

ECOLOGY, BEHAVIOR AND BIONOMICS

Feeding Patterns of the Aquatic Grasshopper *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae) in the Middle Paraná River, Argentina

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Abstract

The aquatic grasshopper *Cornops aquaticum* (Bruner) is native to South America and inhabits lowlands from southern Mexico to Central Argentina and Uruguay. This grasshopper is host-specific to aquatic plants of the genera *Eichhornia* and *Pontederia*. The objectives of this study were to analyze the feeding patterns of the aquatic grasshopper *C. aquaticum* in relationship to development stages and sex and to determine the food consumption rate in their host plant, *Eichhornia crassipes*. Samples were collected from April 2006 to May 2007 in different floodplain lakes of the Middle Parana River. The average consumption was greater in the females (0.127 g food/day \pm 0.051) than in the males (0.060 g food/day \pm 0.025). The feces of 361 nymphs and adults of this locust were examined and the most common tissue fragments found were of the water hyacinth (*E. crassipes*). In the initial nymphal stages (I, II and III), an exclusive consumption of *E. crassipes* was registered, while in the IV and V stages the choice included also other macrophytes. In summary, *C. aquaticum* presents polyphagy in the field, feeding on six macrophytes of different classes and families.

Introduction

The diet breadth of grasshoppers varies from strict monophagy to extreme polyphagy. Between these extremes there are species exhibiting varying degrees of selectivity of the food they eat. The essential difference among polyphagous, oligophagous and monophagous species is one of sensitivity to deterrents (Bernays & Chapman 1994). Isely (1944) showed that grasshoppers are conveniently classified as grass-feeders (graminivorous), forb-feeders (forbivorous), or a mix of the two (ambivorous or mixed feeders). Joern (1986) pointed out that the most oligophagous species are grass feeders, while monophagous- and polyphagous species are forb-feeders. Forbs are generally considered a higher

quality food than grasses for most herbivores because of their higher nitrogen, phosphorus and sugar contents (Randolph *et al* 1995).

The feeding patterns of nymphs and adults of a given species of grasshopper are similar, and vary according to seasonal changes in the availability and quality of food (Gangwere 1961), and the processes of learning (Bernays & Bright 1991). The aquatic grasshopper *Cornops aquaticum* (Bruner) is native to South America and inhabits lowlands from southern Mexico to Central Argentina and Uruguay (Adis *et al* 2007). It is host-specific to aquatic plants of the genera *Eichhornia* (Pontederiaceae) and *Pontederia* (Pontederiaceae) (Adis & Victoria 2001, Adis & Junk 2003). Gangwere & Ronderos (1975) suggested that the high degree of specificity of

this grasshopper depends on the mandible type and it is classified as parenchyma-forbivorous because this acrids eats the parenchyma of plants with wide leaves.

Very little is known concerning the Orthoptera species that inhabit moist or wet environments because usually such species do not become pests. Nevertheless, *C. aquaticum* could have potential use for biological control of the water hyacinth, *Eichhornia crassipes* weed, and is planned to be released in South Africa for this purpose (Oberholzer & Hill 2001). This macrophyte is considered the world's most important aquatic weed (Center 1994, Wright & Purcell 1995) because it invades aquatic ecosystems on almost every continent, reproducing rapidly, dispersing easily, displacing indigenous floras, and causing problems in reservoirs, fisheries, irrigation schemes, and transportation routes (Timmer & Weldon 1967, Mitchell & Thomas 1972, Gopal 1987, Ogwang & Molo 2004).

The objectives of this study were to analyze the feeding patterns of the aquatic grasshopper *C. aquaticum* in relationship to development stages and sex and to determine the food consumption rate in their host plant, *E. crassipes*.

Material and Methods

Study sites

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

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

Consumption rate

Cornops aquaticum adult grasshoppers were collected with entomological nets in the spring (November) of 2007. Thirty grasshoppers of each sex were transported to the laboratory to determine their consumption rate of the host plant *E. crassipes*. After 2h of fasting, the grasshoppers were weighed and placed individually in vials with *E. crassipes* leaves. After 24h, the grasshoppers, the food remaining and the feces were oven-dried (at 60°C for 72h or constant mass) and weighed in an OHAUS

balance (accuracy of 10⁻⁵ g).

The biomass gained and the food consumed were calculated from the difference between the initial and the final dry weights. The initial dry weight of the grasshoppers and the leaves were derived from the fresh weight and a conversion factor, which was obtained by dividing the product of the dry weight/fresh weight of 10 grasshoppers of each sex and 50 leaves of water hyacinth with the same characteristics of those used in the experiments (Pereyra 1995).

The consumption rate, growth and feeding efficiency were calculated using the following nutritional indexes (Pereyra *et al* 1996): i) rate of relative consumption: ingested food/mean dry weight of individual/day, ii) rate of relative growth: biomass gained/mean dry weight of individual/day, and iii) efficiency of ingested food conversion: (gained biomass/ingested food) x 100.

Diet composition

The diet composition of *C. aquaticum* was determined by microanalysis of the feces under an optical microscope (400x) according to Arriaga (1981, 1986). Individuals (152 nymphs and 209 adults) were sampled fortnightly with an entomological net from 2006-2007. Each individual collected was immediately placed in a paper tube for a period of 24h and the feces collected, clarified with 10% potassium hydroxide (KOH) and mounted on a slide. Twenty microscope fields were randomly selected for each sample (feces of one individual) where at least one epidermic tissue piece was present (Sheldon & Roger 1978).

The anatomy of leaves of all the macrophytes recorded in the floodplain lakes was previously analyzed. The epidermal tissues were identified based on cellular characteristics (epidermal cells, stomata, trichomes or hairs, etc) and photographs were taken under the optical microscope. The vegetal tissues observed in the feces of *C. aquaticum* were compared with these reference collections to identify the plant species consumed.

Frequency of occurrence was calculated for each food item present based on the number of fields containing this particular food item.

Statistical analysis

The data collected were grouped among four seasons (autumn, winter, spring and summer) to conduct statistical analyses. Factorial design (2^k) was used to test differences in feeding rates between development stages and sex. The individuals that consumed water hyacinth exclusively were excluded in this test. The level of probability that was considered significant was P<0.05. All analyses were conducted using the software SPSS Statistics.

Results

The daily consumption was higher for females (0.127 g food/day \pm 0.051) than for males (0.060 g food/day \pm 0.025). An average consumption of 0.093 g food/day was noted for adults of both sexes.

The female adults presented high values in all nutritional indexes in comparison with the male adults. The relative consumption rate average, relative growth rate and ingested food conversion efficiency obtained for *C. aquaticum* are shown in Table 1.

The feces of 361 grasshoppers were examined (152 nymphs and 209 adults), and plant tissues of six species were identified. The most common tissue fragments found in the feces were of the water hyacinth, representing 90.4% of all samples. Others plant species consumed were *P. repens* (3.6%), *L. peploides* (3.6%), *Panicum* sp., *Polygonum* sp. and one unidentified grass (2.4%). The epidermal structures (epidermal cells, stomas, trichomes or hairs) of the three most consumed plants are shown in Fig 1.

A total of 298 individuals consumed exclusively *E. crassipes*, 52 individuals, *E. crassipes* and other plants and 11 non-*E. crassipes* host plants.

In the initial nymphal stages (I, II and III, n = 51), only *E. crassipes* was consumed, while in the stages IV and V (n = 86) other macrophytes were also consumed (mainly *L. peploides* and *P. repens*). The proportion of non-*E. crassipes* host plants in the diet was greatest in stage VI (n = 15), reaching 40%. The adults' diet composition was dominated by *E. crassipes*, reaching 77.6% in the female individuals (n = 94) and 81.7% in the male individuals feces (n = 115).

The amplitude of diet of *C. aquaticum* is different according to the development state, being the adult females those that present greater niche breadth, consuming the six plants registered in feces (Fig 2)

There were no significant differences between the

Table 1 Nutritional indexes of aquatic grasshopper *Cornops aquaticum*. Data expressed in grams.

	Females	Males
Daily consumption (food plant/grasshopper)	0.127 \pm 0.051	0.060 \pm 0.025
Mean weight of grasshoppers	0.087 \pm 0.008	0.049 \pm 0.005
Increase of daily weight by grasshopper	0.006 \pm 0.004	0.002 \pm 0.001
TCoR (ingested food/mean dry weight of grasshopper/day)	1.462 \pm 0.556	1.241 \pm 0.489
TCrC (gained biomass/mean dry weight of grasshopper/day)	0.071 \pm 0.044	0.049 \pm 0.024
ECl (%) (gained biomass/ingested food) x 100	7.448 \pm 4.831	5.074 \pm 2.535

botanical composition and the stages of development (P = 0.955) and sex (P = 0.251) of *C. aquaticum*, demonstrating that the election of the nutritional items depends neither on the stage of development nor on the sex of the grasshoppers (Table 2).

Discussion

The daily consumption by individual in *C. aquaticum* was greater in females than in males. Similar results available when the daily consumption of aquatic (Amorim & Adis 1994) and terrestrial grasshoppers were evaluated (Gangwere 1959, de Wysiecki 1986, Sánchez & de Wysiecki 1990, Mariottini 2009). In coincidence with Lockwood *et al* (1996), females consume greater amounts of food than males because they have higher protein demands for egg production.

When *E. crassipes* was the host plant, the relative consumption rate of *C. aquaticum* populations of the

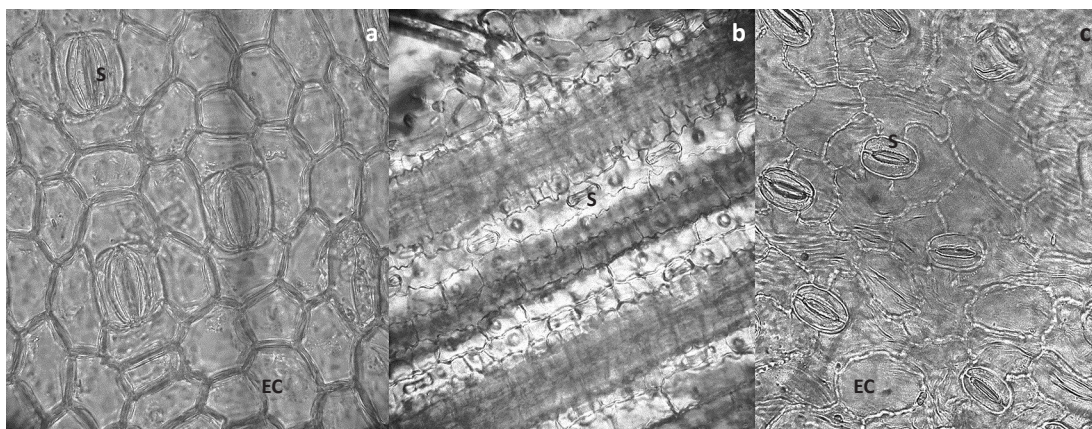


Fig 1 The epidermal structures of the plants more consumed for *Cornops aquaticum*. The photographs were taken under optical microscope (400x). A: *Eichhornia crassipes*, B: *Paspalum repens* and C: *Ludwigia peploides*. S: stoma. EC: epidermal cell. T: trichoma.

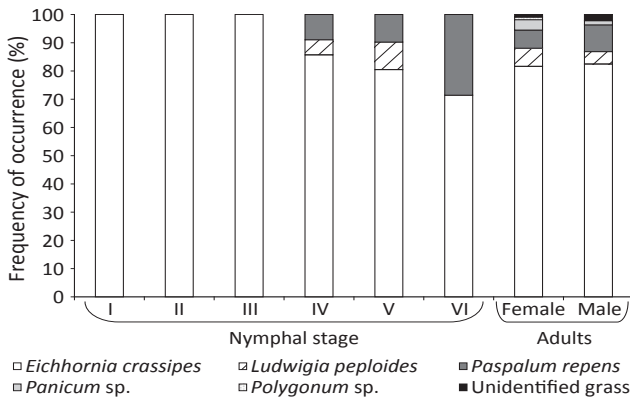


Fig 2 Frequency of occurrence of the different aquatic plants consumed by *Cornops aquaticum* in the different development stages.

Central Amazonia was 0.9 g food/g individual/day, and the individual consumption per day was 0.0522 g in males and 0.0837 g in females (Adis & Junk 2003), recording slightly higher values than in our study. Amorim & Adis (1994) reported a lower relative consumption rate of adult males (0.135 g food/g individual/day) and adult females (0.229 g food/g individual/day) of the semiaquatic grasshopper *Stenacris fissicauda fissicauda* (Bruner) compared to that of *C. aquaticum*. Thus, the consumption capacity of *C. aquaticum* was greater when considering that the dry weight of *C. aquaticum* is greater than that of *S. fissicauda fissicauda*.

Comparing the relative consumption rate obtained, the aquatic grasshopper *C. aquaticum* consumes a larger amount of food than the terrestrial *S. fissicauda fissicauda* and *Dichroplus pratensis* Bruner (Pereyra *et al* 1996). By coincidence, Cyr & Pace (1993) reported that aquatic herbivores consumed greater quantities of biomass than their terrestrial counterparts.

The efficiency of *C. aquaticum* to convert the ingested

food was higher in females than in males, concurring with the results obtained by Sánchez & de Wysiecki (1990) and de Wysiecki & Sánchez (1992) for *D. pratensis*.

Fragments of *E. crassipes* tissues were observed in more than 90% of the diet composition of *C. aquaticum*. Coincidentally, Ferreira & Vasconcellos Neto (2001) also found that 90% of what is consumed by this grasshopper in Brazil is represented by Pontederiaceae. There are several reports of the high specificity of *C. aquaticum* with different genera of the family Pontederiaceae (Silveira Guido & Perkins 1975, Medeiros 1984, Vieira & dos Santos 2003, Lhano *et al* 2005). This relationship may be caused by three different reasons: 1) the water hyacinth is the macrophyte dominant in the Middle Paraná River (Marta 1977, Bayo *et al* 1981); 2) the very low amount of deterrent substances and 3) high concentrations of nitrogen; and 4) the adequate petiole structure (abundant aerenchymatic tissue), allowing optimal conditions for the development of eggs (endophytic oviposition) (Boeger & Adis 2007)

Early instars (I, II and III) of *C. aquaticum* consumed water hyacinth leaves exclusively. This finding agrees with that reported by Sword & Dopman (1999) for *Schistocerca lineate* (Scudder), which represent a more extreme situation in which the early stages are monophagous. However, the later instars and adults become polyphagous. The greater variety of mixed foregut contents in later instars might also suggest their greater mobility (Bernays & Chapman 1994). In contrast, early instars of *Chorthippus parallelus* (Zetterstedt) were observed to feed frequently on three or four of the grass species, suggesting that they require a wider range of grass species (Bernays & Bright 2001).

Bennett (1971, 1974) and Carbonell (1981) demonstrated that *C. aquaticum* could eat another variety of aquatic plant (*Commelina sp.*), but their life cycle is associated with *Eichhornia* because other vegetal species were unsuitable for their endophytic oviposition.

In an experimental study on feeding habits of *C. aquaticum*, the acceptance of six aquatic macrophytes species was detected, indicating that these plants can represent alternative resources, but are not essential for the development of the species (Vieira & dos Santos 2003). *Ludwigia sp.* and *P. repens* are the only plants found in this study, what confirms that the feeding pattern of an herbivore insect in its natural environment would differ from the laboratory conditions, as suggested elsewhere (Bernays & Lewis 1986, Bernays & Simpson 1990, Bernays & Chapman 1994).

The specificity of *C. aquaticum* on *E. crassipes* has been determined for populations of the Pantanal wetlands in Brazil (Lhano *et al* 2005), but those in South Africa also feed on cultivated plants such as *Canna indica* and *Musa paradisiaca* (Oberholzer & Hill 2001).

Table 2 Results obtained of the factorial design (2^k) realized to *Cornops aquaticum* according to sex and stage of development.

Tests of the effects inter-subjects					
Dependent variable: <i>Eichhornia crassipes</i>					
Origin	Sum of square type III	gl	Quadratic mean	F	P
Model	11.013 ^a	4	2.753	28.415	.000
Sex	.131	1	.131	1.355	.251
Stage	.000	1	.000	.003	.955
Sex * stage	.160	1	.160	1.654	.206
Error	3.973	41	.097		
Total	14.986	45			

a. R squared = .735 (R squared corrected = .709)

An important preference for monocotyledonous plants (approximately 95%) was observed in the diet composition of *C. aquaticum* through the whole year in contrast to that revealed by Chapman (1990) that the polyphagous herbivores consume greater proportions of dicotyledons.

In summary, *C. aquaticum* presents polyphagy in the field, feeding on six different species of macrophytes of various classes and families (monocotyledonous: Pontederiaceae and Poaceae; dicotyledonous: Onagraceae and Polygonaceae). Although *C. aquaticum* is considered specific to the genus *Eichhornia*, this grasshopper also feeds on other plant species in the laboratory and in the field. Its acceptance of several plant species in the absence of the preferred host plant could indicate that it is the host plant's relative abundance in the field that determines the *C. aquaticum* diet breadth.

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