

Feeding Habits and Trophic Niche Overlap of Aquatic Orthoptera Associated with Macrophytes

Soledad Capello^{1,*}, Mercedes Marchese^{1,2}, and María L. de Wysiecki³

¹Instituto Nacional de Limnología (INALI-CONICET-UNL), Ciudad Univ., Santa Fe 3000, Argentina

²Facultad de Humanidades y Ciencias-UNL. Ciudad Univ., Paraje El Pozo, Santa Fe 3000, Argentina

³Centro de Estudios Parasitológicos y de Vectores (CEPAVE) (CCT-La Plata- CONICET- UNLP), Calle 2 n° 584, La Plata 1900, Argentina

(Accepted July 27, 2011)

Soledad Capello, Mercedes Marchese, and María L. de Wysiecki (2012) Feeding habits and trophic niche overlap of aquatic Orthoptera associated with macrophytes. *Zoological Studies* 51(1): 51-58. A dietary analysis is a frequent 1st step in studying an animal's ecology, because its diet directly reflects resource use and can provide insights into habitat utilization and competitive interactions. Little is known concerning orthopteran species that inhabit moist or wet environments, because such species do not usually become pests. We hypothesized that aquatic orthopterans feed on only a few macrophytes, and they show trophic niche overlap. Feeding habits of 7 orthopteran species associated with macrophytes, the botanical composition of the diets of these insects, and their trophic niche breadth and overlap were analyzed from the Middle Paraná River, Argentina. The diet composition by a microanalysis of feces under an optical microscope and the frequency of occurrence of each plant, food niche breadth, niche overlap, and food specialization level of every species were determined. Only *Paulinia acuminata*, *Marellia remipes*, and *Cornops aquaticum* exclusively consumed aquatic plants. The water hyacinth (*Eichhornia crassipes*) was the unique macrophyte consumed by all orthopteran species studied, although in different proportions. The greatest trophic niche breadth was shown by *Coryacris angustipennis*, and the highest Berger-Parker index value was found for *C. aquaticum*, which also showed high specificity. The species *C. aquaticum*, *C. angustipennis*, *Conocephalus* sp., and *Scudderia* sp. showed niche overlap; however, they can live in the same habitats because resources are very abundant. This is the 1st analysis of the diet compositions of these species (except *C. aquaticum*), and it is important information to explain orthopteran assemblages associated with macrophytes in this Argentine river.
<http://zoolstud.sinica.edu.tw/Journals/51.1/51.pdf>

Key words: Diet, Herbivores, Orthoptera, Water hyacinth, Paraná River.

Dietary analysis is a frequent 1st step in studying an animal's ecology because it reflects resource use and can provide insights into habitat utilization and competitive interactions (Litvaitis 2000). Thus, partitioning of resources results in a maximization of habitat availability and facilitation of species coexistence which contribute to a determination of community structure (Pianka 1974). Niche overlap may cause the competitive exclusion of a species, or species may avoid

exclusion by employing isolation mechanisms (Gause 1934, Diamond 1978). Therefore, the degree of species overlap in the utilization of resources such as food, space, and shelter has become a valuable approach in studying both community structure and species coexistence. Traditionally, overlap in resource use is quantified as the degree of niche overlap between species, where niche overlap is simply the joint use of a resource (or resources) by 2 or more species

*To whom correspondence and reprint requests should be addressed. E-mail: solecapello@gigared.com

(Hutchinson 1957, Colwell and Futuyma 1971).

Niche overlap between species may be viewed as the volume in multidimensional hyperspace in which 2 or more species maintain viable populations in the presence of one another (Mouillot et al. 2005).

It is important to know an animal's diet in its habitat in order to be aware of its nutritional needs and its interactions with other organisms. For this reason, studies evaluating gut contents try to identify and quantify resources that a species uses, thereby providing information on those resources selected from the choices available in the environment (Tararam et al. 1993). In studies of species interactions and community structure, it is useful to quantify the degree to which 2 species overlap in their utilization of space, food, and other resources, and several measures of niche overlap were proposed (Hurlbert 1978).

Research on both intraspecific and interspecific competition among grasshoppers is very important for understanding the structure and function of the community at high densities (Liu et al. 2007). Belovsky (1985 1997) demonstrated that interspecific competition was strong and was an important factor determining population dynamics and distributions of grasshopper species.

Little is known concerning orthopteran species that inhabit moist or wet environments because such species do not usually become pests. Among them, the most studied species are the acrids *Cornops aquaticum* and *Paulinia acuminata*. *Cornops aquaticum* is studied due to its possible liberation in nonnative areas as a biological control agent of its host plant, *Eichhornia crassipes* (Bennett 1970, Silveira Guido and Perkins 1975, Ferreira and Vasconcellos-Neto 2001, Oberholzer and Hill 2001, Adis and Junk 2003, Adis et al. 2008), which is one of most important invasive weeds globally. Moreover, *Paulinia acuminata* was studied as a potential biological control agent for *Salvinia molesta* (Carbonell 1964 1980, Forno 1981, Sands and Kassulke 1986, Thomas and Room 1986, Vieira and Adis 2000). *Salvinia molesta*, one of the world's most noxious aquatic weeds, is notorious for dominating slow-moving and quiescent fresh waters (Mitchell et al. 1980). Its rapid growth, vegetative reproduction, and tolerance to environmental stress make it an aggressive, competitive species known to impact aquatic environments, water use, and local economies.

To our knowledge, there are no previous studies concerning the trophic niche chara-

cterization of these aquatic insects. We hypothesized that orthopterans which live on aquatic plants feed on only a few macrophytes, and they show trophic niche overlap. Thus, the objectives of this study were to analyze the botanical composition of the diets of different orthopteran species associated with macrophytes, and measure their trophic niche breadth and overlap.

MATERIALS AND METHODS

Study area

Samples were collected from Apr. 2006 to May 2007 in 2 floodplain lakes of the Middle Paraná River, Argentina. The selected sites differed in their degree of connectivity with the main channel, being either permanently (31°38'43.77"S, 60°34'35.07"W) or temporarily connected to the Paraná River (31°40'14.40"S, 60°34'44.43"W).

The vegetation of these floodplain lakes is directly associated with the hydrologic regime of the Paraná River, because the species richness varies according to the water level (Sabattini and Lallana 2007). In spite of differences in the connectivity of the lakes, the most important macrophytes at both sites were the same: *E. crassipes*, *Paspalum repens*, *S. herzogii*, *Pistia stratiotes*, *Ludwigia peploides*, *Echinochloa* sp., and *Polygonum* sp.

Data collection

Orthopterans are not usually considered to be aquatic insects. However, some of their members are linked to freshwater habitats mainly by a relationship to an aquatic host plant. Species that cannot develop without fresh water, especially for egg laying and nymph development, are considered to be primary members of the freshwater biota (Amédégnato and Devriese 2008).

Seven orthopteran species associated with macrophytes were selected: 5 belonged to the suborder Caelifera (*Tucayaca gracilis* (Giglio-Tos 1897), *C. aquaticum* (Bruner 1906), *Marellia remipes* Uvarov 1929, *P. acuminata* (De Geer 1773), and *Coryacris angustipennis* (Bruner 1900)), and 2 belonged to the suborder Ensifera (*Conocephalus* sp. Brongniart 1897 and *Scudderia* sp. Stål 1873).

Cornops aquaticum, *P. acuminata*, and *M.*

remipes have physiologically, ethologically, and morphologically adaptive strategies that allow them to permanently live in the aquatic habitats on floating or rooted plants (Bentos-Pereira and Lorier 1991).

Diet composition

Diet compositions of these orthopterans were determined by a microanalysis of their feces under an optical microscope (400x) according to Arriaga (1981a b 1986). Individuals (568 adults) were sampled every 2 wk with an entomological net in 2006-2007. Each insect collected was immediately placed in a paper tube for a period of 24 h, and the feces was collected, clarified with 10% potassium hydroxide (KOH), and mounted on a slide (Capello et al. in press). Twenty microscope fields were randomly selected for each sample (comprising the feces of 1 individual) in which at least 1 piece of epidermal tissue was present (Sheldon and Roger 1978).

The anatomy of leaves of all macrophytes recorded in these floodplain lakes was previously analyzed. Epidermal tissues were identified based on cellular characteristics (epidermal cells, stomata, trichomes, hairs, etc.), and photographs were taken under an optical microscope. Vegetal tissues observed in the feces of the orthopterans were compared to reference collections to identify the plants species consumed.

Statistical analysis

The frequency of occurrence was calculated for each food item based on the number of fields containing a particular food item.

Food niche breadth was calculated as the Shannon-Wiener index (H):

$$\text{FNB} = - \sum p_i \log_2 p_i;$$

where FNB is the food niche breadth of species *i*, and p_i is the frequency of occurrence of species *i* in the diet of the orthopteran. The larger the numerical value of FNB is, the wider the food niche breadth is.

The food niche overlap index was calculated using the Pianka index in the statistical program EcoSim 7.72 (Gotelli and Entsminger 2009). This index is symmetrical, and it assumes values of 0 to 1, with 0 indicating that a resource is used by a single species, and 1 indicating complete diet overlap or certain resource consumption. Values

of > 0.60 indicate overlap between species.

To determine the level of food specialization of each orthopteran species, the index of dominance of Berger-Parker (d) was calculated by the following formula (Magurran 1988):

$$d = N_{\max} / N;$$

where N is the number of all recorded food components (taxa), and N_{\max} is the number of specimens from taxon *i* (the most numerous taxon in the diet). The Berger-Parker index (d) varies between 1/N and 1. A value closer to 1 indicates higher specialization in the choice of food, while a value closer to 1/N is typical of species that are general feeders (polyphagous).

A factorial correspondence analysis (FCA) was applied to determine relationships between orthopterans species and the plants consumed. Significant differences in diet compositions (aquatic and/or terrestrial) between orthopterans were analyzed by the Kruskal-Wallis test at a 5% significance level. The software XLSTAT (Win) (free version: <http://xlstat.softonic.com>) was used for these statistical analyses.

RESULTS

We examined 568 fecal samples of 5 grasshopper's species (*C. aquaticum*, *P. acuminata*, *M. remipes*, *T. gracilis*, and *C. angustipennis*) and 2 tettigonids (*Scudderia* sp. and *Conocephalus* sp.) to determine the composition of their diets. Only 3 species of grasshoppers (*P. acuminata*, *M. remipes*, and *C. aquaticum*), exclusively consumed aquatic plants, while *Conocephalus* sp. (38.30%) and *C. angustipennis* (27.84%) consumed higher percentages of terrestrial plants (Fig. 1).

When comparing aquatic and terrestrial plants by the Kruskal-Wallis test in relation to the microanalysis of feces of each species, no significant differences were observed ($p > 0.05$).

Eichhornia crassipes was a unique aquatic plant consumed by all orthopteran species examined, although in different proportions. The highest consumption of this macrophyte was by *C. aquaticum* (91.21%), while the lowest value was recorded by the acrid *P. acuminata* (4.31%). Conversely, *Azolla* sp. was the aquatic plant selected least often by orthopterans, being consumed only by *P. acuminata* (Table 1).

The highest trophic niche breadth was shown

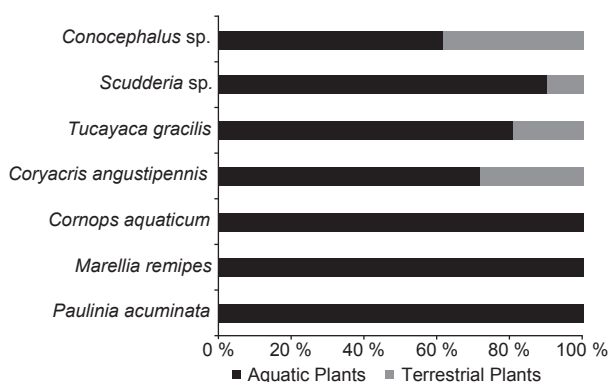


Fig. 1. Percentages of consumption of different plants (aquatics and terrestrial) for each species of Orthoptera.

by *C. angustipennis* (1.19), and the lowest was by *C. aquaticum* (0.38), with only a few vegetal species consumed. In addition, the highest Berger-Parker index value was reached by *C. aquaticum* (0.91), thus showing high specificity (Table 1).

The highest trophic niche overlaps (Pianka index) obtained were between *C. aquaticum* and *C. angustipennis* (0.842) and between *Conocephalus sp.* and *Scudderia sp.* (0.841). On the other hand, species showing the lowest niche overlap were *P. acuminata* and *T. gracilis* (0.015) (Table 2).

Four groups were established according to the results obtained by the FCA, with each species

Table 1. Percentage consumed (% C) and frequency of occurrence (FO) of each plant in the diets of Orthoptera

	Caelifera										Ensifera			
	<i>Paulinia acuminata</i> n = 40		<i>Marellia remipes</i> n = 30		<i>Cornops aquaticum</i> n = 209		<i>Coryacris angustipennis</i> n = 64		<i>Tucayaca gracilis</i> n = 100		<i>Scudderia sp.</i> n = 65		<i>Conocephalus sp.</i> n = 60	
	% C	FO	% C	FO	% C	FO	% C	FO	% C	FO	% C	FO	% C	FO
<i>Alternanthera sp.</i>	0	0	0	0	0	0	0.59	1.56	0	0	23	56.92	12.00	38.33
<i>Azolla sp.</i>	<u>51.13</u>	77.50	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eichhornia crassipes</i>	4.31	17.50	18.65	36.60	<u>91.21</u>	<u>96.66</u>	<u>46.54</u>	<u>65.62</u>	15.90	55.33	12.20	36.92	7.90	33.33
<i>Hydrocleis nymphoides</i>	0	0	<u>77.18</u>	<u>86.66</u>	0	0	0	0	0	0	0	0	0	0
<i>Hydrocotyle sp.</i>	0	0	0	0	0	0	1.98	1.56	0	0	0	0	0	0
<i>Ludwigia peploides</i>	1.38	5.00	0	0	4.08	9.56	3.53	3.12	0	0	<u>54.00</u>	<u>87.69</u>	<u>41.80</u>	66.66
<i>Nymphoides sp.</i>	2.38	10.00	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oxycaryum cubense</i>	0	0	0	0	0	0	1.02	3.12	0	0	0	0	0	0
<i>Paspalum repens</i>	0	0	0.17	3.33	4.23	9.09	12.85	25.00	<u>65.30</u>	<u>85.33</u>	0	0	0	0
<i>Panicum prionites</i>	0	0	0	0	0.33	1.91	3.13	4.68	0	0	0	0	0	0
<i>Pistia stratiotes</i>	3.75	10.00	1.33	10.00	0	0	0	0	0	0	0	0	0	0
<i>Polygonum sp.</i>	0	0	0	0	0.15	2.87	2.54	3.12	0	0	1.30	10.77	0	0
<i>Salvinia sp.</i>	37.06	<u>80.00</u>	2.97	3.33	0	0	0	0	0	0	0	0	0	0
Terrestrials plants	0	0	0	0	0	0	27.84	42.12	18.80	35.33	9.50	33.85	38.30	<u>70.00</u>
Shannon-Wiener index	1.12		0.68		0.38		1.19		0.49		0.99		0.85	
Berger-Parker index	0.51		0.77		0.91		0.64		0.80		0.60		0.68	

n, number of individuals analyzed of each species. The highest values of percentage of consumed (%C) and frequency of occurrence (FO) of each plant in the composition of the diet of each orthopteran species can be observed in italics and underlined.

Table 2. Niche overlap among different orthopteran species (the highest values are underlined)

	<i>Paulinia acuminata</i>	<i>Marellia remipes</i>	<i>Coryacris angustipennis</i>	<i>Tucayaca gracilis</i>	<i>Scudderia sp.</i>	<i>Conocephalus sp.</i>
<i>Cornops aquaticum</i>	0.069	0.234	<u>0.842</u>	0.270	0.240	0.151
<i>Paulinia acuminata</i>		0.036	0.058	0.015	0.033	0.023
<i>Marellia remipes</i>			0.195	0.055	0.047	0.028
<i>Coryacris angustipennis</i>				0.537	0.305	0.472
<i>Tucayaca gracilis</i>					0.087	0.204
<i>Scudderia sp.</i>						<u>0.841</u>

The values that are in italics and underlined indicate a food niche overlap among the species. Only values of > 0.60 indicate overlap between species.

exhibiting adaptive strategies to living in an aquatic habitat. *Cornops aquaticum*, *P. acuminata*, and *M. remipes* were separated in individual groups, while the remaining species were included in a single group. Thus, the diet of the aquatic acrids had a specific composition, while *T. gracilis*, *C. angustipennis*, *Conocephalus* sp., and *Scudderia* sp. shared major proportions of common vegetal species (Fig. 2).

DISCUSSION

Although all orthopteran species studied consumed aquatic plants, *C. aquaticum*, *P. acuminata*, and *M. remipes* fed only on macrophytes, showing higher dependence on aquatic habitats. These species present ethologic, physiological, and ecological adaptations to living in aquatic environments. These adaptations include a general morphology with a fusiform habitus for species living only in water and that are used to swimming under water. These species also have a strong hind femur and expanded hind tibiae, including spines and modified spurs. In

some species, the presence of dense hairs on the margins of the tibiae also helps reinforce their efficiency in aquatic habitats. This modification of the hind tibiae is more or less generalized within all the groups linked to water, but varies from weakly to strongly develop in most aquatic species (Carbonell 1957a, Amédégnato 1977, Roberts 1978). These grasshoppers also show modifications in their ovipositor allowing them to utilize macrophytes as substrata on which to deposit eggs (endophitic or ephyphitic oviposition) and produce lower egg numbers compared to terrestrial species (Braker 1989).

Coryacris angustipennis, *T. gracilis*, *Scudderia* sp., and *Conocephalus* sp. consumed high proportions of terrestrial plants. Thus, by consuming aquatic and terrestrial plants, these species act as an important energy link between aquatic and terrestrial systems. These interrelationships are very important in river basins (Jackson and Fisher 1986, Gray 1989 1993), because rivers may provide resources to terrestrial herbivores. For example, *Paratettix aztecus* and *P. mexicanus* (Orthoptera: Tetrigidae), small species that generally live near river banks, obtain 88%-

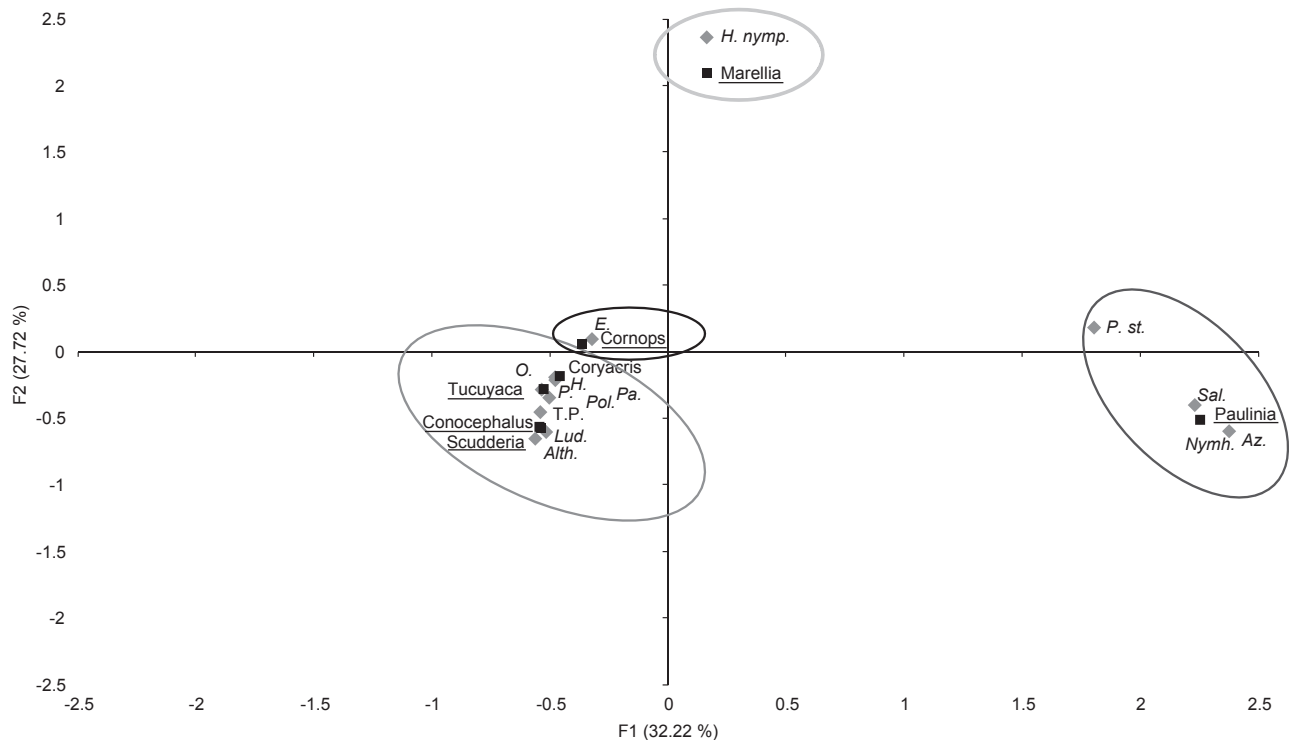


Fig. 2. Factorial correspondence analysis (FCA) between orthopteran species (■ and underline) and the macrophytes (◆) consumed. *E.*, *Eichhornia crassipes*; *H. nymph.*, *Hidrocleis nymphoides*; *P. st.*, *Pistia stratiotes*; *Sal.*, *Salvinia* sp.; *Az.*, *Azolla* sp.; *Nymh.*, *Nymphoides* sp.; *O.*, *Oxycaryum cubense*; *H.*, *Hidrocotyle* sp.; *P.*, *Paspalum repens*; *Pa.*, *Panicum prionites*; *Pol.*, *Polygonum* sp.; *T.P.*, terrestrial plants; *Lud.*, *Ludwigia peploides*; *Alth.*, *Alternanthera* sp.

100% of their carbon from the alga *Cladophora glomerata* (Bastow et al. 2002).

Picaud et al. (2003) considered that 60% of acrid species are polyphagous, but they can include a degree of specialization according to the plants consumed (Crawley 1983, Chapman 1990). Thus, the high preference of *M. remipes* for *H. nymphoides* (a scarce plant species) can be explained by structural modifications for life on the horizontal surface of floating leaves and for feeding on their upper surfaces. Although this species is phytophilous, it has characteristic geophilous features, such as the generally depressed shape of its body, the position of its eyes on the upper part of the head, and the reduced pretarsal arolia (Carbonell 1957a b).

All of the orthopterans studied are polyphagous, because plants of different genera were consumed. According to Bernays and Chapman (1994) and Bernays and Minkenberg (1997), a mix of plants in the diet can improve the nutrient balance and increase survival and fecundity (Unsicker et al. 2008). Although herbivorous insects' preferences are a balance between plant inhibitor substances and phagostimulants, a higher orthopteran preference was determined by inhibitor substances (Bernays and Chapman 1994).

Consumption of *E. crassipes* by all species studied compared to all other plants consumed can be explained by the leaf roughness, pathway of photosynthesis (C_3 plant), and higher cover in the Paraná River system. Thus, it is a very valuable and palatable resource for invertebrate herbivores. However, the highest consumption of the water hyacinth occurred by *C. aquaticum*, which corresponds to a report by Ferreira and Vasconcellos-Neto (2001) in Brazil where it was represented by the Pontederiaceae, especially *E. crassipes*. In addition, a high specificity of *C. aquaticum* for different genera of the family Pontederiaceae was reported (Silveira Guido and Perkins 1975, Medeiros 1984, Viera and Santos 2003, Lhano et al. 2005).

Food niche breadth and overlap analysis

The highest niche breadth was exhibited by *C. angustipennis* (1.19) which consumed different proportions of 8 types of plant (aquatic and terrestrial) and shared the principal food (*E. crassipes*) with *C. aquaticum*. However, there was no competition between the 2 species due to this food niche overlap because the water hyacinth is not a limited resource; it is the most abundant plant

in the Paraná River system.

Paulinia acuminata, commonly considered a possible agent of biological control for *S. molesta* (Carbonell 1964 1980, Forno 1981, Sands and Kassulke 1986, Thomas and Room 1986, Vieira and Adis 2000) also presented a high niche breadth (1.12) by selecting 6 aquatic plant species for its diet, including *E. crassipes*, *L. peploides*, and *Nymphoides* sp. as a new record. Carbonell et al. (2006) reported *S. auriculata*, *Pistia stratiotes*, *Lemna* sp., *Limnobium leavigatum*, *Spidorella intermedia*, and *Azolla filiculoides* in the diet spectrum of *P. acuminata*.

Conocephalus sp. and *Scudderia* sp. showed similar food niche breadths and niche overlap. This similarity in diet compositions might be a key reason for the high competition between these species (Liu et al. 2007), but they are able to partition terrestrially available resources and coexist. In spite of limited information on orthopterans that live on aquatic plants, food niche overlap between many orthopteran species was reported in terrestrial environments (Ueckert and Hansen 1971, Sheldon and Rogers 1978).

The coexistence in the same habitats of the 7 orthopteran species studied can be explained by positive associations that favor mutual occurrence and by the high availability of abundant resources.

Acknowledgments: The authors dedicate this work to the memory of Dr. J. Adis. This study was financed in part by CONICET.

REFERENCES

- Adis J, W Junk. 2003. Feeding impact and bionomics of the grasshopper *Cornops aquaticum* on the water hyacinth *Eichhornia crassipes* in Central Amazonian floodplains. *Stud. Neotrop. Fauna Environ.* **38**: 245-249.
- Adis J, CF Sperber, EG Brede, S Capello, MC Franceschini, M Hill et al. 2008. Morphometric differences in the grasshopper *Cornops aquaticum* (Bruner, 1906) from South America and South Africa. *J. Orthopt. Res.* **17**: 141-147.
- Amédégnato C. 1977. Etude des Acridoidea centre et sud Américains (Catantopinae, sensu lato) Anatomie des genitalia, classification, repartition, phylogenie. PhD dissertation, University Paris VI, Pierre et Marie Curie, Paris.
- Amédégnato C, H Devriese. 2008. Global diversity of true and pygmy grasshoppers (Acridomorpha, Orthoptera) in fresh water. *Hydrobiologia* **595**: 535-543.
- Arriaga MO. 1981a. El uso de los caracteres histofoliales en el estudio de hábitos alimentarios de Acridiidae. Parte I. *Phy. Secc. C* **39**: 61-74.
- Arriaga MO. 1981b. El uso de los caracteres histofoliales en

- el estudio de hábitos alimentarios de Acridiidae. Parte II. Phys. Secc. C **40**: 1-13.
- Arriaga MO. 1986. Metodología adaptada al estudio de hábitos alimentarios en insectos herbívoros. Com. Mus. Argentino Cien. Nat. Bernardino Rivadavia **2**: 103-111.
- Bastow JL, JL Sabo, JC Finlay, ME Powers. 2002. A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers. Oecologia **131**: 261-268.
- Belovsky GE. 1985. Comparison of activity cycles, activity times, and feeding times for ten prairie herbivores. Natl. Geogr. Soc. Res. Rep. **1979**: 1-9.
- Belovsky GE. 1997. Optimal foraging and community structure: the allometry of herbivore food selection and competition. Evol. Ecol. **11**: 641-672.
- Bennett FD. 1970. Insects attacking water hyacinth in the West Indies, British Honduras and the U.S.A. Hyacinth Control J. **8**: 10-13.
- Bentos-Pereira A, E Lorier. 1991. Acridomorfos acuáticos (Orthoptera, Acridoidea) I. Adaptaciones morfológicas. Rev. Bras. Zool. **35**: 631-653.
- Bernays EA, B Chapman. 1994. Host-plant selections by phytophagous insect. Chapman and Hall. New York, 312 pp.
- Bernays EA, OPJM Minkenbergh. 1997. Insect herbivores: different reason for being a generalist. Ecology **78**: 1157-1169.
- Braker HE. 1989. Evolution and ecology of oviposition on host plants by acridoid grasshoppers. Biol. J. Linnean Soc. **38**: 389-406.
- Capello S, ML de Wysiecki, M Marchese. 2010. Feeding patterns of the aquatic grasshopper *Cornops aquaticum* Bruner (Orthoptera, Acrididae) in the Middle Paraná River, Argentina. Neotrop. Entomol. (In press)
- Carbonell CS. 1957a. Observaciones bioecológicas sobre *Marellia remipes* Uvarov (Orthoptera, Acridoidea) en el Uruguay. Univ. de la República, Facultad de Humanidades y Ciencias, Montevideo, Uruguay.
- Carbonell CS. 1957b. The external anatomy of the South American semi-aquatic grasshopper *Marellia remipes* Uvarov (Acridoidea, Pauliniidae). Smithsonian. Misc. Coll. **137**: 61-97.
- Carbonell CS. 1964. Hábitat, etología y ontogenia de *Paulinia acuminata* (DE GEER), (Acridoidea, Pauliniidae) en el Uruguay. Rev. Soc. Uruguaya Entomol, **6**: 39-48.
- Carbonell CS. 1980. Orthoptera. In SH Hurlbert, G Rodriguez, N Dias dos Santos, eds. Aquatic biota of tropical South America. Part 1, Arthropoda. San Diego, CA, 323 pp.
- Carbonell CS, MM Cigliano, C Lange. 2006. Acridomorph (Orthoptera) species of Argentina and Uruguay/ Especies de Acridomorfos (Orthoptera) de Argentina y Uruguay. Publications on Orthopteran Diversity. The Orthopterists Society at the Museo de La Plata, La Plata. http://140.247.119.225/OrthSoc/Images/books/Carbonell_CD/INDEX.HTM
- Chapman RF. 1990. Food selection. In RF Chapman, A Joern, eds. Biology of grasshoppers. New York: J. Wiley, pp. 39-72.
- Colwell RK, DJ Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology **52**: 567-576.
- Crawley MJ. 1983. Herbivory. The dynamics of animal-plant interactions. Oxford, UK: Blackwell Scientific Publications, 437 pp.
- Diamond JM. 1978. Niche shifts and rediscovery of interspecific competition. Am. Sci. **66**: 322-331.
- Ferreira SA, J Vasconcellos Neto. 2001. Ecology, behavior and bionomics of *Cornops aquaticum* in Poconé, Brazil. Neotrop. Entomol. **30**: 523-533.
- Forno IW. 1981. Progress in the exploration for biological control agents for *Salvinia molesta*. In Proceedings of the 5th International Symposium on Biological Control of Weeds, Brisbane, pp. 167-173.
- Gause GF. 1934. The struggle for existence. Williams Wilkins, reprinted by Hafner Publishing Company, 1969. New York.
- Gray LJ. 1989. Emergence production and export of aquatic insects from a tallgrass prairie stream. SW Nat. **34**: 313-318.
- Gray LJ. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. Am. Midl. Nat. **129**: 288-300.
- Gotelli NJ, GL Entsminger. 2009. EcoSim: null models software for ecology. Version 7. Jericho, VT: Acquired Intelligence and Kesey-Bear. Available at <http://garyentsminger.com/ecosim.htm>
- Hurlbert SH. 1978. The measurement of niche overlap and some relatives. Ecology **59**: 67-77.
- Hutchinson GE. 1957. Concluding remarks. Cold Spring Harbor Symp. Quantitative Biol. **22**: 415-427.
- Jackson JK, SG Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. Ecology **67**: 629-638.
- Lhano MG, J Adis, MI Marques, LD Batirola. 2005. *Cornops aquaticum* (Orthoptera, Acrididae, Leptysminae) aceitação de plantas alimentares por ninfas vivendo em *Eichhornia azurea* (Pontederiaceae) no Pantanal norte, Brasil. Amazoniana **18**: 397-404.
- Litvaitis JA. 2000. Investigating food habits of terrestrial vertebrates. In L Boitani, TK Fuller, eds. Research techniques in animal ecology. Controversies and consequences. Columbia Univ. Press, New York, USA, pp. 165-190.
- Liu CZ, SR Zhou, L Yan, FN Huang. 2007. Competition among the adults of three grasshoppers (Orthop., Acrididae) on an alpine grassland. J. Appl. Entomol. **131**: 153-159.
- Magurran AE. 1988. Diversidad ecológica y su medición. Barcelona: Vedral. 200 pp.
- Medeiros MLM. 1984. Insetos associados á *Eichhornia crassipes* (Mart.) Solm-Laubach, flutuação sazonal e biologia do *Cornops aquaticum* (Bruner, 1906) (Orthoptera: Acrididae). Master thesis, Mestre em Ciências Biológicas, Univ. Federal do Paraná, Brasil, 105 pp.
- Mitchell DS, T Petr, AB Viner. 1980. The water fern *Salvinia molesta* in the Sepik River, Papua New Guinea. Environ. Conserv. **7**: 115-122.
- Mouillot D, W Stubbs, M Faure, O Dumay, A Tomasini, JB Wilson, T Do Chi. 2005. Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. Oecologia **145**: 345-353.
- Oberholzer IG, MP Hill. 2001. How safe is the grasshopper *Cornops aquaticum* for release on water hyacinth in South Africa? In MH Julien, MP Hill, TD Center, J Ding, eds. Biological and integrated control of water hyacinth, *Eichhornia crassipes*. ACIAR Proc. **102**: 82-88.
- Pianka ER. 1974. Niche overlap and diffuse competition. Proc. Nat. Acad. Sci. USA **71**: 2141-2145.
- Picaud F, E Bonnet, V Gloaguen, D Petit. 2003. Decision making for food choice by grasshoppers (Orthoptera:

- Acrididae): comparison between a specialist species on a shrubby legume and three graminivorous species. *Environ. Entomol.* **32**:680-688.
- Roberts HR. 1978. A revision of the tribe Leptysmini except the genus *Cylindrotettix* (Orthoptera: Acrididae: Leptysminae). *Proc. Acad. Nat. Sci. Phil.* **129**: 33-69.
- Sabattini R, VH Lallana. 2007. Aquatic macrophytes. In M Iriondo, JC Paggi, MJ Parma, eds. *The Middle Paraná River. Limnology of a subtropical wetland*. Argentina: Springer-Verlag, pp. 205-224.
- Sands DPA, RC Kassulke. 1986. Assessment of *Paulinia acuminata* (Orthoptera: Acrididae) for the biological control of *Salvinia molesta* in Australia. *Biocontrol* **31**: 11-17.
- Sheldon J, L Rogers. 1978. Grasshopper food habits within a shrubsteppe community. *Oecologia (Berl.)* **32**: 85-92.
- Silveira Guido A, BD Perkins. 1975. Biological and host specificity of *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae), a potential biological control agent for water hyacinth. *Environ. Entomol.* **4**: 400-404.
- Tararam AS, Y Wakabara, MB Eqüi. 1993. Hábitos alimentares de onze espécies da megafauna bêmica da plataforma continental de Ubatuba, SP. *Pub. Esp. Inst. Oceanogr.* **10**: 159-167.
- Thomas PA, PM Room. 1986. Taxonomy and control of *Salvinia molesta*. *Nature* **320**: 581-584.
- Ueckert DN, RM Hansen. 1971. Dietary overlap of grasshoppers on sandhill rangeland in northeastern Colorado. *Oecologia* **8**: 276-295.
- Unsicker SB, A Oswald, G Köhler, WW Weisser. 2008. Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia* **156**: 313-324.
- Vieira MF, J Adis. 2000. Aspectos da biologia e etologia de *Paulinia acuminata* (De Geer), 1773 (Orthoptera, Pauliniidae), um gafanhoto semi-aquático, na Amazônia Central. *Acta Amazôn.* **30**: 333-346.
- Vieira MF, AC Santos. 2003. Duração do ciclo de vida de *Cornops aquaticum* (BRUNER, 1906) (Orthoptera: Acrididae: Leptysminae) e aspectos de seu comportamento alimentar na Amazonia central. *Acta Amazôn.* **33**: 711-714.