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3 **Postembryonic development and population parameters of *Alpaida veniliae***

4 **(Araneae, Araneidae), reared in the laboratory.**

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17 Running head: BENAMU ET AL. DEVELOPMENT AND DEMOGRAPHY OF

18 *ALPAIDA VENILIAE*.

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21 **Abstract.** We studied postembryonic development from hatching to adult stage and determined
22 life history traits and population parameters of *Alpaida veniliae*. It is one of the most
23 abundant species of the orb weaving guild of the spider community of soybean crops in
24 Buenos Aires province, Argentina. The first three instars occurred inside the egg sac, and
25 nymph IV (spiderlings) started the dispersion from it. *Alpaida veniliae* female achieved greater
26 adult size and larger adult longevity than the male. Mean fecundity, mean number of egg sacs
27 per female, mean number of eggs per egg sac, as well as the net reproductive rate, the
28 intrinsic rate of increase (r), the generation time (T), and the reproductive values (V_x) of
29 three cohorts, were determined under laboratory conditions, indicating a relatively high
30 capacity for growth. Their biological and ecological attributes indicate the importance
31 of conservation this predator as a natural enemy of soybean crop pests.

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34 **Keywords:** spiders; generalist predators; soybean; life history traits; population growth rates.

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47 **Introduction**

48 Arthropod predators can be very effective in reducing the density of phytophagous
49 arthropods in agroecosystems as well as in unmanaged habitats (Nyffeler et al. 1994;
50 Wyss et al. 1995; Barbosa and Wratten 1998; Rypstra et al. 1999). Currently, there is a
51 growing interest in the potential of generalist predators as biological control agents of
52 pests (Riechert and Lockley 1984; Riechert and Bishop 1990; Symondson et al. 2002).

53 The reappraisal of conservation of natural enemies as biological control agents
54 has started to change the current dogma and creating new management perspectives for
55 pests (Nyrop et al. 1998). Accordingly, management practices to preserve predaceous
56 arthropods in agro-ecosystems seem to be a sound alternative to pesticides (Ehler 1998).

57 Spiders are relevant components of the natural assemblages of predatory
58 arthropods of most agroecosystems (Turnbull 1973; Young & Edwards 1990; Wise
59 1993; Sunderland *et al.*, 1997; Sunderland & Greenstone 1999). Field and laboratory
60 studies of spider predation rates indicate that the impact of the spider assemblages may
61 contribute significantly to decrease pest population abundance in many crops (Wise
62 1993; Sunderland & Greenstone 1999; Nyffeler 1999; Maloney et al. 2003; Danişman et
63 al. 2007). Normally, spider communities have high abundance, richness and diversity in
64 agroecosystems throughout the crop growing season, (Riechert and Lockley 1984;
65 Benamú and Aguilar 2001; Maloney et al. 2003; Beltramo et al. 2006). Another
66 important feature of their life history, pointed out by Harwood and Obrycki (2005), is
67 the advantage of spiders over specialist natural enemies due to their sit-and-wait
68 strategy that allow them attack pests once they arrive, by surviving on alternative preys.

69 In transgenic soybean crops of Buenos Aires province, Argentina, the spider
70 *Alpaida veniliae* (Keyserling 1865) (Araneae, Araneidae), is one of the most abundant
71 species of the orb weaving guild of the spider community. Saavedra et al. (2007)

72 reported the importance of *A. veniliae* predation on herbivore insect populations on rice
73 crops. However, to date, there is little information on the biology and the ecology of this
74 species. In view of *A. veniliae* might be a potential natural enemy of some soybean pests
75 that could be integrated in future pest management programs, basic studies of its
76 biology and ecology are needed.

77 The objectives of this work were to study the postembryonic development and
78 the population parameters of *Alpaida veniliae*, in laboratory.

79

80 **Material and methods**

81 A laboratory colony was reared, starting with 30 juvenile females, 10 adult gravid
82 females and 10 adult males of *A. veniliae*, collected from two transgenic soybean crops
83 located at Chivilcoy (35° 01' S, 60° 06' W) (Buenos Aires, Argentina). Spiderlings
84 emerging from the egg-sacs were followed to obtain a mass-rearing population. In the
85 laboratory, we individually reared juveniles and adult couples, to allow mating, in 500
86 ml glass jars. Juveniles and adults were provided with an *ad libitum* supply of
87 *Drosophila melanogaster* and *Musca domestica* adults. Laboratory conditions were $25 \pm$
88 2° C, $75 \pm 5\%$ RH, and a photoperiod of 16:8 (L: D) h. This colony provided the
89 necessary individuals to study the different life traits and the population parameters.

90

91 *Postembryonic development*

92 To determine postembryonic development, 16 egg masses were individually reared in 6
93 cm diameter plastic Petri[®] dishes. Dishes were disposed on trays of expanded
94 polystyrene with pieces of moistened cotton to prevent the eggs from drying, and
95 covered with plastic film to avoid contamination by fungi and mites. They were kept in
96 an environmental chamber at $25 \pm 0.5^\circ$ C, $75 \pm 5\%$ R.H. and 16:8 L: D, h. Different

97 postembryonic stages, from hatching to adult stage, were determined according to
98 Galiano (1991), which considers that development begins with the rupture of the
99 chorion (hatching), remaining the first instar inside it. The second instar appears after
100 detaching the embryonic cuticle, which is considered the first molt, and the subsequent
101 instars are numbered sequentially. At instar IV, individuals (spiderlings) abandon the
102 egg-sac and start a free life.

103 As it was impossible to separate individual eggs from the egg mass, we
104 determined the intrachorionic development by daily examination under binocular
105 microscope of 978 eggs from different egg masses, but not separated from them.
106 Spiderlings coming out the egg-sac, were individually kept in Petri dishes, and daily
107 checked until reaching the adult stage. We measured the length and width of
108 cephalothorax of 50 individuals of each instar, 50 adult males, and 50 adult females,
109 immediately after the molt. To measure instar I and II we previously submerged some
110 egg masses in liquid glycerin to transparent membranes, and randomly selected 50
111 individuals of each. Differences in development times and morphological measurements
112 among juveniles, and in adult longevity, total life span, and in cephalothorax size
113 between adult sexes were tested with ANOVA or Kruskal Wallis test. Means or
114 medians were separated by the least significant differences (LSD) multiple range test or
115 Box and Wisker plot method, respectively. A 0.05 significance level was chosen for all
116 statistical analysis.

117

118 *Life history traits*

119 To assess male and female longevity, we followed the surviving individuals, used to
120 study postembryonic development, until the end of their lives as adults. Additionally, 22
121 newly emerged male and female adults, randomly selected, were paired and placed in

122 500 ml plastic vials to determine the mean number of days from mating to the first
123 oviposition (pre-reproductive period), the mean fecundity (mean number of eggs per
124 female), the mean number of eggs per egg sac, and the mean percentage of egg
125 hatching.

126

127 *Population parameters*

128 Three cohorts (i.e. a group of individuals born within the same short interval of time)
129 selected from the laboratory colony were used to construct three age specific life tables
130 and estimate the population parameters. Spiderlings of each cohort were placed
131 individually in 6cm diameter Petri[®] dishes with a piece of moistened cotton on the
132 bottom, and fed *ad libitum Drosophila melanogaster* up to the IV instar, and then fed
133 *Musca domestica* to the adults. From a group of 100 eggs we measured the percentage
134 of hatching and corrected the initial number of spiderlings of each cohort to perform the
135 calculations of the population parameters starting from the eggs.

136 Thus, the initial number of eggs of each cohort was of 897, 429 and 483 eggs,
137 respectively. Once a week we checked survival of each cohort until death of all
138 individuals. Spiders were sexed in the fifth nymph. Cohort survival (proportion of the
139 initial female cohort alive at age x) and fecundity (mean number of female offspring
140 produced per female of age x) were estimated. From fifth instar to adult stage we
141 calculated the mean sex ratio [(male / (male + female))] and used this value to correct
142 age-stage specific survival values from birth, assuming that the sex ratio was similar
143 from birth to fifth. Three of the surviving females of each cohort, chosen at random,
144 were paired with males coming from the colony, and housed individually in 500 ml
145 plastic vials to estimate age specific fecundity. We constructed age-specific survival (l_x)

146 and fecundity (m_x) curves at weekly intervals, and calculated the following
147 demographic parameters:

148 Net reproductive rate (R_o), that is the mean number of female offspring produced
149 per female per generation

$$150 \quad R_o = \sum_{x=0}^n l_x m_x \quad [1]$$

151

152 Intrinsic rate of increase (r), that is the mean number of female offspring
153 produced per female per time unit.

$$154 \quad r \approx \frac{\ln R_o}{T} \quad [2]$$

155

156 Generation time (T) that is the mean age of the parents of all the offspring
157 produced by a single cohort.

$$158 \quad T = \frac{\sum_{x=0}^n x l_x m_x}{R_o} \quad [3]$$

159

160 Reproductive values (V_x), that is the contribution to the future population that
161 one female of age x will make. It is measured relative to that of the first age, which is
162 considered equal to 1.

$$163 \quad V_x = \frac{e^{rx}}{l_x} \sum_{y=x+1}^n e^{-ry} l_y m_y \quad [4]$$

164

165 Where x is the age class and n the oldest age class.

166

167 **Results**

168 *Postembryonic development*

169 The egg sac of *A. veniliae* is yellow and shaped like a dome. It has three layers of fibers
170 surrounding the mass of eggs, which is pink, darkening as it develops and it measures
171 3.82 ± 1.1 mm (mean \pm SD; $n=16$) in length, and 3.23 ± 0.7 mm (mean \pm SD; $n= 16$) in
172 width. Hatching occurred in two steps within the egg sac. During the first, the individual
173 broke the chorionic membrane. This is considered the instar I, which is intrachorionic,
174 still wrapped in the embryonic cuticle, the body bent at right angle with the legs folded
175 under the cephalothorax and no visible segmentation of the legs. The rupture of
176 chorionic membrane took place 6.33 ± 0.5 days after oviposition (Table 1). During the
177 second step, at approximately 24 h from breaking the chorionic membrane, the
178 embryonic cuticle is detached, dragging the egg membranes, resulting in the freeing of
179 the legs from the cephalothorax and the emergence of instar II. The instar III had the
180 cephalothorax and legs free and extended parallel to each side of the body, with little
181 sketches of segmentation at the level of the trochanter-femoral joint. They had no hair
182 nor pigmentation, only a slight red pigmentation in their eyes, and fed on the chorion,
183 which dries and become increasingly crumpled inside the ootheca. Instar IV
184 (spiderlings) had hair, tarsal nails and eyes, and started the dispersion from the egg sac.
185 At this point, spiderlings were also able to spin a simple type of silk for capture prey.
186 Cannibalism was not observed inside the egg sac. It was possible to discriminate sex in
187 instar V, because it was easy to see the palp of the male. Females had nine instars, while
188 males had only eight.

189 Developmental time of juveniles and adults and cephalothorax size of *A. veniliae*
190 is shown in Table 1 and 2, respectively. Earlier instars, particularly from the first to the
191 third, had shorter developmental time than later ones (Kruskal-Wallis, $H = 5212.62$; P
192 $=0.001$, $n= 3164$). Adult male longevity was much shorter than that of female, as well as
193 the total male life span.

194 Cephalothorax length was similar until instar VI, and then successively
195 increased to adult ($H= 475.90$; $P = 0.001$). Cephalothorax width differed between instar
196 II to III and remained similar until instar VII when it increased with age ($H= 466.84$; P
197 $= 0.001$). Adult females had a longer and wider cephalothorax than adult males (length:
198 $H = 24.75$; $P = 0.001$; width: $H= 78.24$; $P= 0.001$).

199

200 *Life history traits*

201 Females had a longer total life span than males, living approximately 62 days longer
202 ($F= 105$; $df =1, 78$; $P< 0.001$). Adult female longevity was approximately 42 d longer
203 than that of the male ($H= 57.43$; $P= 0.001$) (Table 1). After 6.7 ± 2.6 (mean \pm SD) d
204 from copulation, females laid the first egg sac. Mean (\pm SD) female fecundity was
205 740.91 ± 329.16 eggs. The mean (\pm SD) number of egg sacs deposited by a female was
206 4.59 ± 2.04 , and the mean (\pm SD) number of eggs per egg sac was 161.39 ± 32.17 . The
207 percentage of egg hatching was 95.02%.

208

209 *Population parameters*

210 The age-specific survival curves showed some variations at initial ages between cohorts
211 (Fig. 1). In cohort 1 survival sharply decreased during the first four weeks of life,
212 indicating a high mortality at the first instars. Survival in cohorts 2 and 3 remained very
213 high during the first six weeks, after which it suffered a pronounced reduction. From

214 this moment on, patterns of survival were rather similar, declining gradually to reach
215 zero between the 28th and 29th week of cohort life span. Cohort survival had values
216 ranging from 10 to 15 % when females started oviposition. Fecundity curves exhibited
217 two or three peaks, reaching the maximum fecundity from week 21 to week 23.

218 Population parameters were similar between cohorts and indicated a relatively
219 high capacity for growth (Table 3). Generation time ranged approximately from 19 to
220 24 weeks, and the maximum reproductive values (Fig. 2) were at the ages of 20, 23 and
221 24 weeks of the female life span, in cohort one, two, and three, respectively. The sex
222 ratio differed between cohorts and was biased towards females in the three cohorts.

223

224 **Discussion**

225 The aforementioned research has increased the knowledge of some basic biological and
226 ecological attributes of *A. veniliae*, an abundant species of the orb weaving guild of the
227 spider community in soybean agroecosystem.

228 The major web types (e.g., scattered, sheet, and orbs) are reported to be
229 specifically adapted to particular habitat structures and to the capture of specific prey,
230 being the orb-web capable of capturing a wider range of taxa than other web types
231 (Turnbull, 1973).

232 Web-building spiders are, directly or indirectly, important mortality factors of
233 pests. According to Greenstone (1999), pests are an important part of the diet of web-
234 building spiders. Moreover, Harwood et al. (2001, 2003) have reported that cereal
235 spiders have a non-random web location strategy, which is directly related to prey
236 density. This strategy allows the spiders to increase the frequency with which the insects
237 fall into his web when prey density is high, although not feed directly on them.

238 Saavedra et al. (2007) studied the predation rate of *A. veniliae* in rice crops,
239 concluding that the predatory behaviour of this spider could have strong implications
240 on the regulation of two phytophagous species inhabiting this crop. Moreover the high
241 prey capture capacity, *A. veniliae* exhibits many attributes that are considered desirable
242 for natural enemies and make them relevant predators of pests **MARCO QUIEN DICE**
243 **ESTO!!!**. Among them, temporal synchronization with preys, high fecundity, high
244 population growth potential, predation at juvenile and adult stages, and the orbicular
245 web **(Bellows and Fisher, 1999)**.

246 Flórez et al. (2002) also reported one more nymphal instar in the female than in
247 the male of the related species *A. variabilis*, under both greenhouse and field conditions,
248 but a smaller female and male longevity than that of *A. veniliae* determined in this
249 study. However, the greater longevity of *A. veniliae* females compared to males
250 registered in the present study is coincident with findings of other authors in
251 phylogenetically unrelated species (Gardner 1965; Bailey 1968; Jackson 1978; Mansour
252 et al. 1980).

253 Fecundity curves indicated that *A. veniliae* is iteroparous, which means that the
254 female reproduces repeatedly during its lifetime. The mean female fecundity coincided
255 with that found for other spiders (Foelix 1996), but it was considerably higher than that
256 of other *Alpaida* species, such as *A. variabilis* (76.5 ± 34 eggs per female) (Flórez et al.
257 2002). However, fecundity comparisons are difficult to make because there are not data
258 on female size or biomass, only cephalothorax width, and female size, among other
259 factors, is very related to fecundity.

260 The mean number of days from mating to the first oviposition of *A. veniliae* was
261 much shorter than that of other species of the same genus, e.g. *A. variabilis* (15.25 ± 2.6

262 d) (Flórez et al. 2002). A short prereproductive period is an important trait for a natural
263 enemy of pests, because it contributes to population growth.

264 Since the three studied cohorts came from the same colony and were reared
265 under identical conditions of food, temperature, humidity and photoperiod, we assumed
266 that variations among survival curves registered at initial ages, revealed the natural
267 inter- population variations.

268 Seeing as males may copulate several times with different females through their
269 lives, the highest proportion of females found in the studied cohorts (sex ratio biased
270 towards females) would indicate another positive feature that would promote population
271 increase. But, whether this potential would be expressed in field conditions is difficult
272 to predict and deserves more research.

273 Unfortunately, there is very little information about population parameters from
274 others spiders to compare with this study. Boulton & Polis (1999) have calculated some
275 life history parameters of *Diguetia mojavea* (Diguetidae) under field conditions in
276 southern California. However, results are not easy to compare since that family is not
277 closely related to Araneidae, and conditions like food, temperature and photoperiod that
278 greatly affect development and growth rate were different.

279 In addition to the high abundance of *A. veniliae* in the soybean spider
280 community, their biological and ecological attributes indicate the importance of
281 conservation this predator as a natural enemy of soybean crop pests. However, more
282 research to elucidate the significance of their predator role in pest suppression of
283 soybean crops is needed.

284

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286

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292

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