall survival was 79.73%, obtaining 1,130.40 viable individuals per female (see Montezano et al. 2013, Table I); the average duration of the life cycle (43.99 days), corresponds to 8.29 generations per year (n); and the environmental resistance as null. In other words, each female could generate more than 86 sextillion offspring.

This relatively high value can also be obtained using published data for other representatives of *Spodoptera*. For example, for *S. exigua*, at 26°C, using data from Greenberg et al. (2001), considering an average lifespan of seven days, for larvae fed with cabbage, cotton, pepper, pigweed and sunflower, we get approximate values of 2.1 x 10²⁶, 3.8 x 10³³, 3.6 x 10²⁸, 5.4 x 10³⁷ and 1.6 x 10²⁸, respectively. For *S. eridania*, at 27°C, using data from Parra et al. (1977) and considering a sex ratio of 0.5 or 1:1, gives roughly 6.6 x 10²³ and 6.8 x 10¹⁸, for larvae reared on cotton and soybean, respectively.

The maximum rate of population increase occurred between the 36th and 37th day, during the 5th week of life, represented by the crossing of the survival and specific fertility lines (Figure 1). This rate is relatively dislocated towards the beginning of the adult stage, especially driven by the higher fertility and low mortality of imagos shortly after emergence. These observations agree with other studies conducted with representatives of *Spodoptera* where higher values of fecundity are observed during the first few days, from the second or third to the seventh (i.e. Kehat and Gordon 1975, Sadek 2001, Bavaresco et al. 2004, Murúa and Virla 2004).

The net reproductive rate (Ro) was 353.90 females per generation, similar to values described for other *Spodoptera* representatives on different host plants: for *S. exigua* - 377.11 on *Chenopodium album* Linn. - Chenopodiaceae and 342.11 on cabbage - *Brassica napus* Linn. Brassicaceae (Farahani et al. 2011); for *S. exigua* - 359.3 on cotton - *Gossypium hirsutum* Linn - Malvaceae, 342.2 on sunflower - *Helianthus annuus* Linn. - Asteraceae, and the maximum value of 596.0 on pigweed - *Amaranthus retroflexus* Linn. - Amaranthaceae (Greenberg et al. 2001); for *S. cosmioides* - 313.6 on castorbean - *Ricinus communis* Linn. - Euphorbiaceae and 380.7 on onion - *Allium cepa* Linn. - Liliaceae (Bavaresco et al. 2003); and for *S. frugiperda* - 372.2 on cotton (leaf), 363.2 (leaf and boll), 330.5 on millet (leaf), 421.8 on soybean (leaf) and 501.7 on corn (leaf) (Barros et al. 2010). Due to the great variability of

The mean generation time (T) of 37.19 days was above the maximum described for *S. exigua* of ~31.6, at 26°C (Greenberg et al. 2001, Farahani et al. 2001) and for *S. frugiperda* of ~30.8, at 25°C (Barros et al. 2010). However, it was less than the minimum observed for *S. cosmioides* of ~47.2, at 26°C (Bavaresco et al. 2003).

The daily intrinsic rate of increase (rm) and the daily finite rate of increase (λ) of *S. albula* obtained in the present study were: rm = 0.158 and λ = 1.171, respectively. These relatively low values, resemble those obtained for *S. cosmioides* (Bavaresco et al. 2003) which had a higher mean generation time (T), compared with that of *S. exigua* (Greenberg et al. 2001, Farahani et al. 2011) and *S. frugiperda* (Barros et al. 2010).

The parameters calculated for *S. albula* resemble some of the values obtained with certain host plants of *S. cosmioides* (Bavaresco et al. 2003), *S. exigua* (Greenberg et al. 2001, Farahani et al. 2011), and *S. frugiperda* (Barros et al. 2010). However, one must consider that there are great variations between values for the same species, especially due to temperature and host plant or artificial diet (i.e. Parra et al. 1977, Mattana and Foerster 1988, Ali and Gaylor 1992, Greenberg et al. 2001, Bavaresco et al. 2003, 2004, Busato et al. 2005, Santos et al. 2005, Azidah and Sofian-Azirun 2006, Sá et al. 2009, Barros et al. 2010, Farahani et al. 2011). Furthermore, Murúa et al. (2008) showed huge variations between biological and reproductive parameters between cohorts of *S. frugiperda* from different locations and host plants in Argentina.

*S. albula* shares diverse biological characteristics with the other representatives of the genus, considered key pests of various cultures. Among the analyzed parameters, the relatively long duration of the biological cycle is noted and should be further studied to assess whether it is responsible for the greater importance of this species in warmer regions, such as in Central America (i.e. Alcaraz Vieco 1962, González-B 1966, Stoyan and Machado 1970, Gloria-B 1975, Hallman 1979, 1983, Novo Padrino et al. 1984, 1985, Páez Gázquez and Novo Padrino 1987, Armstrong 1994, Vázquez et al. 1999, Pruett and Guamán 2001, Semillas del Caribe 2010), where the life cycle is shortened as a function of temperature.

This study indicates the importance of particularizing every aspect of the reproductive biology, since many details can compromise the data of reproductive parameters and the full expression of the biotic potential of *S. albula* and other Lepidoptera. In this way, when a single couple of *S. frugiperda* was used (Murúa et al. 2008) in comparison to multiple couples per cage (Milano et al. 2008), it caused a reduction in the mating number, in turn, it was associated with an increase in longevity and in the pre-oviposition period, leading to a decrease in fecundity and fertility.

Our results also indicate concerns for the need of a better understanding of the reproductive parameters of *S. albula* in the field, such as studies which include the collection of adults of other species using light traps (Sadek 2001), in order to compare with data obtained in the laboratory so that more reliable relationships can be inferred.

The reduction or delay in the number of copulations negatively influencing the population parameters indicates the relevance of identification studies (Bestmann et al. 1988, Dunkleblum et al. 1995) and the use of pheromones to retard or prevent
the mating of *S. albula* in nature, in mating disruption procedures (Cardé and Minks 1995), as a strategy for the Integrated Management of this species.

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**RESUMO**

Este trabalho objetivou avaliar o potencial biótico e parâmetros da tabela de vida e fertilidade de *Spodoptera albula* (Walker, 1857) em condições controladas (25 ± 1°C, 70 ± 10% UR e fotofase de 14 horas). Avaliou-se a longevidade, períodos de pré, pós e oviposição, fecundidade e fertilidade de 13 casais. A longevidade das fêmeas (13,500 dias) foi significativamente maior que a dos machos (11,154 dias). A duração dos períodos médios de pré, pós e oviposição foram de 2,615, 1,769 e 9,385 dias, respectivamente. A fecundidade média foi de 1.417,69 ovos e a fertilidade 1.340,401 larvas por fêmea. Em média, as fêmeas copularam 1,231 vezes. Observou-se forte correlação positiva entre número de cópulas e a fecundidade (r = 0,847, p < 0,001) e, forte correlação negativa, entre o número de cópulas e a duração do período de pré-oviposição (r = -0,762, p = 0,002), e a longevidade (r = -0,788, p = 0,001). O potencial biótico de *S. albula* foi estimado em 8,768 x 10^22 indivíduos/fêmea/ano. A taxa líquida de reprodução (Ro) foi de 353.904 vezes por geração e o tempo médio de uma geração (T) foi de 37,187 dias. A taxa intrínseca de aumento (λ) foi de 1,105, com uma razão finita de aumento (ρ) de 3,019.

**Palavras-chave:** lagarta-militar, desenvolvimento, fecundidade, reprodução espermatóforo.

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