ECOLOGY, BEHAVIOR AND BIONOMICS

Demographic Study of Two Population Outbreaks of *Elasmoderus wagenknechti* (Liebermann) (Orthoptera: Tristiridae) in the Transitional Desert of Chile

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Estudo Demográfico de Dois Surtos Populacionais de *Elasmoderus wagenknechti* (Liebermann) (Orthoptera: Tristiridae) no Deserto Transicional do Chile

RESUMO - Sob certas condições ambientais, diversas espécies de gafanhotos que habitam áreas de campos, como as áreas entre vales do deserto transicional do Chile, podem experimentar surtos populacionais. Uma dessas espécies é *Elasmoderus wagenknechti* (Liebermann), espécie endêmica. Nós estudamos dois surtos que ocorreram em 1996 e 1999. Os objetivos da pesquisa foram (1) estimar alguns parâmetros demográficos associados aos eventos acima indicados, e (2) comparar os parâmetros entre os eventos. Os parâmetros estudados foram densidade (indivíduos/m^2), razão sexual, fertilidade da fêmea (i.e., ovos/fêmea), e a relação entre a fertilidade e o tamanho corporal da fêmea. O intervalo da densidade do evento foi estimado entre 0,2 e 0,4 indivíduos/m^2 em 1996, e entre 0,5 e 0,6 indivíduos /m^2 em 1999. Foram encontradas diferenças (análise de variância) na densidade entre os locais para o mesmo evento, e entre os eventos. As fêmeas foram mais numerosas que os machos em alguns locais estudados (e.g., Lomas del Sauce). Foi estimado um intervalo médio de 27-39 ovos/fêmea, existindo diferenças entre os locais no evento de 1996, mas não no evento de 1999. Para fêmeas de longitude corporal de 30-35 mm. foi detectada uma relação linear entre número de ovos/fêmea e tamanho corporal. Em conclusão, a magnitude do evento na área de estudo é específica do local; além do que para os parâmetros demográficos examinados existe uma acentuada variabilidade entre locais e entre os eventos.

PALAVRAS-CHAVE: Inseto de campo, biologia populacional, zona semi-árida, inseto endêmico, ecologia de pastagens

ABSTRACT - Under certain environmental conditions, several species of grasshoppers inhabiting rangeland areas (e.g., inter-valleys) of the Chilean transitional desert can irrupt demographically. One of them is *Elasmoderus wagenknechti* (Liebermann), an endemic species. We studied two outbreaks occurred in 1996 and 1999. The objectives of the research were to (i) estimate some demographic parameters associated with the aforementioned events, and (ii) compare between them the population parameters. The parameters we studied were density (ind/m^2), sexual proportion, female fertility (i.e., eggs/female), and the relationship eggs/female versus female size. Density (ind/m^2) ranged from 0.2 to 0.4 in 1996 and from 0.5 to 0.6 in 1999. ANOVA-tests registered differences in density among study sites and between years. In some of the study sites, females were more abundant than males (e.g., Lomas del Sauce). Females fertility ranged from 27 to 39 eggs per female, with significant differences among sites in 1996 but not in 1999. For females of 30-50 mm body size, a linear relationship was detected between egg number/female and body size. It is concluded that the *E. wagenknechti* outbreaks are site-specific in the study area and that the demographic parameters examined show a high variability among sites and between events.

KEY WORDS: Rangeland insect, population biology, semi-arid zone, endemic insect, grassland ecology

Population outbreaks of animal species living in rangeland ecosystems of the Chilean transitional desert have been observed to occur in oligochaetes, gastropods, mites, insects, and rodents. However, available formal knowledge is quite asymmetrical. Rodent population outbreaks are well studied and literature is abundant (Jiménez *et al.* 1992, Meserve *et*

al. 1995, Gutiérrez *et al*. 2000), whereas, it is limited about insects (e.g., Fuentes & Campusano 1985, Cepeda-Pizarro *et al*. 2003) and mites (Cepeda-Pizarro unpublished data); very poor concerning oligochaetes (Santelices *et al*. 1973), and anecdotal with gastropods (J. Cepeda-Pizarro, pers. obs.). Knowledge about grasshopper outbreaks is rather modest and circumstantial (Moroni 1972, Toro 1972).

In the recent years, a possible relationship between the local ecosystem dynamics and the El Niño-Southern Oscillation event (ENSO) has called the attention of several researchers (Dillon & Rundel 1990, Meserve *et al*. 1995, Jaksic 1998, Gutiérrez *et al*. 2000). Regarding fauna, this interest has been mainly focused on small mammals (Meserve *et al*. 1995, Lima *et al*. 1999a, b) and much less on other taxa. Despite their abundance, insect outbreaks are not well studied and understanding about characteristics of the phenomenon is limited (Fuentes & Campusano 1985, Cepeda-Pizarro *et al*. 2005a, 2005b).

The locally named "langosta de Combarbalá", *Elasmoderus wagenknechti* (Liebermann), is an endemic and common rangeland species of north-central Chile (Cigliano 1989), capable of population out-breaking. Its range extends from Tal-Tal (25º22'S; 70º31'W) in the Atacama Desert to Salamanca (31º46'S; 70º58'W) in semi-arid Chile (Cigliano 1989, Elgueta *et al*. 1999). Although *E. wagenknechti´*s outbreaks have been reported by locals since 1940, studies are rather preliminaries (Moroni 1972, Toro 1972). *E. wagenknechti* irrupted in north-central Chile in 1996 and 1999. We took advantage of the events to examine in some detail a set of characteristics of the phenomena. In a former work (Cepeda-Pizarro *et al*. 2003), we analysed morphometric characteristics and sexual dimorphism of individuals. In the present work we look at some demographic characteristics of the outbreak. In doing this study we asked the following questions: i) Which are the population density and female proportion? ii) Which are the female fertility characteristics, particularly egg number/female and the relationship egg number to female size? and finally iii) Were there demographic differences between events and among sites where the outbreak took place? We advanced the existence of an event-and-site effect on the demographic characteristics of the outbreak. The aims of the research were to i) estimate some demographic parameters associated with the irruptive events of 1996 and 1999, and ii) compare some demographic characteristics of them.

Material and Methods

Study area. The examined *E. wagenknechti* outbreaks occurred in the Combarbalá countryside (Limarí Province, IV Region of Coquimbo, Chile, 31º10'S; 71º00'W). The presence of gentle slopes in flat or nearly flat sectors, mixed with low hillocks interrupted by small ravines and narrow valleys, gives to the general landscape of the area a rugged appearance (Gastó & Contreras 1979). Soil type is aridisol (Orthids; Camborthids) in most of the sites, coarse textured and poorly developed (Luzio & Alcayaga 1992). The area has a Mediterranean subtropical semiarid climate, with warm and dry summers and wet-temperate winters (Novoa & Villaseca 1989). Mean annual rainfall is ~210 mm, highly variable among years (yearly range: 22.8-608.2 mm). Wet years have been associated to ENSO (Dillon & Rundel 1990, Gutiérrez *et al*. 2000). According to Gajardo (1993), plant formation corresponds to an inland scattered chaparral. Vegetation is not directly influenced by sea and is present both in the flat grounds and in the mountain range. *Adesmia microphylla* Hook. et Arn., *Atriplex semibaccata* R. Br., *Lithraea caustica* (Molina) Hook. et Arn., *Colliguaja odorifera* Molina, *Gutierrezia resinosa* (Hook. et Arn.) S.F. Blake, and *Flourensia thurifera* (Molina) D.C. are the most typical plant species found in the area. "Aguas lluvias" (i.e., hillsides used to grow rainfed crops such as wheat or barley, frequently abandoned as a barren piece of land after cultivation) are quite common. Desertification is severe and, for this reason, the original vegetation is highly altered, remaining only degraded and scattered patches of it (Gastó & Contreras 1979, Squeo *et al*. 2002). The outbreak sites were Agua Amarilla (31°06´S; 71°26´W, 725 msl), El Huacho (31°02´S; 71°11´W, 775 msl), La Ciénaga (31°02´S; 71°06´W, 800 msl), Quebrada Grande (31°09´S; 71°16´W, 700 msl), and Lomas del Sauce (31°03´S; 71°03´W, 700 msl) (Fig. 1). These sites are protected from direct sea influence by a chain of low-altitude hills.

Demographic analysis. The fieldwork was made on springtime of 1996 and 1999, before insecticide application by the Chilean governmental agency "Servicio Agrícola y Ganadero" (SAG). The sites evaluated in 1996 were Lomas del Sauce, Quebrada Grande and La Ciénaga; in 1999, they were Agua Amarilla, El Huacho and Lomas del Sauce. The following population parameters were estimated: i) density (ind/m^2) and dry biomass (mg/m^2); ii) female proportion; and iii) females fertility. Density measures were conducted in September (1996) and October (1999), in sectors occupied by scattered chaparral. Sampling was carried out during two days, between 10:00 am and 5:30 pm. The estimate of the mean density of grasshoppers (ind/m^2) was obtained by counting the individuals found in 30 rectangular strips of 10 x 1.2 m (12 m^2) per site. The strip was achieved by walking 15 normal steps on a straight line (equal to 10 m in length) and simultaneously seeing a perpendicular line 1.2 m long. Although grasshoppers are easily recognized in the field because of their toad-shaped form and jumping habit, special care was taken on recognizing and counting the male over the female's dorsum, a common characteristic of the species (Toro 1972). Dry biomass was estimated according to Cepeda-Pizarro *et al.* (2003).

Female proportion was estimated from randomly formed groups of specimens. These groups were formed by capturing the insects by hand (one team of collectors) or using an entomological net (two teams of collectors), as they were found in a given amount of time (e.g., 10 or 15 min). Captures were made between 10:00 am and 3:00 pm, during two days. The collected specimens were dead by ethyl acetate gases and kept as a group until time of processing. Although sex recognition and counting was facilitated by the strong sexual dimorphism shown by the species (*sensu* Cepeda-Pizarro *et al.* 2003), confirmation of sex was assured by examination of external genitalia. A group of females (n = 304) was separately captured for fertility analysis as well. These females were killed with ethyl acetate gases and kept in glycerinated alcohol (70%)

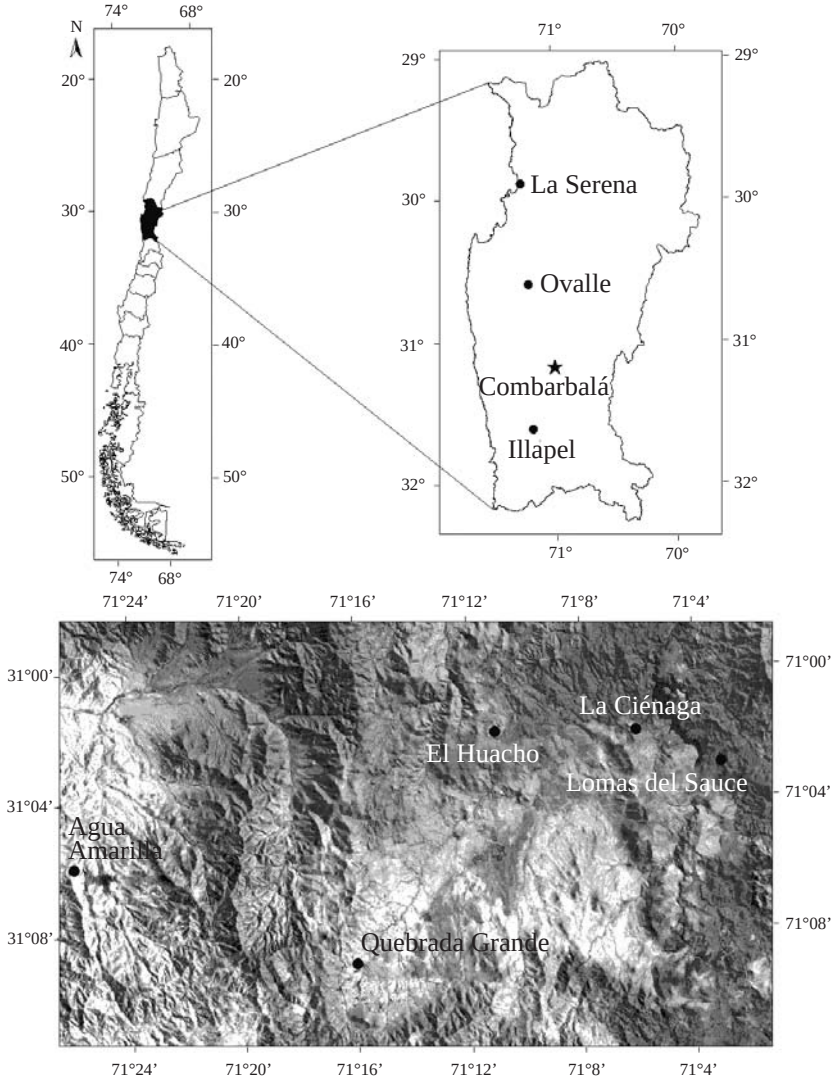

Fig. 1. Geographic location of five study sites (Agua Amarilla: 31°06´S; 71°26´W; El Huacho: 31°02´S; 71°11´W; La Ciénaga: 31°02´S; 71°06´W; Quebrada Grande: 31°09´S; 71°16´W; Lomas del Sauce: 31°03´S; 71°03´W), in the area of Combarbalá in north-central Chile.

until dissection to count and measure the eggs. The mean egg number/female and the relationship egg number/female to female size were estimated. Female size was measured as body length, using a Digitimatic caliper (Mitutoyo-500 1 ± 0.02 mm), following Cepeda-Pizarro *et al*. (2003).

Statistical analysis. Differences in density among sites and between events were statistically assessed by analysis of variance (ANOVA-tests); in case of F-significant, LSD-tests were used (Montgomery 1984). ANOVA and LSD-tests were also utilized to compare the differences among sites and between events in the female fertility analysis. The observed differences in female proportion were evaluated with the test of proportions, using 0.5 as null hypothesis (Domènech-Massons 1977); in turn, the relationship between egg number/female and female size was checked with linear regression analysis (Draper & Smith 1966). Calculations and estimates of the parameters were made with the Statistix program (Anonymous 1996). To apply the ANOVAs, the original values were square root or arc sine-transformed to fit the test assumptions (Montgomery 1984).

Results

Density. ANOVA-tests showed differences in density between events ($F_{1, 178} = 19.50$, $P < 0.0001$, Table 1). Differences were detected among sites for the 1996 event ($F_{2,87} = 3.72$; $P < 0.027$), but not for the 1999 event ($F_{2,87} = 0.19$; $P < 0.824$) (Table 1). Between events, the mean density was higher in 1999 (0.5 ind/m^2; 280.6 mg/m^2 of dry biomass) than in 1996 (0.3 ind/m^2; 130.89 mg/m^2) (Table 2). In 1996, mean density ranged between 0.2 and 0.4 ind/m^2 (1700 to 3700 ind/ha; 88.80 to 191.85 mg/m^2 of dry biomass), being the mean

Table 1. ANOVA-values for site and year effect of the event over density of *E. wagenknechti* (Orthoptera: Tristiridae) in two population outbreaks recorded in rangeland sites of north-central Chile. Density is provided as nº ind/m^2.

Event	Source of variation	df	MS	F	P (F)
1996	Among sites	2	0.33	3.72	< 0.0270
	Error	87	0.09		
1999	Among sites	2	0.06	0.19	< 0.8240
	Error	87	0.30		
1996/99	Between event	1	3.80	19.50	< 0.0001
	Error	178	0.19		

Table 2. *E. wagenknechti* mean density in two population outbreaks recorded on rangeland sites of north-central Chile.

Event	Site	ind/m^2 ± se	ind/ha	mg/m^2 ± se[1]
1996	Lomas del Sauce	0.4 ± 0.07 a, a	3700	191.85 ± 35.8 a
	La Ciénaga	0.2 ± 0.03 b	2200	111.68 ± 15.4 b
	Quebrada Grande	0.2 ± 0.06 b	1700	88.80 ± 28.9 b
	Mean event	0.3 ± 0.05 a	2500	130.89 ± 26.7 a
1999	Lomas del Sauce	0.6 ± 0.10 a, a	5600	289.21 ± 52.5 a
	Agua Amarilla	0.6 ± 0.10 a	5800	297.80 ± 52.0 a
	El Huacho	0.5 ± 0.10 a	4900	254.85 ± 50.3 a
	Mean event	0.5 ± 0.10 b	5400	280.6 ± 51.6 b

[1]Given the strong difference of body size between sexes, the biomass is expressed as the averaged dry weight between male and female dry weight (137.7 and 423.6 mg respectively). Values followed by the same letter are not statistically significant (LSD-test, P < 0.05). n = 30 quadrants of 10 x 1.2 m per site.

density of Lomas del Sauce (0.37 ind/m^2) significantly higher than that of the remaining sites (Table 2). In the 1999 event, mean density of grasshoppers ranged between 0.5 and 0.6 ind/m^2 (4900 to 5600 ind/ha; 254.85 to 297.80 mg/m^2 of dry biomass); with no significant differences among sites (Table 2). The mean density in Lomas del Sauce, a site measured in both years, was higher in 1999; nevertheless, this difference proved to be non-significant (Table 2).

Female proportion and fertility. Female proportion ($P_{♀}$) varied between years ($F_{1,31}$ = 24.78; P < 0.001; Table 3). Differences were detected among sites in 1996 ($F_{2,12}$ = 10.59; P < 0.002; Table 3), but not in 1999 ($F_{2,15}$ = 0.03; P < 0.973; Table 4). The mean values of $P_{♀}$ were 0.80 (1996) and 0.51 (1999). The high value obtained in 1996 is due to the contribution of the Lomas del Sauce site ($P_{♀}$ = 0.96; Table 4). Whereas the mean $P_{♀}$-1996 deviated significantly from the expected value 0.5 (z = 7.71, P < 0.001), the mean $P_{♀}$-1999 did not (z = 0.003, P < 0.89). Among the six intra-year comparisons that were carried out (Table 4), a significant

Table 3. ANOVA-values for site and year effect of the outbreak event in the female proportion ($P_{♀}$) in subpopulations of *E. wagenknechti*[1].

Year	Source of variation	df	MS	F	P (F)
1996	Among sites	2	1326.50	10.59	< 0.002
	Error	12	125.20		
1999	Among sites	2	1.14	0.03	< 0.973
	Error	15	41.94		
1996/99	Between years	1	3826.48	24.78	< 0.001
	Error	31	154.41		

[1]arc sine transformation.

Table 4. Female proportion ($P_{♀}$) in subpopulations of *E. wagenknechti* in two population outbreaks[1] recorded in north-central Chile in 1996 and 1999.

Event	Site	n	R	$P_{♀}$ ± se
1996	Lomas del Sauce	7	15-29	0.96 ± 0.02 b
	Quebrada Grande	4	13-21	0.68 ± 0.04 a
	La Ciénaga	4	11-19	0.64 ± 0.10 a
	Event	15	11-29	0.80 ± 0.05 a
1999	Lomas del Sauce	6	25-25	0.52 ± 0.03 a
	El Huacho	6	25-25	0.51 ± 0.03 a
	La Ciénaga	6	25-25	0.51 ± 0.06 a
	Event	18	25-25	0.51 ± 0.02
	Total	33	11-29	0.64 ± 0.04

[1]nº of groups (replicates) used to estimated female proportion; R: range for number of individuals/replicate; $P_{♀}$ ± se: female proportion calculated as mean ± standard error. Values followed by the same small letter are not statistically significant (ANOVA Table 3, LSD).

deviation from the expected 0.5 was only detected in the Lomas del Sauce population ($P_{♀} = 0.96$; $z = 8.78$, $P < 0.001$). A deviation nearly to the critical value of the test ($z = 1.86$ calculated versus 1.96 tabulated) was achieved by $P_{♀}$ (0.68) of the Quebrada Grande population in1996. Neither the estimated values of $P_{♀}$ associated to the remaining sites nor the general area average (e.g., 0.64) showed significant deviation of 0.5 (Table 4).

Regarding the mean egg number/female, the ANOVA-tests showed differences among sites in each one of the studied years, but not between years ($F_{1,303} = 3.35$; $P < 0.068$) (Table 5). The mean number of eggs per female was estimated between 27 and 42 in females of 1996, and between 28 and 39 in females of 1999 (Table 6). The most ovigerous female populations corresponded to Quebrada Grande (1996) and El Huacho (1999) (Table 6). For females with the body size of 30-50 mm, a significant linear relationship was estimated between the egg number/female and female size ($F_{1.32} = 13.2$;

Table 5. ANOVA-values for the site and year effect of the outbreak event over egg number/female of *E. wagenknechti*.

Event	Source of variation	df	MS	F	P (F)
1996	Among sites	2	1371.24	10.92	< 0.0001
	Error	152	125.54		
1999	Among sites	2	1547.42	12.84	< 0.0001
	Error	147	120.50		
1996/1999	Between years	1	472.01	3.35	< 0.0680
	Error	303	140.70		

Table 6. Nº of egg/female of *E. wagenknechti* among sites and between years of the outbreak event.

Event	Site	n	Media ± se	Range	CV
1996	Lomas del Sauce	98	37.0 ± 1.00 a	0.00-54.00	26.86
	Quebrada Grande	36	42.1 ± 2.12 b	5.00-82.00	30.13
	La Ciénaga	21	27.8 ± 3.03 c	0.00-54.00	50.50
	Event	155	37.0 ± 0.96	0.00-87.00	32.22
1999	Agua Amarilla	50	28.2 ± 1.91 a	0.00-51.00	47.92
	El Huacho	50	39.0 ± 1.23 b	21.00-52.00	22.41
	La Ciénaga	50	36.2 ± 1.43 b	0.00-56.00	27.94
	Event	150	34.5 ± 0.96	0.00-56.00	34.29

$P < 0.001$) (Fig. 2). Mature eggs are oval in shape; with mean lengths of 4.46 ± 0.09 mm for the major axis and 1.11 ± 0.03 mm for the minor axis; with a mean volume of 3.68 ± 0.17 mm. The egg has an aerolate chorion with rounded poles.

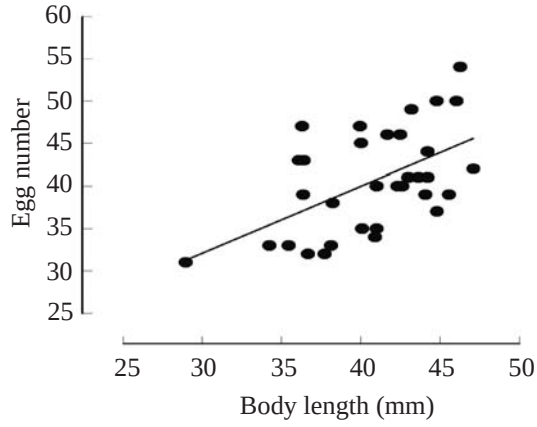

Fig. 2. Relationship between egg number per *E. wagenknechti* female and its body length (L_t, mm), under population outbreak conditions n = 33.

Discussion

According to locals, population outbreaks of *E. wagenknechti* are a recurring phenomenon in the area of north-central Chile. Table 7 shows a 30-years record on available information about outbreaks of *E. wagenknechti* as they have been reported by locals and recorded by the state agency Servicio Agrícola Ganadero. No data on density numbers are available, except those of Moroni (1972), Toro (1972) and the present work. Compared to the abovementioned authors, our estimates of density were much lower. We found densities ranging from 0.25 to 0.54 ind/m^2, in contrast to 10-50 ind/m^2 observed in the 1970-event (Moroni 1972, Toro 1972). Comparatively, densities $\geq$ 9.6 ind/m^2 are considered outbreak levels in rangeland grasshoppers inhabiting the grassland biome of Wyoming (Schell & Lockwood 1997). Although the relatively smaller densities as compared to those reported in literature from other arid/semiarid biomes (Cigliano *et al*. 1995, Torrusio *et al*. 2002), the importance of the event in the Chilean case is given by farmer´s complaints for damage caused by grasshoppers on subsistence crops (Table 7). Owing to rugged landscape, semi arid conditions, and intensive desertification, small farmlands and family orchards attract grasshoppers searching for food of good quality, high water content, and oviposition sites. These complaints usually call the attention

Table 7. Thirty year record of population outbreak occurrences of *E. wagenknechti* during 30 years in rangeland sites of north-central Chile[1].

Year	Outbreak focus	Host plants
1970	Quilitapia, Chipel, Divisadero, Lomas del Sauce, El Huacho Agua Amarilla, Pama, Comunidad Jiménez y Tapia, Fundo Las Añañucas, Quebrada Grande, La Laja Aeródromo de Chingay, Estación La Mostaza, Punitaqui, Camarico Viejo, Ramadilla, Santa Rosa, El Rodeo, Cerro Las Nipas, Parral, Alcones	Native flora: *Cristaria glaucophylla*, *Cistanthe* sp., *Erodium* sp., *Melilotus indica*, *Ephedra* sp., *Viola* sp. Crop attacks not reported.
1971	No data available	
1972	El Huacho, Lomas del Sauce, Quebrada Trujillo, Pama, Chingay, Quilitapia	Native flora: *Gutierrezia resinosa*, *Flourensia thurifera*, *Atriplex semibaccata* Crop attacks: *Phaseolus vulgaris*, *Allium cepa*, *Medicago sativa*, *Vicia faba* and low part of *Pyrus communis* and *Vitis vinifera*
1973	No data available	
1974	Chipel, Quebrada de Lepe, Divisadero, El Huacho, Lomas del Sauce Agua Amarilla, Comunidad Jiménez y Tapia, Quilitapia, Quebrada Grande, Pajarito Blanco, La Cienaga, Cancha de aterrizaje de Quilitapia, Peña Blanca y Chingay.	Native flora: not reported Crop attacks: not reported
1975	Trujillo, Chipel, Lepe, Peñablanca, El Carrizo, Los Romeros, Sauce Bajo, Agua Amarilla, Quebrada de Lepe	Native flora: lightly affected Crop attacks: lightly affected (*Titricum aestivum*, *Medicago sativa*, *Cuminum cyminum*, *Pisum sativum*)
1976	No data available	

Continue

Table 7. Continuation.

Year	Outbreak focus	Host plants
1977	Altos de las Cañuelas de Quilitapia, Agua Amarilla, Cancha de aterrizaje de Quilitapia, Andacollito del Huacho, Majada de la Morra, Cruz Grande del Huacho, Quebrada de Trujillo, Divisadero, Llanos de Bucho, Pama, Chingay, Soruco, Lepe, Cañuelas de Peña Blanca, Quebrada del Huacho	Native flora: lightly affected Crops attacks: lightly affected (cereals, fruit trees)
1978-79	No data available	
1980	Quilitapia, Las Quebradas, El Huacho, El Pacul, Lomas del Sauce, Lepe, Soruco, Cogotí, Pama, Pama Arriba, Blanquillo, Chingay, Placa (Combarbalá)	Native flora: lightly affected Crops attacks: lightly affected
1981-95	No data available	
1996	Agua Amarilla, El Huacho, Lomas del Sauce, Pajarito Blanco, La Cienaga, Quilitapia.	Native flora: lightly affected Crops attacks: lightly affected
1997-98	No data available	
1999	Lomas del Sauce, Agua Amarilla, El Huacho	Native flora: not reported
2000	No data available	

[1]Source of information: Servicio Agrícola y Ganadero SAG (Region of Coquimbo, Chile)

of local newspapers and trigger intensive chemical control conducted by state agencies. These events are noticed as outbreaks by locals (Table 7).

Most of the available information on sexual proportion of grasshopper populations comes from studies conducted in acridids, for which a 1:1 proportion is relationship established (Beingolea 1965, 1995; Joern & Gaines 1990). However, this relationship can be modified under differential mortality (Mulkern 1983) or protandry (del Castillo & Núñez-Farfán 2002). Presently, we have no explanation for the high value of female proportion (0.96) found in Lomas del Sauce in 1996. It is evident from Table 3 that this site has characteristics that favor the *E. wagenknechti* outbreaks.

Very little is known about the reproductive capacity of the Chilean grasshoppers (Elgueta *et al*. 1999). The mean number of eggs per female estimated in this study are close to the values found by Toro (1972) for the 1970-outbreak. Nevertheless, these estimates are much lower than those values reported in the locust-literature (Beingolea 1965, 1995; Joern & Gaines 1990). For instance, Joern & Gaines (op. cit.) have reported values as high as 330 to 642 eggs per female in individuals of *Schistocerca gregaria* Forskal, *Locusta migratoria* (L.) and *Nomadacris septemfasciata* (Serville) (Orthoptera: Acrididae), in solitary phase, kept under laboratory conditions. The most fertile females in our study sites were found in Quebrada Grande (1996) and in El Huacho (1999), with means of 42 and 39 eggs per female, respectively. At present, we have not explored yet the causal relationship and lack of an appropriate explanation for these results.

In conclusion, we have described some demographic characteristics of an endemic species of a Chilean grasshopper, *E. wagenknechti*, which is capable of display population outbreaks. Although abundance levels reached by this grasshopper during outbreaks are far from the levels reached by other species of grasshoppers, the *E. wagenknechti* outbreaks are intense enough to call local attention and provoke farmer´s complaints. Because of this, state agencies keep a permanent monitoring and insecticide control program. Apparently, these outbreaks are related to the desertification stage of the land and soil mismanagement by rainfed cultivation. These and other aspects of the *E. wagenknechti* outbreaks are examined in a further paper.

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References

Anonymous, 1996. Statistix for windows. User´s Manual. Analytical Software. Tallahassee. Florida, 333p.

Beingolea, G.O. 1965. Sumario bio-ecológico de la langosta migratoria sudamericana *Schistocerca cancellata* Serv (*S. Paranensis* Burm.) en el Perú. Rev. Peruana Entomol. Agri. 6: 39-60.

Beingolea, G.O. 1995. Langostas y su control. RAAA/SENASA, Lima, 143p.

Castillo, R.C. del & J. Núnez-Farfán. 2002. Female mating success and risk of pre-reproductive death in a protandrous grasshopper. Oikos 96: 217-224.

Cepeda-Pizarro, J., J. Pizarro-Araya & H. Vásquez. 2005a. Composición y abundancia de artrópodos del Parque Nacional

Llanos de Challe: impactos del ENOS de 1997 y efectos del hábitat pedológico. Rev. Chil. Hist. Nat. 78: 635-650.

Cepeda-Pizarro, J., J. Pizarro-Araya & H. Vásquez. 2005b. Variación en la abundancia de Arthropoda en un transecto latitudinal del desierto costero transicional de Chile, con énfasis en los tenebriónidos epígeos. Rev. Chil. Hist. Nat. 78: 651-663.

Cepeda-Pizarro, J., S. Vega, H. Vásquez & M. Elgueta. 2003. Morfometría y dimorfismo sexual de *Elasmoderus wagenknechti* (Liebermann) (Orthoptera: Tristiridae) en dos eventos de irrupción poblacional. Rev. Chil. Hist. Nat. 76: 417-435.

Cigliano, M.M. 1989. Revisión sistemática de la familia Tristiridae (Insecta: Orthoptera). Bol. Soc. Biol. Concepción (Chile). 60: 89-91.

Cigliano, M.M., W.P. Kemp & T. Kalaris. 1995. Spatio-temporal characteristics of rangeland grasshopper (Orthoptera: Acrididae) regional outbreaks. J. Orthoptera Res. 4: 111-126.

Dillon, M.O. & P.W. Rundel. 1990. The botanical response of the Atacama and Peruvian Desert flora to the 1982-83 El Niño Event, p.487-504. In P.W. Glynn (ed.), Global ecological consequences of the 1982-83 El Niño-Southern oscillation. Elsevier Oceanographic Series 52, Amsterdam, 350p.

Domènech-Massons, J.M. 1977. Bioestadística. Métodos estadísticos para investigadores. Editorial Herder, Barcelona, 662p.

Draper, N.R. & H. Smith. 1966. Applied Regression Analysis. Wiley Series in probability and mathematical statistics. John Wiley and Sons, Inc. New York, 407p.

Elgueta, M., A. Camousseight & C. Carbonell. 1999. Catálogo de los Orthoptera (Insecta) de Chile. Publ. Ocas. Mus. Nac. Hist. Nat. (Chile) 54: 1-60.

Fuentes, E.R. & C. Campusano. 1985. Pest outbreaks and rainfall in the semiarid-region of Chile. J. Arid Environ. 8: 67-72.

Gajardo, R. 1993. La vegetación natural de Chile. Clasificación y distribución geográfica. Editorial Universitaria, Santiago, 165p.

Gastó, J. & D. Contreras. 1979. Un caso de desertificación en el norte de Chile. Boletín Técnico Nº 42. Facultad de Agronomía. Universidad de Chile. Santiago, Chile, 99p.

Gutiérrez, J.R., P.L. Meserve & F.M. Jaksic. 2000. Efectos de la corriente de El Niño sobre la biota terrestre de ecosistemas áridos de Sudamérica, p.91-94. In P. Jiménez-Milón, C. Talavera-Delgado, L. Villegas-Paredes, A. Ortega-Paredes & F. Villasante-Benavides (eds.), Memorias del IV Congreso Latinoamericano de Ecología. Ecología y desarrollo sostenible: Reto de la América Latina para el tercer milenio. Industria Gráfica Regentus, R.S. Ltda. Arequipa, 274p.

Jaksic, F.M. 1998. The multiple facets of El Niño/Southern oscillation in Chile. Rev. Chil. Hist. Nat. 71: 121-131.

Jiménez, J.E., P. Feinsinger & F.M. Jaksic. 1992. Spatio-temporal patterns of an irruption and decline of small mammals in north-central Chile. J. Mammal. 73: 356-364.

Joern, A. & S.B. Gaines. 1990. Populations dynamics and regulation in grasshoppers. p.415-482. In R.F. Chapman & A. Joern (eds.), Biology of grasshoppers. John Wiley and Sons, New York, 576p.

Lima, M., P.A. Marquet & F.M. Jaksic. 1999a. El Niño events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. Ecography 22: 213-218.

Lima, M., J.E. Keymer & F.M. Jaksic. 1999b. ENSO-driven rainfall variability and delayed density-dependence cause rodent outbreaks in western South America: From demography to population dynamics. Amer. Nat. 153: 476-491.

Luzio, W. & S. Alcayaga. 1992. Mapa de asociaciones de grandes grupos de suelos de Chile. Agri. Téc. (Chile) 52: 347-353.

Meserve, P.L., J.A. Yunger, J.R. Gutiérrez, L.C. Contreras, W.B. Milstead, B.K. Lang, K.L. Cramer, S. Herrera, V.O. Lagos, S.I. Silva, E.L. Tabilo, M.A. Torrealba & F.M. Jaksic. 1995. Heterogeneous responses of small mammals to an El Niño (ENSO) event in nor-central semiarid Chile and the importance of ecological scale. J. Mammal. 76: 580-595.

Montgomery, D.C. 1984. Design and analysis of experiments. John Wiley & Sons. New York, 776p.

Moroni, J. 1972. Irrupción de *Elasmoderus rabiosus* (Liebermann) en el Norte Chico (Acrididae, Chilacridinae). Not. Mens. Mus. Nac. Hist. Nat. (Chile) 192: 3-6.

Mulkern, G.B. 1983. Sex ratios of *Melanoplus sanguinipes* and other Acrididae (Orthoptera). J. Kansas Entomol. Soc. 56: 457-465.

Novoa, R. & S. Villaseca. 1989. (eds.) Mapa agroclimático de Chile. Instituto de Investigaciones Agropecuarias, Santiago, 126p.

Santelices, M., V. Irribarra, R. Valdés & F. Silva. 1973. Sobre algunos oligoquetos del Norte Chico. Ans. Mus. Hist. Nat. Valparaíso (Chile) 6: 67-74.

Schell, S.P. & J.A. Lockwood. 1997. Spatial characteristics of rangeland grasshopper (Orthoptera: Acrididae) population dynamics in Wyoming: Implications for pest management. Environ. Entomol. 26: 1056-1065.

Squeo, F.A., G. Arancio, C. Marticorena, M. Muñoz & J.R. Gutiérrez. 2002. Diversidad vegetal en la IV Región de Coquimbo, Chile. p.149-158. In F.A. Squeo, G. Arancio & J.R. Gutiérrez (eds.), Libro rojo de la flora nativa y de los sitios prioritarios para su conservación: Región de Coquimbo. Ediciones Universidad de La Serena. La Serena. Chile, 386p.

Toro, H. 1972. Notas biológicas sobre la langosta de Combarbalá. Idesia 2: 133-136.

Torrusio, S., M.M. Cigliano & M.L. de Wysiecki. 2002. Grasshopper (Orthoptera: Acridoidea) and plant community relationships in the argentine pampas. J. Biogeogr. 29: 221-229.

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