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Sampling and Biostatistics

Survival Analysis and Actuarial Parameters of *Sternechus subsignatus* (Coleoptera: Curculionidae) Adults

María Guillermina Socías,^{1,2,3} Guido Van Nieuwenhove,^{4,5} María Gabriela Murúa,^{1,2,3} Eduardo Willink,^{1,3} and Gerardo Gustavo Liljesthröm^{2,6}

¹Instituto de Tecnología Agroindustrial del Noroeste Argentino (ITANOA) (guillezoo@hotmail.com; gmurua@eeaoc.org.ar; ewillink@ eeaoc.org.ar), ²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) (gerlilj@outlook.com.ar), ³Estación Experimental Agroindustrial Obispo Colombres (EEAOC), Av. William Cross 3150, Las Talitas, (T4101XAC), Tucumán, Argentina, ⁴Instituto de Entomología, Fundación Miguel Lillo, Miguel Lillo 251 (T4000JFE), San Miguel de Tucumán, Tucumán (gavn12004@yahoo.com.ar), ⁵Corresponding author, e-mail: gavn12004@yahoo.com.ar, and ⁶Centro de Estudios Parasitológicos y de Vectores (CEPAVE), Boulevard 120 S/N e/61 y 62 (B1902CHX), Universidad Nacional de La Plata, La Plata, Argentina

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Abstract

The soybean stalk weevil, *Sternechus subsignatus* Boheman 1836 (Coleoptera: Curculionidae), is a very serious soybean pest in the Neotropical region. Both adults and larvae feed on soybean, causing significant yield losses. Adult survival was evaluated during three soybean growing seasons under controlled environmental conditions. A survival analysis was performed using a parametric survival fit approach in order to generate survival curves and obtain information that could help optimize integrated management strategies for this weevil pest. Sex of the weevils, crop season, fortnight in which weevils emerged, and their interaction were studied regarding their effect on adult survival. The results showed that females lived longer than males, but both genders were actually long-lived, reaching 224 and 176 d, respectively. Mean lifetime (I_{50}) was 121.88 \pm 4.56 d for females and 89.58 \pm 2.72 d for males. Although variations were observed in adult longevities among emergence fortnights and soybean seasons, only in December and January fortnights of the 2007–2008 season and December fortnights of 2009–2010 did the statistically longest and shortest longevities occur, respectively. Survivorship data (Ix) of adult females and males were fitted to the Weibull frequency distribution model. The survival curve was type I for both sexes, which indicated that mortality corresponded mostly to old individuals.

Resumen

El picudo del tallo de la soja, *Sternechus subsignatus* Boheman 1836 (Coleoptera: Curculionidae), es una plaga sumamente seria en soja en la región Neotropical. Tanto los adultos como las larvas se alimentan de la soja, causando pérdidas significativas en el rendimiento. La supervivencia de los adultos fue evaluada durante tres campañas de soja bajo condiciones de laboratorio. Se realizó un análisis de supervivencia usando un ajuste paramétrico de supervivencia, a fin de generar curvas de supervivencia e información relevante para mejorar las estrategias de manejo integrado para este gorgojo plaga. Se evaluó el efecto del sexo, la campaña de soja, la quincena de emergencia y la interacción de estos sobre la supervivencia de los adultos. Los resultados mostraron que las hembras vivieron más que los machos y que la longevidad de ambos sexos era prolongada, alcanzando los 224 y 176 días respectivamente. El tiempo medio de vida (I_{50}) fue de 121.88 \pm 4.56 días para las hembras y 89.58 \pm 2.72 días para los machos. Aunque se observaron variaciones en las longevidades de los adultos entre quincenas y campañas de soja, solo las quincenas de diciembre y enero de la campaña 2007–2008 y las quincenas de diciembre de 2009–2010 se destacaron estadísticamente como la más larga y la más corta respectivamente. Los datos de supervivencia (Ix) de hembras y machos adultos fueron ajustados al modelo de distribución de frecuencias de Weibull. La curva de supervivencia fue de tipo I para ambos sexos, lo cual indica que la mortalidad mayormente afecta a los individuos viejos.

Key words: actuarial parameter, longevity, pest management, soybean weevil pest

The soybean stalk weevil, *Sternechus subsignatus* Boheman 1836 (Coleoptera: Curculionidae), is a very serious soybean (*Glycine max* L.) pest present in the Neotropical region (Costilla and Venditti

1990, Hoffmann-Campo et al. 1991, Sosa Gómez et al. 2008, Socías et al. 2011). *Sternechus subsignatus* is extremely harmful, as both larvae and adults damage soybean. Adults feed on stem tissues

fraying them, and if this occurs during early soybean vegetative stages, the damage is irreversible. Plants die and plant stands decrease, which leads to substantial yield losses (Hoffmann-Campo et al. 1991, Casmuz et al. 2009). Moreover, during late vegetative and reproductive stages, gravid females girdle the main stem, fraying the epidermis and cortex to deposit a single egg each, which is covered with fiber and tissue. After egg eclosion, the larvae develop and feed on the medulla inside the stem, and a gall forms on the girdled part (Hoffmann-Campo et al. 1991, Socías et al. 2011). Larval feeding results in sap circulation reduction or interruption in the main stem, which can hinder plant productivity (Hoffmann-Campo et al. 1990). After that, the larvae drop onto the ground and bury themselves to overwinter, later becoming pupae and adults at the end. A new cycle begins when adult weevils emerge from late spring to midsummer, as rainfall increases (Socías et al. 2011).

Life tables are a convenient starting point for understanding some demographic features, but they should only be viewed as tools for performing a more general exploratory survival analysis (Fox 2001). However, most studies on animal survival are based on standard life tables, which show the number of individuals that have survived different stages of their life cycle, along with reproductive output (Bellows and Van Driesche 1999). Survival analyses (i.e., failure time methods) have several important advantages over classical life tables. They allow data to be compared on different time scales, and they do not assume a normal distribution of the failure times of a group. Moreover, they permit standardization of information from survival curves, thus allowing comparison with other results obtained using similar methods (Fox 2001). Furthermore, survival curves can be used to compare survival among different populations or years (Schowalter 2006). Finally, this approach allows visualizing a survival range or survival area, rather than a unique survival point for each age (Núñez-Campero et al. 2012).

Previous studies on *S. subsignatus* (Hoffmann-Campo et al. 1991, Lorini et al. 1997, Silva 1999) showed that female and male adults can live up to 112 to 119 d and 62 to 109 d, respectively. Moreover, these authors observed that although females had a high fecundity, they were able to lay few (1.73) eggs daily (Hoffmann-Campo et al. 1999). Thus, their potential oviposition period could last several weeks, with a consequent overlap of successive development stages in the population (Socías et al. 2011). However, neither a survival analysis nor determinations of the survival curve type have been developed for *S. subsignatus*.

Tuljapurkar and Horvitz (2006) observed that the environment at the time of emergence or birth has effects on age-specific survivorship at all ages, including very advanced ages. Moreover, they observed that environmental conditions also have lasting effects on the remaining life expectancy of individuals. However, seasonal emergence time in other coleopteran species adults was studied by Naranjo and Sawyer (1987), and it was found to have no effects on beetle longevity. Currently, it is not known whether emergence time has an influence on *S. subsignatus* adult longevity.

Longevity and survival are two characteristic and important attributes that vary among insect species. The knowledge of how long an insect pest can live—its mean and maximum longevities—and how it survives is essential for developing effective integrated control programs (Lorini et al. 1997, Socías et al. 2011, Ramalho et al. 2015). Therefore, the aim of the present study was to determine the effects of sex, fortnight of emergence from the soil, and soybean season on adult soybean stalk weevil longevity. Moreover, this study assessed *S. subsignatus* adult survival and its corresponding curve type through survival analysis, using failure time approaches. This is the first attempt to evaluate if the fortnightly conditions or

emergences have effects on adult survival. All these information sources will be useful to define the best moment to control *S. sub-signatus* populations, and to develop a better integrated pest management program against the soybean stalk weevil.

Materials and Methods

Sampling and Laboratory Rearing of *S. subsignatus* Specimens

Plots located on two commercial soybean farms from Tucumán province (Argentina), which had been producing soybean for >5 yr, were chosen for this trial. These served as a reservoir of S. subsignatus larvae and pupae for our longevity assessments along three soybean seasons (2007-2008, 2008-2009, and 2009-2010). Overwintering forms were sampled from early autumn up to early spring on a fortnightly basis. For this purpose, 10 plots of soybean plantations of the previous season were randomly selected for sampling on each farm. Each plot was 1.00 by 0.30 by 0.20 m in length, width, and depth, respectively. Monitoring consisted in sieving the soil sample in situ, with a 20-mesh metallic sieve (Zonitest). All larvae and pupae collected were recorded and placed over sterilized soil, previously obtained from the same field, in plastic containers (850 cc). Then, larvae and pupae were transported to the Estación Experimental Agroindustrial Obispo Colombres (EEAOC) laboratories, where they were kept at $25 \pm 1^{\circ}$ C, with a $70 \pm 10\%$ relative humidity, and under a natural photoperiod.

The climate in Tucumán province is classified as subtropical subhumid-humid (Lamelas et al. 2010), which is characterized by a 25°C mean annual temperature, and dry winters followed by rainy summers. Cumulated annual rainfall reaches 1,100 mm and is distributed from late spring (November) to early autumn (March) (Minetti et al. 2005). We used this information to establish the laboratory conditions abovementioned. Each plastic container was covered with a dark cloth, as larvae and pupae exhibit negative phototropism (Hoffmann-Campo et al. 1991). The containers were moistened periodically until adult emergence to prevent the material from drying. As weevils emergence is strongly correlated with precipitation (i.e., emergence starts and increases as precipitation starts and increases; M.G.S, unpublished data), we used rainfall data from both farms to add the same volume (mm) of water to moisten the soil in the plastic containers. Meteorological data were obtained from automatic weather stations (Weather Monitor II by Davis) belonging to the Agrometeorology Department of the EEAOC.

Ten newly emerged S. subsignatus adults (<24 h) were placed inside cylindrical (12 by 12 cm) plastic cages. Each cage was labeled and covered with a thin cotton organdy cloth, so as to ensure ventilation and prevent insects from escaping. Water was provided by way of a piece of wetted cotton. As a food source, fresh soybean stems were supplied. Water was changed every 2 d, or when it was needed. Adult survival was checked every 48 h, and the cages were cleaned and the soybean stems renewed. Dead adults were removed, labeled, and preserved with 96% ethanol for determining sex, by means of observation of the tibial characteristics pointed out by Rosado-Neto (1987). Subsequently, individuals were dissected to remove genital armor and corroborate sex, by observing either the aedeagus (males) or the spermatheca (females) (Socías 2012). Seventy (i.e., seven replicates [26 $\stackrel{?}{\circ}$ and 44 $\stackrel{?}{\circ}$]), 100 (10 replicates [58 $\stackrel{?}{\circ}$ and 42 $\stackrel{?}{\circ}$]), and 120 adults (12 replicates [71 $\stackrel{?}{\circ}$ and 49 ♀]) belonging to the first, second, and third soybean seasons were obtained, respectively. In total, 290 adults (29 replicates) were used in this study.

Statistical Analysis

Cox Proportional Hazards Models

A Cox proportional hazard model (CPHM) is a semiparametric and well-recognized statistical technique for exploring the relationship between the survival of individuals and several explanatory variables. It allows us to estimate the hazard (or risk) of death or any other event of interest for individuals, given their prognostic variables. In addition, the quantitative impact of these variables on important lifetime variables of interest (such as median survival) can be described (SAS Institute 2008). Therefore, we use this model to test the effects of sex, soybean season, fortnight of emergence, and their interactions on *S. subsignatus* longevity. Then, longevity data corresponding to each significant variable (sex, fortnight, and soybean season, see Table 1) were analyzed with a generalized lineal model (GLMz) and subjected to the Sidak test for multiple comparison of means ($\alpha = 0.05$).

Survival Analysis

A univariate survival analysis was performed for each significant variable obtained from CPHM. This test was used to find significant differences among adult survival times across different groups or subgroups. Therefore, survival times for the two sexes and for each season were compared using the Wilcoxon-Gehan (D) test, which assigns a greater weight to earlier survival points (Gehan 1965, 1975) unlike CPHM. Subsequently, means were separated by the Sidak test ($\alpha = 0.05$). Finally, in order to select the density function and determine the type of survival curve, we fitted survival data to four different distributions (Weibull, exponential, log-logistic, and log-normal) (Fox 2001). The distribution value was chosen with the lowest corrected Akaike information criterion (AICc) value. The Bayesian information criterion (BIC) was used to back up the AICc criterion (Akaike 1974, Burnham and Anderson 2004). For the Weibull distribution, we used the alpha-beta parameterization corresponding to the mean and standard deviation of the normal distribution of the natural logarithm of the time variable (SAS Institute 2008). The shape parameter β if >1, = 1, or <1, respectively, corresponds to the Deevey (1947) type I, II, and III survivorship curves (Pinder et al. 1978). Mean lifetime probability (l_{50}) was estimated with the probability density function (PDF) (Lee and Wang 2003).

For all the statistical analysis, JMP Version 10.0 (SAS Institute 2008) and SPSS version 22.0 (IBM Statistics 22.0 Version, SPSS 2013) programs were used.

Results

CPHM analysis revealed that sex, soybean season, and the interaction of fortnight and soybean season factors had significant effects

Table 1. Proportional hazard model testing for the effects of sex, soybean season, fortnight, and their interactions on *Sternechus subsignatus* adult longevity

Factors	df	χ^2	p value
Sex	1	43.71	<0.001*
Soybean season	2	26.32	< 0.001*
Fortnight	4	1.29	0.263
Sex × Soybean season	2	0.47	0.495
$Sex \times Fortnight$	3	0.03	0.857
Soybean season × Fortnight	4	5.78	0.016*
Sex × Soybean season × Fortnight	3	3.62	0.057

^{*}p value < 0.05.

on *S. subsignatus* adult longevity (Table 1). Sex had a significantly influence on longevity, so much so that females (121.88 ± 4.56) lived significantly longer than males (89.58 ± 2.72). Similarly, soybean seasons showed significantly different impacts on adult longevities along the three seasons. Adults of the first soybean season were the longest-living ones (136.22 ± 6.93 d), followed by adults of the 2008-2009 (101.85 ± 3.34 d) and 2009-2010 (88.95 ± 3.72 d) seasons. Longevity of adults emerging in different fortnights was similar among soybean seasons and within the same season. However, only significant statistical differences between fortnights 2 (December) and 1 and 2 (January) in the 2007-2008 season, and fortnights 1 and 2 (December) in the 2009-2010 season were observed (Fig. 1).

The survival analysis showed that sex and soybean season had a significant effect on adult survivorship (sex [D=29.70; df=1, 289; P<0.01], soybean season [D=39.18; df=2, 289; P<0.01], and fortnight [D=3.71; df 4, 289; P=0.45]).

The life table actuarial parameters obtained from the survival analysis, both for *S. subsignatus* males and females, are shown in Table 2. Figures 2 and 3 show survivorship (*lx*) and daily life table expectancy (*ex*) curves, respectively, for both sexes and the standard deviation for each survival event.

The AICc and BIC values resulting from the comparison of the four kinds of survival models proposed in this study are presented in Table 3. The Weibull distribution had the best fit for male and female survival curves. The parameters obtained were $\alpha\!=\!100.72\pm2.91$ and $\beta\!=\!2.87\pm0.18$ (Cramer–von Mises W test of goodness of fit; W–S = 0.536, $P\!=\!0.25$) for males, and $\alpha\!=\!137.46\pm4.91$ and $\beta\!=\!2.53\pm0.18$ (Cramer–von Mises W test of goodness of fit; W–S = 0.246, $P\!=\!0.25$) for females. The β parameters (>1) values from Weibull distribution indicated that the survival curves for both sexes belonged to type I.

Table 4 shows that Weibull distribution had the best fit to the data of the first and second soybean season survival curves. The parameters obtained were $\alpha=152.79\pm7.11$ and $\beta=2.73\pm0.30$ (Cramer-von Mises W test of goodness of fit; W–S=0.789, P=0.25), and $\alpha=113.61\pm3.60$ and $\beta=3.22\pm0.24$ (Cramer-von Mises W test of goodness of fit; W–S=0.089, P=0.25), respectively. While the third soybean season survival curve best fitted a log-normal distribution, the P-values from Kolmogorov's D goodness of fit (D=0.124, P=0.010) for the empirical distribution function tests were <0.05, indicating that the data did not support a lognormal model. Therefore, we accepted the second best fit option, the Weibull distribution. The parameter estimates were $\alpha=100.68\pm4.16$ and $\beta=2.31\pm0.16$ (Cramer-von Mises W test of goodness of fit; W–S=0.123, P=0.25).

The mean lifetime probability (l_{50}) estimated from PDF was 88.63 d for males (95% confidence bounds: [83.20, 94.42]), and 119.90 d (95% confidence bounds: [109.92, 128.62]) for females. Overall, males had a significantly lower survival age than females (Table 5).

The l_{50} for the first, second, and third soybean seasons were 133.57 d (95% confidence bounds: [120.52, 148.02]), 101.38 d (95% confidence bounds: [94.61, 108.62]), and 79.42 d (95% confidence bounds: [72.83, 86.61]), respectively. Adults from the second soybean season had a significantly greater survival than those from the third soybean season (Table 5).

Discussion

This is the first study of *S. subsignatus* weevil survival parameters, and its results showed that there are longevity differences between the

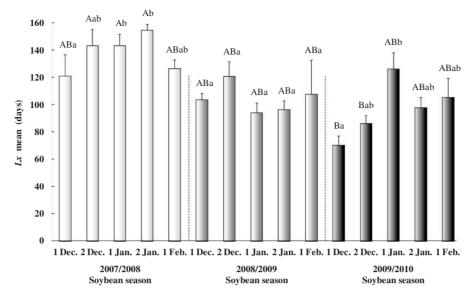


Fig. 1. Longevity of Sternechus subsignatus adults (mean ± SE [d]) considering the three soybean seasons under study. Lowercase letters indicate differences among fortnights of the same season, and capital letters indicate differences among fortnights of different seasons.

Table 2. Life table parameters of *Sternechus subsignatus* male and female adults

Age (d)	Males			Females						
	N	qx	рx	lx	ex	N	qx	px	lx	ex
0	236	0.09	0.91	1.0	66.67	201	0.07	0.93	1.00	88.05
8	215	0.1	0.9	0.91	69.0	186	0.11	0.89	0.93	89.16
16	193	0.08	0.92	0.82	68.47	166	0.14	0.86	0.83	95.57
24	178	0.09	0.91	0.75	64.0	143	0.05	0.95	0.71	97.05
32	162	0.07	0.93	0.69	59.76	136	0.06	0.94	0.68	92.17
40	150	0.09	0.91	0.64	54.59	128	0.08	0.92	0.64	87.74
48	136	0.04	0.96	0.58	50.46	118	0.02	0.98	0.59	85.41
56	130	0.06	0.94	0.55	44.31	116	0.04	0.96	0.58	78.56
64	122	0.1	0.9	0.52	38.77	111	0.00	1.0	0.55	73.67
72	110	0.04	0.96	0.47	34.0	111	0.01	0.99	0.55	66.0
80	106	0.16	0.84	0.45	27.0	110	0.08	0.92	0.54	58.67
88	89	0.19	0.81	0.38	23.25	101	0.07	0.93	0.5	58.0
96	72	0.18	0.82	0.31	21.6	94	0.04	0.96	0.47	61.33
104	59	0.27	0.73	0.25	19.11	90	0.08	0.92	0.45	57.0
112	43	0.23	0.77	0.18	17.43	83	0.12	0.88	0.41	52.5
120	33	0.27	0.73	0.14	12.29	73	0.12	0.88	0.36	49.71
128	24	0.58	0.42	0.1	6.86	64	0.11	0.89	0.32	46.86
136	10	0.1	0.9	0.04	22.0	57	0.11	0.89	0.28	41.82
144	9	0.11	0.89	0.04	15.00	51	0.04	0.96	0.25	36.0
152	8	0.5	0.5	0.03	8.00	49	0.06	0.94	0.24	28.73
160	4	0.75	0.25	0.02	5.33	46	0.17	0.83	0.23	21.82
168	1	0.5	0.5	0.00	0.00	38	0.18	0.82	0.19	18.0
176	1	0.5	0.5	0.00		31	0.35	0.65	0.15	16.4
184						20	0.2	0.8	0.1	12.8
192						16	0.63	0.38	0.08	6.4
200						6	0.33	0.67	0.03	12.0
208						4	0.5	0.5	0.02	8.0
216						2	0.25	0.75	0.01	8.0
224						2	0.75	0.25	0.01	

N—cohort; qx—mortality period (probability of dying in the interval x to x+1); px—survival period (probability of surviving from x to x+1); lx—survival fraction (proportion of individuals that survive from x to x+1); and ex—life expectancy.

sexes. Despite the great potential for damage due to a prolonged adult longevity in the field, there are few studies which address biological features of this pest and the ecological conditions that favor its development. The little literature there is available comes from Brazil, and nothing is revealed there in relation to its natural enemies.

Our results showed that sex had a significant effect on weevil longevity, with females living significantly longer than males. This longevity difference was also observed by Hoffmann-Campo et al. (1991), Lorini et al. (1997), and Silva (1999) in Brazil, though with some differences in survival days in each case. These authors found that longevity under laboratory conditions for females and males was 118.7 and 69.4 d, 119 and 109 d, and 112.5 and 62.9 d, respectively. Hoffmann-Campo et al. (1991) showed that the mean lifetime probability (l_{50}) was reached approximately when females were 120 d old and when males were 50 d old, which coincides with our results only in what concerns females: our male values were almost twice as those found by these authors.

Other authors have also reported great longevities in other weevil species. Gold et al. (2001) noted that Cosmopolites sordidus (Germar, 1824) adults lived up to an average of 5-8 mo, with some surviving >2 yr. Homalinotus coriaceus (Gyllenhal, 1836) has a longevity of 398 d for males, and 468 d for females (Sarro et al. 2004). Tatar and Carey (1994) propose a mechanistic explanation for differences in mortalities between males and females, which should be considered as absolute and relative mortality force patterns in each sex. These authors argue that in the case of Callosobruchus maculatus (F., 1775), a pest of stored legumes, age-dependent mortality processes are evident only after a particular age for each sex. This difference may be caused by an earlier depletion of juvenile-derived metabolites in males. Males are smaller than females when hatching, and may begin adult life with fewer energy reserves than females. Williams (1957) argued that a shorter longevity or a "more rapid senescence" in males is an indirect result of the extrinsic risk they run when mating. Because resources and energy in organisms are limited, sexual behavior patterns in animals are the result of selective pressures acting differentially on males and females, allocating these resources for growth, survival, and reproductive efforts (Martín-Vivaldi and Cabrero 2002).

In their metabolic theory, Brown et al. (2004) posed how metabolic rate varies with body size and temperature. This theory

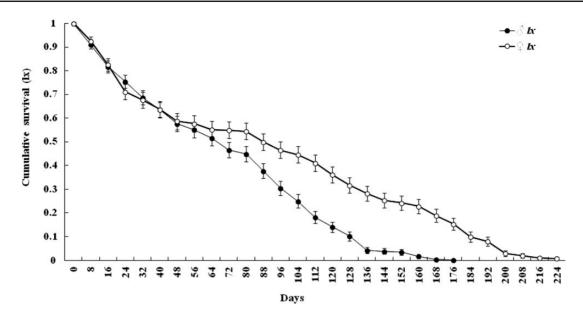


Fig. 2. Mean survivorship (Ix) curves for Sternechus subsignatus male and female individuals from three seasons (2007–2010). Bars through points represent ± SD.

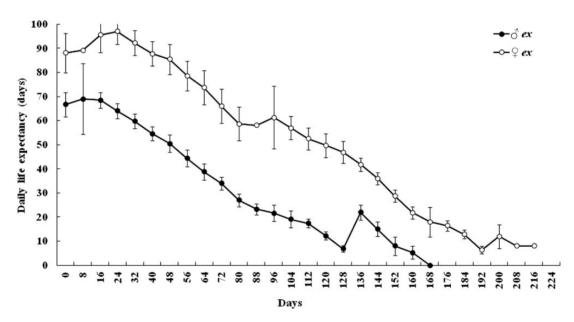


Fig. 3. Mean daily life table expectancy (ex) curves for Sternechus subsignatus male and female individuals from three seasons (2007–2010). Bars through points represent \pm SD.

Table 3. Comparison of survival models fitted to four kinds of distributions for male and female of *Sternechus subsignatus*, using the indexes of the corrected AICc and the BIC

Distribution	M	ale	Fen	Female	
	AICc	BIC	AICc	BIC	
Weibull	1604.8	1610.90	1454.14	1459.86	
Log-normal	1625.24	1631.34	1485.76	1491.48	
Log-logistic	1620.02	1626.12	1488.12	1493.85	
Exponential	1782.44	1785.51	1568.85	1571.73	

Table 4. Comparison of survival models fitted to four different distributions for three soybean seasons of *Sternechus subsignatus*, using AICc and BIC indexes

Distribution	Soybean	season 1	Soybean	Soybean season 2		Soybean season 3		
	AICc	ICc BIC		BIC	AICc	BIC		
Weibull Log-normal Log-logistic Exponential	1765.19 1764.14	1769.42 1768.37	1074.88	1084.22 1080.11	1254.14 1261.66	1259.67		

Table 5. Survival comparisons of *Sternechus subsignatus* male and female adults, both within and between soybean seasons

Season 1	♂ vs ♀		Season 2	♂ vs	♂ ♀vs		\$
	Wilcoxon	p		Wilcoxon	p	Wilcoxon	p
2007–2008	23.174	0.001	2008–2009	0.155	0.693	24.833	0.001
			2009-2010	1.188	0.276	26.641	0.001
2008-2009	0.445	0.505	2009-2010	14.584	0.001	0.162	0.688
2009-2010	7.430	0.006					

The left side of the table shows, at first instance, the differences between male and female adults for each soybean season. The right side of the table shows, secondarily, the differences between soybean seasons, i.e., season 1 versus season 2 (Wilcoxon–Gehan test, $\alpha = 0.05$).

predicts how metabolic rate controls ecological processes such as life history attributes, which include development rate, mortality rate, age at maturity, life span, population growth rate, etc. Almost all characteristics of organisms vary predictably with body size. These theories could explain the difference in longevity observed between *S. subsignatus* males and females, because adults show a marked sexual dimorphism in favor of females, which are usually larger (Rosado-Neto 1987).

Adult longevity was also affected by soybean season and the specific fortnight considered. Statistical differences among fortnights of the same season and fortnights of different seasons were observed but, in general, adult longevity remained the same. During the three soybean cycles under study, adult longevity for each sex was recorded, and in 2007-2008 and 2008-2009, we observed similar longevities for females and males. However, during the last soybean season, 2009-2010, the mean longevities of both females and males were shorter than in the previous two seasons, even though longevity ranges for both sexes were identical to the ones recorded in the previous two years. Such differences in adult longevity may be due to increased mortality in the early weeks of adult life, which affects mean longevity values for each sex. The causes for such deaths are still unknown, but we may draw the hypothesis that they have to do with a decline or variation in the nutritional quality of the host plant, as a food source. This may have affected larval development in the field during the 2008-2009 season, thus hindering subsequent adult survival in the 2009-2010 season. Juvenile insects grow noticeably, so the quantity and quality of food that they can secure for themselves have crucial implications for their adult life. Therefore, larval growth and larval stage duration are critically dependent on food quality (Speight et al. 2008). Progeny vigor in many insect species may also be affected by plant quality variations (Awmack and Leather 2002). In this sense, Silva (1998) and Socías et al. (2015) (unpublished data) pointed out that both S. subsignatus emergence onset and its peak are generally determined by rainfall and water "stress" suffered by the host plant. Thus, a dry year can affect future insect population, because it may be prevented from obtaining adequate food and accomplishing full development (Silva 1998). Larvae suffer nutritional stress under these adverse soil moisture circumstances, because they are feeding on plants that represent scarce and lower quality food sources. As a consequence, the population either does not complete larval stage or evolves into adults with a lower body mass, possibly on account of their lower rate of nutrient assimilation and their higher energy consumption (Silva 1999). Based on what Silva (1998, 1999) argues, we may infer that the significantly shorter adult longevities observed in some soybean seasons might be attributed to variability in host plant quality or quantity. For S. subsignatus, whose individuals emerge in the same season (summer)

over a period of 60–90 d (Socías et al. 2011), it is reasonable to expect that there should be no differences in the mean longevities of individuals that emerged in different fortnights. However, the observed differences between the first fortnights of the first and last soybean seasons are probably due to environmental changes that strongly affected these individuals. Over the course of the life of an individual, environmental changes accumulate to determine both the average and variance of life expectancy and survivorship (Tuljapurkar and Horvitz 2006).

Curve fitting is useful in demography studies, as it can be used basically for smoothing data, enabling forecasting, facilitating comparisons, increasing precision, and drawing inferences from censored data (Carey 1993). In the present study, the lowest AICc and BIC values were used to select the best fitted curve, and for S. subsignatus female and male adults, the survivorship data (lx) were best fitted by the Weibull frequency distribution model. Survivorship data can be effectively summarized using the shape and scale parameters of this frequency distribution. The shape parameter controls the rate of change of the age-specific mortality rate, as well as the general form of the survivorship curve (Pinder et al. 1978). According to Deevey (1947) and based on Weibull parameters, the survival curve was type I. This indicated that mortality mostly affected old individuals, i.e., specimens at the end of their maximum life span (Begon et al. 2006). Type I survivorship curves are most common in univoltine insect species, and this may be related to the scarcity of host plants in another season. In temperate latitudes, most species have seasonal and synchronous reproduction, and life cycles are commonly annual or univoltine. Price et al. (2011) argued that "such insects have life cycles synchronized with their food supply, which flushes in spring and ages through the season until leaf fall, with rapid changes in availability and suitability of food, imposing usually a single window in the annual cycle in which food is suitable for young larvae to become established." Among many life history stages of univoltine insects, the larval feeding period may be most strongly constrained by the environment, with respect to seasonality (Isawa 1991).

Mean life expectancy data are essential for determining the average lifetime of insects in the field, as well as for deciding on the appropriate time for pest control. The long life span and high survival rates of S. subsignatus adults recorded in this study, plus the high fecundity of females (Hoffmann-Campo et al. 1991, Lorini et al. 1997, Silva 1999), the relatively low or null impact of natural enemies (Lorini et al. 1990), and the high survival level of hibernating stages under the ground (Socías 2012) constitute a complex scenario where controlling this pest becomes difficult. Adults are the only developmental stage susceptible to control by a combination of cultural and chemical practices, in contrast to eggs and active larvae (which are endophytic), and hibernating larvae and pupae (which are buried under the ground) (Socías 2012). Therefore, all control and management strategies, such as rotation with grasses, trap crops, delayed sowing dates, seed treatments, and foliar applications should be directed to adults, as it is the stage that ensures the spacetime continuity of the species. The knowledge of adult survival rates, together with a deep understanding of S. subsignatus biological characteristics, will allow designing systems for insect control that maximize cultural practices aimed at reducing insect population densities in soybean crops.

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