

## ECOLOGY, BEHAVIOR AND BIONOMICS

### Host Plants of the Grasshopper *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae) in the Wetland of Poconé, MT, Brazil

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#### Plantas Hospedeiras de *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae) no Pantanal de Poconé-MT

RESUMO – O gafanhoto *Cornops aquaticum* (Bruner) vive permanentemente sobre macrófitas aquáticas em áreas alagáveis. Suas plantas hospedeiras e sua preferência alimentar foram determinadas a partir de observações de campo, análise de conteúdo intestinal e testes alimentares em laboratório. A especificidade para oviposição foi estudada através da coleta de macrófitas cujos pecíolos potencialmente conteriam ovos desse gafanhoto. Parte da amostra foi dissecada em laboratório e o restante mantido em caixas d'água teladas para se verificar a eclosão de ninfas. *C. aquaticum* alimentou-se e ovipositou em *Eichhornia azurea* e *Pontederia cordata* (Pontederiaceae) no campo. Dos 140 intestinos analisados 75% continham tecidos de Pontederiaceae. No laboratório, entretanto, os gafanhotos aceitaram espécies de outras famílias. Os testes de aceitabilidade mostraram que foram aceitas 16 das 19 espécies oferecidas separadamente. As sete espécies de plantas aceitas com maior frequência foram selecionadas para as medidas das taxas de alimentação. Não houve diferença significativa entre o consumo das mesmas pelos gafanhotos. Quando quatro ou cinco espécies foram oferecidas simultaneamente, as espécies hospedeiras do campo nem sempre foram preferidas. O fato de maior número de espécies de plantas ter sido aceito no laboratório é um bom indicativo de que o espectro de plantas hospedeiras deve estar sendo determinado por outros fatores ecológicos além da química da planta. A seleção de plantas hospedeiras por *C. aquaticum* pode estar relacionada principalmente à abundância relativa das espécies de macrófita no campo e à proteção contra predação que esta oferece. Se considerada apenas a parte emersa das macrófitas, *E. azurea* representava o recurso mais abundante nas áreas alagadas. Além disso, a coloração críptica do gafanhoto sobre esta espécie possivelmente diminui o risco de predação. Portanto, embora seja potencialmente polífago, *C. aquaticum* apresenta uma considerável oligofagia no campo, alimentando-se e ovipositando sobre três espécies da família Pontederiaceae.

PALAVRAS-CHAVE: Herbivoria, gafanhoto, dieta, planta-hospedeira.

ABSTRACT – The grasshopper *Cornops aquaticum* (Bruner) lives permanently on aquatic macrophytes in floodplains of tropical South America. Its host plants and feeding preference were determined by field observations, crop analysis and feeding tests in the laboratory. Macrophytes were sampled and their petioles were examined for potential egg deposition in order to reveal host plant specificity. Sub-samples were dissected in the laboratory and eggs were counted directly whereas the rest of the sample was kept in net-covered water tanks aiming to verify hatching of nymphs. *C. aquaticum* fed and oviposited on *Eichhornia azurea* and *Pontederia cordata* (Pontederiaceae) in the field. Out of 140 fore-guts analyzed from free-living grasshoppers, 75% contained Pontederiaceae tissues. In the laboratory, however, it accepted plant species from other families. Tests of acceptance revealed that from 19 plant species offered, one by one, 16 were accepted. The seven plant species, which were accepted with highest frequency, were selected for tests of feeding rates. These rates were equal for all seven species. When four or five food plant species were offered simultaneously, the host species were not always preferred. The fact that in the laboratory more host-plant species were accepted than in the field indicates that the host range in the field is determined by other ecological factors than the plant chemistry. Host plant

selection by *C. aquaticum* can be related to the relative abundance of the macrophyte species in the field and to the protection, which they offer against predation. Considering the emerging parts of the macrophytes, *E. azurea* represents the most abundant resource in the floodplains. Moreover, the cryptic coloration of the grasshopper on *E. azurea* lessens predation risk. That is why, apart from being potentially polyphagous, *C. aquaticum* presents a considerable oligophagy in the field, feeding on few species of Pontederiaceae.

KEY WORDS: Insecta, herbivory, diet.

The selection of food sources in Acridoidea is governed by a complex series of factors, which include the availability and development stage of the host plant as well as the behavior, physiology and ecology of the insect (Gangwere 1961, Mulkern 1967, Otte & Joern 1977). Besides, according to Bernays & Chapman (1978), the chemical composition of the plant is the main factor. The feeding habits of nymphs and adults of a given grasshopper species are similar and may vary according to seasonal changes in the availability and condition of the food source (Gangwere 1961), and learning processes (Bernays & Bright 1991). The Acridoidea are, with no exceptions, phytophagous and the majority of species is polyphagous (Bernays & Bright 1991, 1993) and lay their eggs in the soil or on superficial debris, but some species oviposit inside the leaves or plant tissues (braker 1989).

*Cornops aquaticum* (Bruner) is a semi-aquatic grasshopper with endophytic oviposition and is widespread from Northeast Argentina and Uruguay to Mexico (De Zolessi 1956). The species presents a series of adaptations to the aquatic environment (Bentos-Pereira & Lorier 1991) living permanently on floating plants of the genus *Eichhornia* (Pontederiaceae), more specifically on *E. crassipes* (Mart.) Solms and *E. azurea* (Sw.) Kuntl (Bennet 1968, 1970; Mitchell & Thomas 1972) probably because other plants do not provide them an adequate substrate for oviposition (Carbonell 1981). Despite being indicated for biological control of *E. crassipes* (Bennett & Zwolfer 1969, Andres & Bennett 1975, Silveira-Guido & Perkins 1975) little is known about this grasshopper's use of their host plants.

In this research work, *C. aquaticum* was observed considering some issues related to its selection of host plants, such as: 1) which are the host plants used for feeding and oviposition in the field? 2) Is there temporal difference in the feeding preference? 3) Are there differences between feeding preference (among individuals and between sexes) in the laboratory and in the field?

## Material and Methods

**Area of Study.** Field studies were carried out at Fazenda Ipiranga (16° 24' S and 56° 40' W) located at the Cuiabá/Bento Gomes/Paraguaizinho Wetland, also known as Wetland of Poconé according to the Radambrasil Project / 1982 (Allen & Valls 1987) in an area that remains humid or flooded during the dry season, locally called as "Corixo Birici", during 1993. The Poconé Wetland presents well defined dry and rainy seasons. The flooding generally occur in December, when rainfalls are intense, reaching its maximum by February or March. In 1993, the heaviest rainfalls occurred in February

(370 ml) and the overflow extended until early May reaching the level of 1.4 m. From that month on, with the rainfall reduction, the draining started and from July to November a characteristic dry period with low monthly pluviosity occurred, with a minimum of 0 ml of rain in July and the level of the water reaching 20 cm in November. Evidently, variations of these periods occur from year to year. The air average temperature varied from 18.2°C in July to 25.0°C in January. Between May and October, the thermal amplitudes were large, with a variation of 18°C (min. 9°C and max. 27°C) occurring on a single day in July. The values for the monthly average relative humidity do not change much remaining between 83.4% and 91.6%. Although, between May and October the minimum values had been lower.

**Natural History.** During 1993, weekly sections of direct observations on resting and feeding sites, movement and behavior of *C. aquaticum* as well as on presence of predators were carried out.

**Feeding Preference in the Field.** To evaluate the feeding preference of *C. aquaticum* and to compare this behavior between wet and dry seasons as well as between sexes, 70 grasshoppers (35 males and 35 females) were collected in May, 1993 (wet season) and again in October, 1993 (dry season). These samples were all kept in 70% alcohol. In the laboratory, an analysis of the insect fore-gut contents was performed according to the technique described by Isely & Alexander (1949) and Mulken & Anderson (1959). To identify the intestinal content, microscope slides of plant tissues from aquatic macrophyte species of emerging leaves found in the area as well as microscope slides of the fore-gut contents of grasshoppers fed in the laboratory with the same plant species were prepared and compared with those containing the intestinal content of grasshoppers collected in the field. All the content of each fore-gut was placed on a single slide due to its reduced size. All slides were photographed. Data on relative abundance of macrophyte species found in the field were obtained from Anajde Lemes do Prado (Doctor degree thesis in preparation) using the sites method (Mantovani & Martins 1990) along a 100 m transect on gradient of flooding starting from the "corixo". To calculate the relative frequency of the macrophyte species only the emerging parts of the plants (those parts above the water surface), which represented a potential source of food for the grasshopper, were considered. The comparison between frequency of plant species in the field and in the intestines of the grasshoppers was done using the Qui-square test.

**Feeding Tests in the Laboratory.** For the acceptability and feeding preference tests, about 20 grasshoppers and samples of macrophytes were weekly collected from January to December, 1993. The insects were collected using an entomological net and placed into screened cages. These 25 cm x 27 cm x 40 cm cages were built with wooden frames and had a glass sheet in one side to allow visualization and a small door on the top side for insects and plants handling. The macrophytes were taken to the laboratory using water-filled bowls and plastic bags. These samplings were performed in the day preceding the acceptability and feeding preference tests. Previous to each test the grasshoppers were kept in the cages with no feeding for 24h. This period of time was rigorously respected due to the fact that insects deprived of food and water for long periods of time become more stressed and less selective. Besides, the order of preference achieved under these conditions may reflect the need of water balance and not exactly a feeding preference (Emlen 1966, Lewis 1982, Bernays 1991). Each insect was used only once to avoid the possibility of learning that could mislead results (Szentesi & Bernays 1984, Lee & Bernays 1990).

**Feeding Tests in the Laboratory – Acceptability.** In order to verify if *C. aquaticum* would feed on other species in the absence of the host plant, acceptability tests were carried out. The term acceptability, according to Singer (1986), is used to describe the possibility that a plant will be accepted when found. From the 48 aquatic macrophyte species present in the area (Prado *et al.* 1994), 19 were selected (Table 1). These species had emerging parts, i.e., structures exposed above the water sheet, which could serve as source of food for the grasshopper. At every week, from January to May, each plant species brought from the field were separately fed to grasshoppers individually kept in cages. The whole plant was placed in the cage on a polyethylene tray containing water collected in the field. At least 10 replications for each plant species were used, thus using a minimum of 190 grasshoppers. The test lasted until the plant was accepted or, in case of rejection, until the death of the grasshopper. Tests in which the insects died in the first two days were excluded from results since death could be attributed to stress and not necessarily to rejection. The following qualitative categories of consumption, according to Johnson and Mündel (1987),

Table 1. Relative frequencies of macrophytes species in the field (Frc) and in the fore-gut content of *C. aquaticum* (Frg) during the draining and dry seasons at the “Corixo Birici”, Ipiranga Farm, Poconé Wetland – 1993, acceptability (Ac) and consumption categories (Co) per species in the laboratory (0 = null; 1 = slight; 2 = moderate; 3 = severe)

Family	Species	Draining season		Dry season		Ac	Co
		Frc <sup>(1)</sup>	Frg	Frc	Frg		
Acanthaceae	<i>Justicia laevilinguis</i>	0	0	0	0	9	1
Alismataceae	<i>Echinodorus paniculatus</i>	0	0	6,3	0	9	3
Alismataceae	<i>Echinodorus sp.</i>	2,5	1,9 <sup>(3)</sup>	0	0	10	3
Amaranthaceae	<i>Alternanthera phylloxeroides</i>	0	0	3,1	0	1	0
Cyperaceae	<i>Eleocharis cf. acutangular</i>	0	1,9 <sup>(3)</sup>	0	0	9	3
Cyperaceae	<i>Eleocharis cf. elegans</i>	0	0	0	0	9	3
Cyperaceae	<i>Eleocharis cf. minima</i>	0	0	0	0	9	3
Convolvulaceae	<i>Ipomoea carnea fistulosa</i>	0	0	0	0	0	0
Convolvulaceae	<i>Ipomoea cf. aquatica</i>	0	0	0	0	0	0
Euphorbiaceae	<i>Caperonia castaneifolia</i>	2,1	0	0	0	9	3
Hydrophyllaceae	<i>Hydrolea cf. spinosa</i>	10,4	0	0	0	9	1
Lamiaceae	<i>Hyptis cf. lorentziana</i>	0	0	0	0	1	1
Memnyanthaceae	<i>Nymphoides aff. indica</i>	2,1	0	0	0	1	0
Onagraceae	<i>Ludwigia inclinata</i>	25,0	0	9,4	0	10	1
Onagraceae	<i>Ludwigia sedioides</i>	6,3	0	18,8	0	5	1
Poaceae	<i>Hymenachne amplexicaule</i>	4,2	0	0	0	-	-
Pontederiaceae	<i>Eichhornia azurea</i>	31,3	96,3	37,5	98,0 <sup>(2)</sup>	10	3
Pontederiaceae	<i>Pontederia cordata</i>	6,3	0	6,3	0	10	3
Rubiaceae	<i>Diodia cf. kuntzii</i>	0	0	0	0	3	1
Salviniaceae	<i>Salvinia cf. auriculata</i>	0	0	15,6	0	1	1

(1) Calculation performed from unpublished data provided by Anajde Lemes do Prado. Null frequencies indicate that the species were not present only at the Prado transect, although sparsely present in the area of study of the present research work.

(2) Not possible to distinguish between *E. azurea* and *P. cordata* in the fore-gut content of *C. aquaticum*.

(3) Not possible to distinguish the species, only the genus in the fore-gut content of *C. aquaticum*.

were attributed: null (0); slight (1); moderate (2); and severe (3). The association between the consumption categories and acceptance frequency of each species was tested by the Kendall method (Conover 1980).

#### Feeding Tests in the Laboratory – Feeding Preference.

From the eight most consumed and most accepted species in the previous test (Table 1), three presented low abundance in November and December, since they occur preferentially during the draining and dry seasons. Therefore, only five species were used in these tests: *E. azurea* and *P. cordata* (both Pontederiaceae); and *Eleocharis minima*, *Eleocharis cf. elegans*, and *Eleocharis cf. acutangular* (all Ciperaceae). A total of four tests were carried out. In each one, the plant species were simultaneously offered. To guarantee the same proportion of each food source in a given cage the plants offered had approximately the same biomass. Five replications for males and five replications for females were carried out with a single grasshopper per cage. The first test was conducted in November (dry season) in which the species *E. azurea*, *P. cordata*, *El. minima* and *El. cf. elegans* were offered simultaneously. After 24h, signs of herbivory were recorded on each plant providing data on frequency of herbivory for each plant species. In the flooding period (December), the species *El. cf. acutangular* was added to test the effect of the increment of food items offer on the herbivory preference (test 2). To evaluate temporal variations on *C. aquaticum* preference, these two tests were repeated in the flooded season (tests 3 and 4). For the tests 2, 3 and 4 the following data were recorded after a 24h period: a) the first macrophyte species visited; and b) the species showing feeding signs, as in test 1. During these tests (2 to 4) data on the position of the grasshoppers inside the cages were recorded every two hours intervals. This frequency of individuals on each plant species allowed to verify the use of the plant not only as a feeding item but as resting sites and possible protection sites for the grasshoppers as well. Data on frequency of grasshoppers on each plant species (tests 2 to 4) as well as on the frequency of feeding signs on each plant species (for all tests) were statistically analyzed using the Qui-square test.

**Specificity for Oviposition.** The specificity of *C. aquaticum* for oviposition was verified by weekly field observation besides dissection and maintenance in laboratory of macrophytes brought from the field. Samples of these plants, whose petioles dimension might harbor *C. aquaticum* oviposition, were weekly collected in the field from January to December. In the laboratory, measurements such as total length and length and diameter of the petiole of part of the leaves collected were taken in order to verify the preference for size of petioles for oviposition. These plants were than dissected to detect the presence of egg masses and dimension and number of eggs. After dissection the plants were oven-dried at 70°C for dry weight data record. Part of the samples brought from the field were maintained in the laboratory for observation of nymphs hatching. In order to verify the best conditions for maintenance of the different species, the plants were arranged into 500 L net-covered water tanks or in aquariums and polyethylene trays at room temperature and natural light intensity.

## Results

**Natural History.** *C. aquaticum* was frequently found on patches of *E. azurea* and *P. cordata*, flying away from them only when disturbed. Generally the grasshoppers used to concentrate on clusters of the first species being also found in a more sparse manner on area of *P. cordata*. These grasshoppers rested and fed on petioles as well as on the leaf sheets, making easily identifiable marks, characterized by longitudinal scrapings of the epidermis. Besides the mentioned host species marks very similar to those produced by *C. aquaticum* were also found on the macrophytes *El. cf. elegans* and *Eleocharis paniculatus*. These marks were well differentiated from those caused by other groups of herbivorous insects present on the plants such as Coleoptera and other Orthoptera.

When disturbed, the insects used to hide behind petioles and leaves or fly to other plants located a few meters away. The displacement was generally small. In sites where the host plants were concentrated, this displacement was approximately 3 m. Although, in areas of lower macrophytes density, they used to fly up to 10 m. Displacements between distant patches were not observed. They were rarely seen out of flooded areas, even on host plants which were located on recently dried sites.

Either males or females were difficult to visualize due to their cryptic coloration. Many times it was necessary to provoke some disturbance in the environment in order induce them to fly and to be seen. Both are green, although the males possess a narrow yellow stripe on the sides of the head and pronotum. Males are also smaller and faster than females. These grasshoppers were more visible on *P. cordata* due to the architecture of the plant. This species has longer and thinner petioles as well as smaller leaves than *E. azurea*. Evidently the denser was the plant population the more difficult was to locate the grasshoppers.

During the flooded and part of draining periods (January to May) males and females were green and during the dry period they changed color becoming brown. Although food was available during this period, mortality was high being common to find several dead grasshoppers on the macrophytes. During the dry season *E. azurea* leaves also became brown even in flooded areas.

Concerning possible *C. aquaticum* predators, predation attempts by fish were observed when the grasshoppers dived. Other potential predators were observed in the field. Some birds such as “cafezinho” (*Jacana jacana*) and “bem-te-vi” (*Pitangus sulphuratus*) were seen feeding on invertebrates on the aquatic macrophytes.

**Feeding Preference in the Field.** From a total of 140 fore-guts analyzed, it was possible to identify the contents of 105 (75%). Out of these, 102 contained Pontederiaceae tissues (97%), two contained *Eleocharis* tissues and one contained *Echinodorus* tissues. Only one species found in the fore-gut of a single male collected during the draining period was not identified. The remaining 34 microscope slides were too much damaged being difficult the recognition of the plant tissues.

The structures of *E. azurea* could not be distinguished from *P. cordata* on the slides containing fore-guts of

grasshoppers collected in the field. Although these differences were clear when slides of fresh tissues of both species were examined. The distinction between these species and the other species present in the area, however, was easily done.

The fore-guts of grasshoppers collected during the draining period (n=54) and dry period (n=51) contained 96.3% and 98% of Pontederiaceae tissues (*E. azurea* and *P. cordata*), respectively. The majority of males or females consumed Pontederiaceae in the field (Fig. 1).

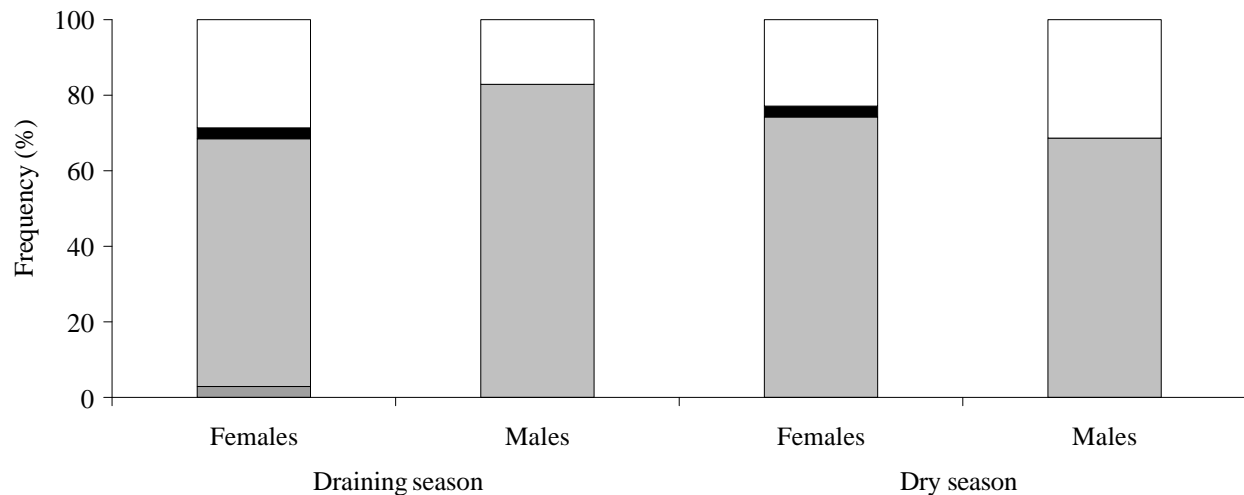


Figure 1. Percentage of aquatic macrophyte species in the fore-gut contents of males and females *C. aquaticum* collected during the draining and dry seasons at the Poconé wetland, state of Mato Grosso, Brazil, in 1993. (Pontederiaceae: gray; *Eleocharis* sp.: black; *Echinodorus* sp.: striped; and non-identified material: white)

When absolute frequencies of macrophyte species in the field were compared with those found in the grasshoppers' fore-guts the differences were highly significant either in the draining period ( $\chi^2 = 87$ ; gl = 19;  $P < 0.001$ ) or dry period ( $\chi^2 = 62.25$ ; gl = 19;  $P < 0.001$ ) indicating feeding preference. The most frequent macrophyte species in the field either in the dry season or in the draining season was *E. azurea* (Table 1), which formed dense patches that practically covered all the flooded area.

**Feeding Tests in the Laboratory – Acceptability.** Out of 19 macrophyte species pertaining to 13 families, 16 species pertaining to 12 families were accepted and from these only seven were abundantly consumed (Table 1). The consumption categories attributed were positively correlated to the frequency of acceptance of the macrophyte species by the grasshopper, i.e., the most frequently accepted plants were also the most damaged ones ( $\tau = 0.784$ ;  $n = 19$ ;  $P < 0.01$ ). Generally, when the grasshopper was placed on the plant it would move the antennae, touching the leaf with them and than with its mouth apparatus. In some cases, as with *Ipomea*, as the insect was placed on the plant, it would immediately jump to the cage walls. Males and females rejected *Alternanthera phylloxeroides*, *Ipomea carnea* and *Ipomea* cf. *aquatica*. Beside these species the males also rejected *Hyptis* cf. *lorentziana*, while females also rejected

*Nymphoides* aff. *indica* and *Salvinia* cf. *auriculata*.

The more frequently accepted species were *E. azurea*, *P. cordata*, *Ec. paniculatus* and *Ludwigia inclinata* (Fig. 2). However, considering the consumption category the last one was only slightly consumed. The most consumed species were the first three already cited, followed by *Caperonia castanaefolia*, *Echinodorus* sp., *El. cf. acutangular*, *El. cf. elegans* and *El. minima*. Although, these last ones had not always been accepted.

#### Feeding Tests in the Laboratory – Feeding Preference.

The first plant species visited by the females was *E. azurea* (tests 2, 3, and 4) while the males initially visited, in each test, different species: *El. cf. elegans* in the test 2; *El. minima* in the test 3; and *E. azurea* in the test 4 (Fig. 3a, 4a, 5a).

In the choice of the host plant for feeding (herbivory marks) there were significant differences between sexes only in the test 1 (dry season). In this test males preferred *P. cordata* and *E. azurea* while females preferred *El. cf. elegans* and *El. minima* ( $\chi^2 = 10.65$ ; gl = 3;  $0.001 < P < 0.005$ ) (Fig. 6). Although a female preference for *E. azurea* in the tests 3 and 4 (flooded period) was detected the difference between males and females were not significant (test 2:  $\chi^2 = 4.16$ ; gl = 4;  $0.50 < P < 0.25$ ; test 3:  $\chi^2 = 3.57$ ; gl = 3;  $0.50 < P < 0.25$ ; test 4:  $\chi^2 = 0.87$ ; gl = 4;  $P < 0.99$ ) (Fig. 3b, 4b, 5b).

When feeding preference was analyzed independently of sex, there was no significant difference of herbivory marks on the different macrophyte species. Individuals fed on all plant species offered (test 2:  $\chi^2 = 3.5$ ; gl = 4;  $0.50 < P < 0.25$ ; test 3:  $\chi^2 = 3.57$ ; gl = 3;  $0.50 < P < 0.25$ ; test 4:  $\chi^2 = 1.99$ ; gl = 4;  $0.75 < P < 0.50$ ) (Fig. 3b, 4b, 5b).

Concerning frequency of grasshoppers on macrophyte species, in the tests 2 and 4 (dry x flooded periods) there was no significant differences between sexes (test 2:  $\chi^2 = 1.96$ ; gl = 4;  $0.75 < P < 0.50$ ; test 4:  $\chi^2 = 5.98$ ; gl = 4;  $0.25 < P < 0.10$ ). Both were found with higher frequency on *E. azurea* and *P.*

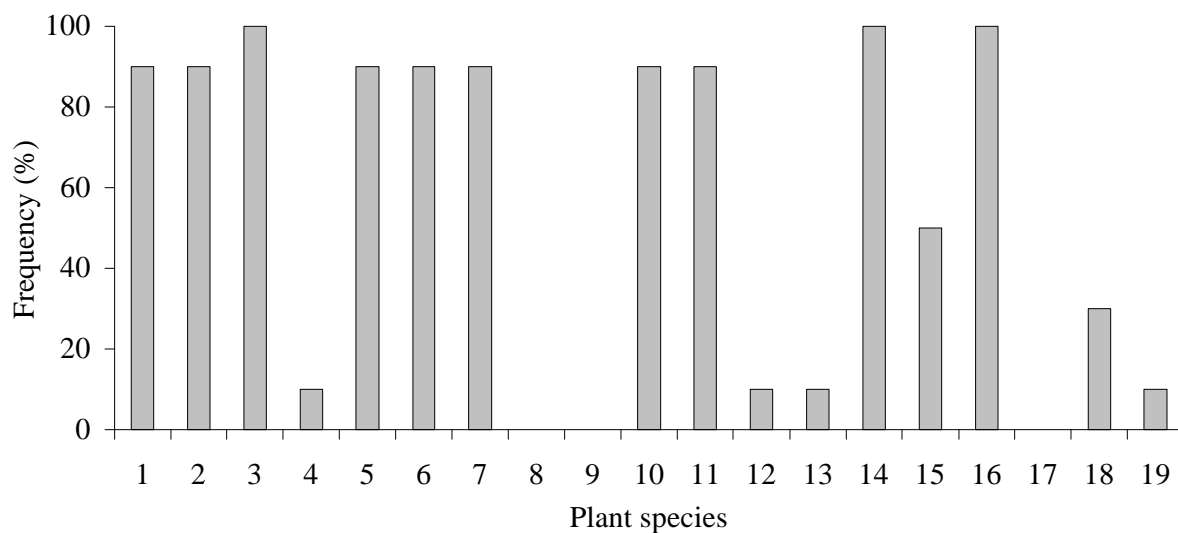


Figure 2. Frequency of acceptability of aquatic macrophyte species by *C. aquaticus* in laboratory: 1. *J. laevilinguis*; 2. *Ec. paniculatus*; 3. *Echinodorus sp.*; 4. *A. phylloxeroides*; 5. *El. cf. acutangular*; 6. *El. cf. elegans*; 7. *El. cf. minima*; 8. *I. carnea fistulosa*; 9. *I. cf. aquatica*; 10. *C. castaneifolia*; 11. *H. cf. spinosa*; 12. *H. cf. lorentziana*; 13. *N. aff. indica*; 14. *L. inclinata*; 15. *L. sedioides*; 16. *E. azurea*; 17. *P. cordata*; 18. *D. cf. kuntzii*; 19. *S. cf. auriculata*.

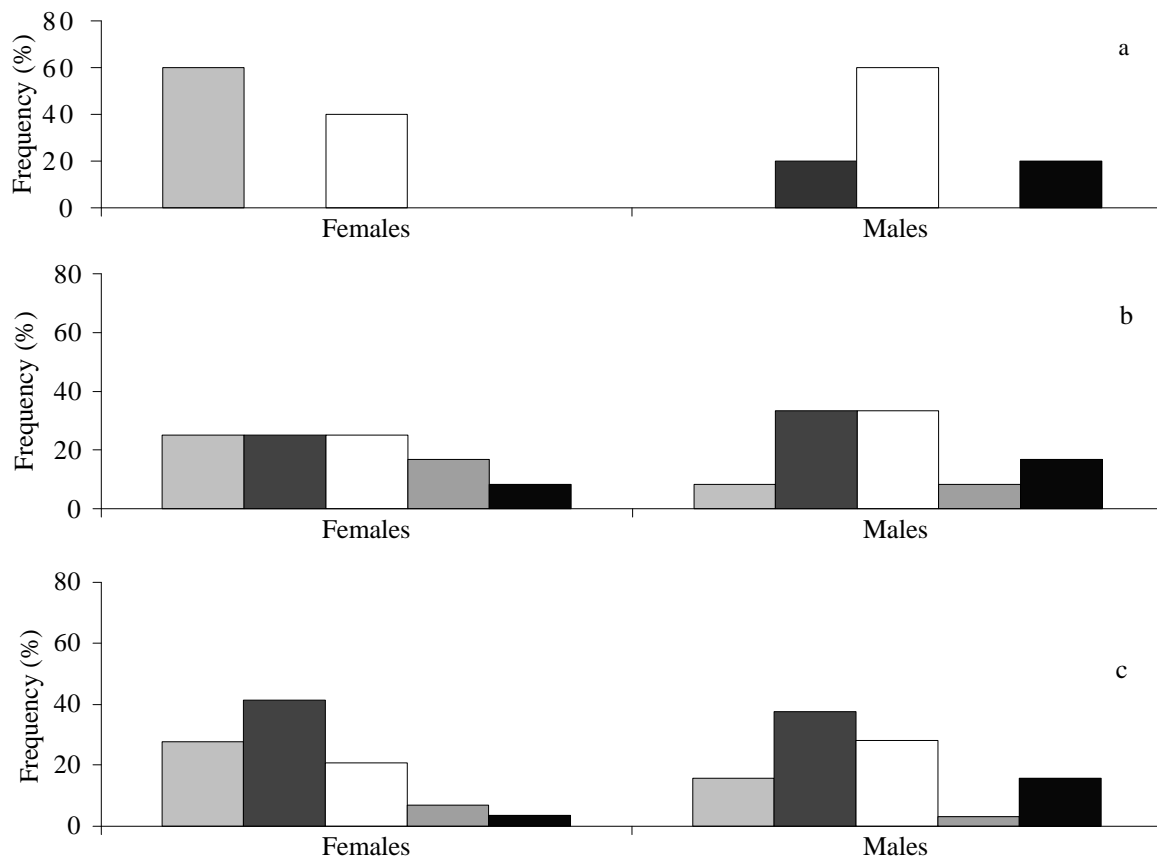


Figure 3. Preference in the laboratory – test 2: percent frequency of (a) first choice (n=5 for both sexes), (b) herbivory (n=12 for both sexes), (c) grasshoppers on each species of macrophyte (females, n=29; males, n=32 (*E. azurea*: gray; *P. cordata*: black; *El. cf. elegans*: white; *El. cf. minima*: stripped; *El. cf. acutangular*: dotted)

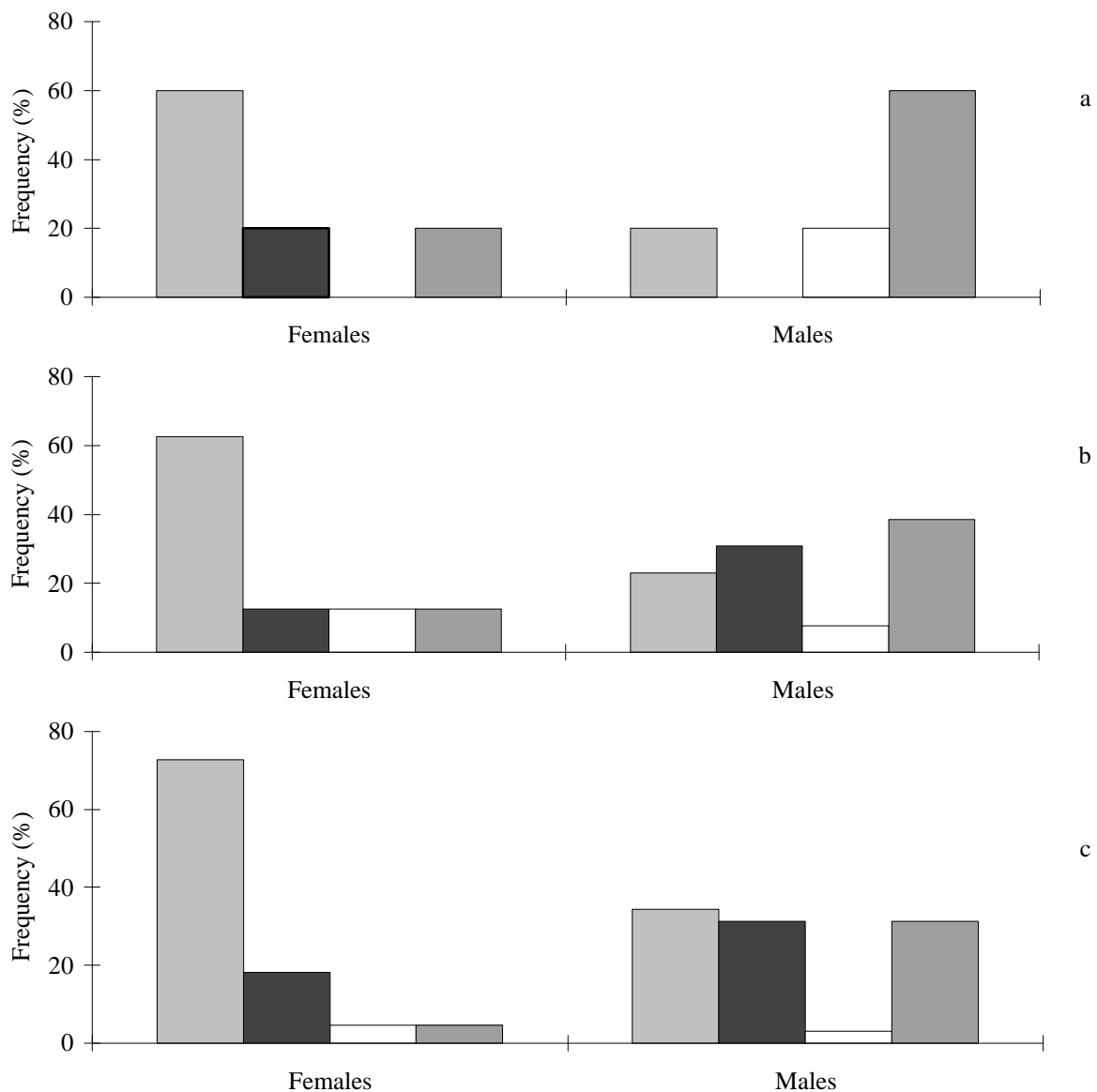


Figure 4. Preference in the laboratory – test 3: percent frequency of (a) first choice (n=5 for both sexes), (b) herbivory (females, n=8; males, n=13), (c) grasshoppers on each species of macrophyte (females, n=23; males, n=32 (*E. azurea*: gray; *P. cordata*: black; *El. cf. elegans*: white; *El. cf. minima*: stripped))

*cordata* (Fig. 3c, 5c). Only in the test 3 the difference was significant; females preferred *E. azurea*, while males fed equally on *E. azurea*, *P. cordata* and *El. minima* ( $\chi^2 = 9.32$ ;  $gl = 3$ ;  $0.01 < P < 0.05$ ) (Fig. 4c). When the analysis was performed independently of sex, the frequency on *E. azurea* was significantly higher in the test 3 ( $\chi^2 = 23.78$ ;  $gl = 3$ ;  $P < 0.01$ ) (Fig. 4c) and in the test 4 ( $\chi^2 = 51.15$ ;  $gl = 4$ ;  $P < 0.01$ ) (Fig. 5c), and on *P. cordata* in the test 2 ( $\chi^2 = 22.19$ ;  $gl = 4$ ;  $P < 0.01$ ) (Fig. 3c).

**Specificity for Oviposition in the Laboratory.** It was not possible to observe oviposition in the field. In the plants dissected in the laboratory two egg masses were found on *P. cordata* among 477 leaves dissected, and none on *Ec.*

*paniculatus* and *E. azurea* (Table 2). It was not possible to establish any correlation between size of petioles and preference for oviposition due to the reduced number of egg masses found.

Hatching of nymphs was not observed on the plants kept in aquariums in the laboratory. These plants decayed in a few days, mainly *E. azurea*, probably due to the pruning needed to reduce the excessive size of the branches. In the water tanks, however, the macrophytes remained vigorous and nymphs were observed on *E. azurea* and *P. cordata*. These nymphs completed their development in the water tanks up to the adult phase.

In the feeding rates tests, previously cited, one female oviposited on the petiole of *P. cordata* and on four occasions

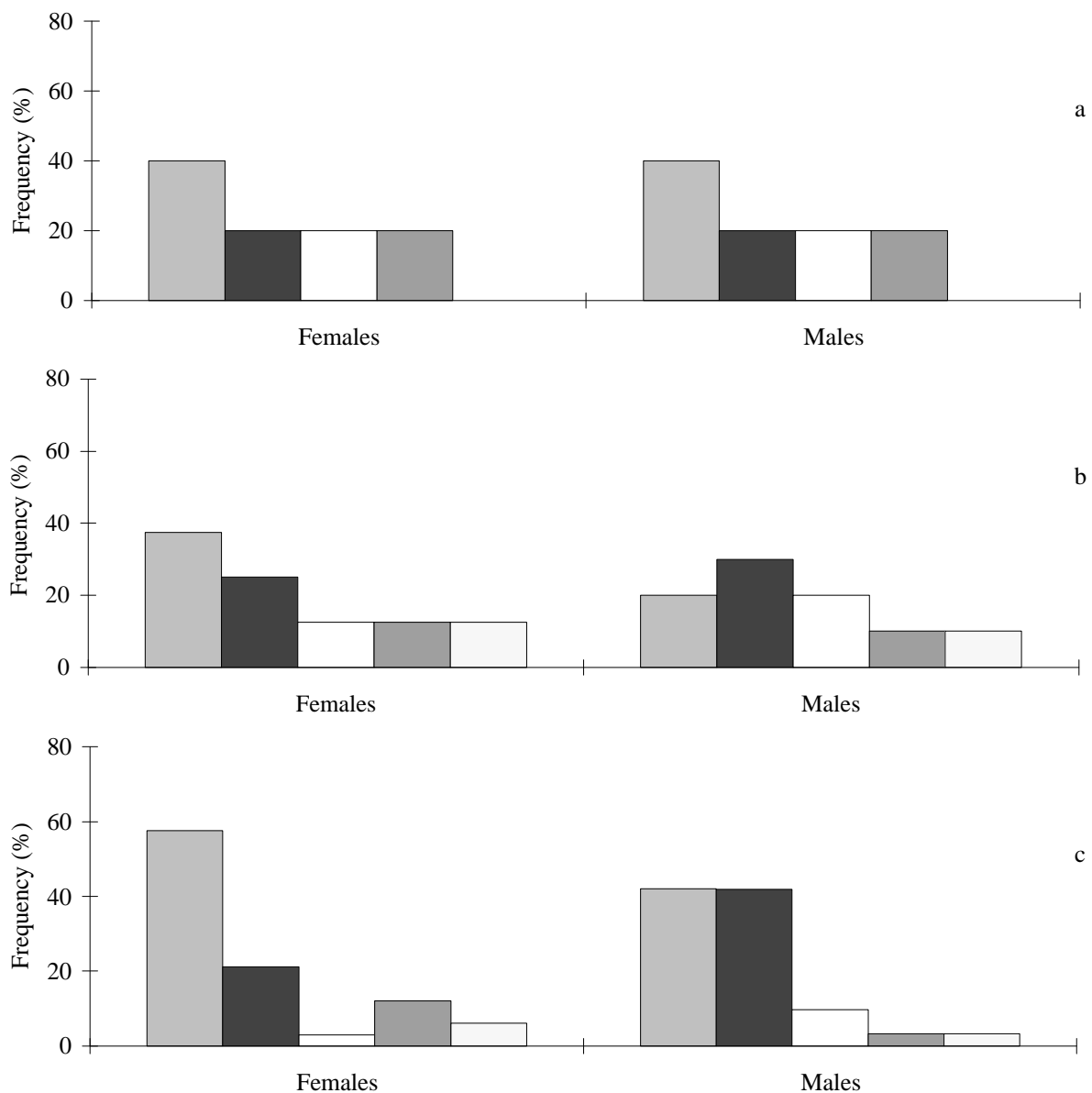


Figure 5. Preference in the laboratory – test 4: percent frequency of (a) first choice (females, n=5; males, n=9), (b) herbivory (n=12 for both sexes), (c) grasshoppers on each species of macrophyte (females, n=33; males, n=31 (*E. azurea*: gray; *P. cordata*: black; *El. cf. elegans*: white; *El. cf. minima*: striped; *El. cf. acutangular*: dotted)

the females deposited their eggs on the walls of the cages when the plant species tested were *E. azurea*, *P. cordata*, *El. cf. acutangular* and *El. cf. elegans*.

### Discussion

Selection of *E. azurea* as host plant may be related to a higher protection against predation. *C. aquaticum*, besides using the architecture of the plant to hide, also present cryptic coloration. Its visualization on *E. azurea* leaves is difficult mainly if the leaf density is large. Relations between coloration and habitat were also found for other grasshoppers (Gill 1979, Eterovick *et al.* 1997).

The *C. aquaticum* color change during the dry season guarantees its cryptic characteristic, since the leaves of *E. azurea* also become brown during the dry season. This grasshoppers' color change is probably not related to the age of the insect once senescent insects during the flooded season do not present this color alteration. The color of grasshoppers in a general way may be affected by the availability of vitamins in the feeding diet, particularly by the lack of beta-carotene. Carotenoids probably contribute directly for the constitution of green and yellow colors and its absence may result in insects with abnormal coloration (Bernays & Chapman 1978). Changes in the plant quality during the dry season (Da Silva *et al.* 1994) may be responsible by *C. aquaticum* color changes.



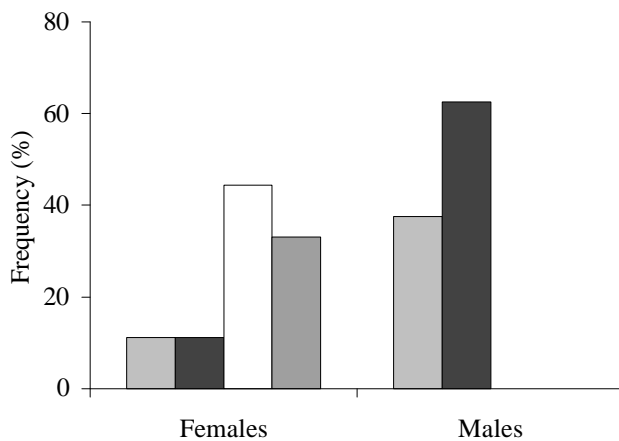


Figure 6. Preference in the laboratory – test 1: percent herbivory frequency (females, n=9; males, n= 8) (*E. azurea*: gray; *P. cordata*: black; *El. cf. elegans*: white; *El. cf. minima*: stripped)

The probability of the plant in being found either in space as in time is determinant on the choice of a host plant (Feeny 1976, Miller & Strickler 1984). The spatial predictability seemed to be determinant on the host range of *C. aquaticum*, which fed on *E. azurea*, the most abundant food source in the field and the predominant species in almost all water ponds of the Poconé Wetland (Da Silva 1989). According to the Emlen (1966) model, even if another species was richer and more efficiently used by a given insect, the most common species would still be preferred. This was observed by Rowell (1985) for two allopatric species of grasshoppers of the genus *Rhachicreagra*.

The alteration of plant communities in the area is intense during flooded, draining, dry and flooding seasons (Prado *et al.* 1994). The plant species alternate during the year and many of them go through morphological changes in order to adapt themselves to such a dynamic environment. The aerial leaves of *E. azurea*, however, are available as long as the water sheet is present. That occurred all year round, in 1993. Although *E. azurea* was available in the “Corixo Birici” during practically all the year, its quality may have been altered from one period to another with variations on the nutrient content. During the dry season, there is higher concentration of nitrogen in the plant tissues due to the availability in the soil and smaller biomass production (Da Silva 1993). However, as alterations on *C. aquaticum* feeding preference did not occur from draining to dry seasons, a

possible variation in the host plant quality did not interfere on the order of preference in the field. The high *C. aquaticum* adult mortality observed during the dry season may also be related to thermal stress due to the wide daily thermal amplitude in that period.

The grasshoppers’ feeding on a higher number of macrophyte species in the laboratory than in the field may indicate that the diet amplitude may be determined by other ecological factors besides plant chemistry. The reproductive behavior may be another important aspect in the choice of the host plant for insects that mate on the host plant (Jaenike 1990).

From the moment that the plant is reached, its physical structure – texture, pubescence, turgescence, growth mode – may play an important role on the selection of food (Mulhern 1967). Mechanical receptors allow textural sampling of particular loci, which they contact and may generate information about the configuration of the superficies that are undistinguishable by vision, for example substrates for oviposition (Miller & Strickler 1984). Beside these receptors, some grasshopper species possess sensorial organs, to detect the odor of the host plant, located in the antennae (White & Chapman 1990). This seems to occur with *C. aquaticum* due to its behavior of touching the plant surface with the antennae as soon as it lands on it.

Tasting gives the best information about plant composition. Thus, when plant presenting herbivory signs are considered, if only the test 1 had been carried out (Fig. 6) it could be concluded that females and males had distinct preferences. On the contrary of what was expected the females would not prefer the host plants; these plants would be only used for oviposition. However, when results of the other tests were analyzed there was a displacement of the preference towards the host species *E. azurea*, for the females and *P. cordata* for the males.

If the plant chosen by an insect for resting and feeding also has to offer protection against predation, a preference for *E. azurea* would be expected, considering the architecture of the plant. However, when the 2h-interval observation data, concerning to plants preferred for feeding and also for resting, were considered, only females confirmed this hypothesis and only in the tests 3 and 4 (Fig. 3c, 4c, 5c).

Other aspects to be considered are the increment on the food offer from four to five species in the tests of feeding preference and the season in which each one was carried out. It is expected that the bigger the number of food items available the higher the grasshopper selectivity. This analysis was not feasible because there was a temporal difference between the tests of feeding preference 1 and 2. However,

Table 2. Number, mean total length (TL) and dry weight of dissected leaves of *E. azurea*, *Ec. paniculatus* and *P. cordata* in the laboratory and number of egg masses of *C. aquaticum*.

Species	Number	CT (X ±SE) (cm)	Dry weight (g)	Egg masses
<i>E. azurea</i>	539	24,5 ± 0,63	1314,5	0
<i>Ec. paniculatus</i>	194	53,0 ± 3,53	118,9	0
<i>P. cordata</i>	477	32,0 ± 0,56	206,5	2

between tests 3 and 4, which were carried out exactly on the same day, the increase in the number of species did not affect the order of preference for the females.

Considering the males, the frequency on the host plants increased with the increase of the variety of species offered. In relation to the plant species with herbivory signs, no changes in the preference occurred between the tests. It was possible to conclude that the increase was due to the choice of sites for resting and not for feeding.

When results obtained for the frequency of grasshoppers on each plant species are compared it is easy to perceive the similarity between tests 3 and 4, in relation to females. Between these tests as well as between the tests 1 and 2, a temporal difference existed which may have influenced the results. Although partially conflicting results have been found in the literature for daily variation on secondary compounds in plants, there is a general agreement that the concentration of these compounds changes along the year or along growth season (Swain 1963). Sperber (1991), studying temporal variation on the diet of the grasshopper *Abracris dilecta* (Walker), found no significant changes in the number of plants consumed between rainy and dry seasons. In Pantanal, however, the environmental modifications imposed by climatic changes and mainly by the hydrological cycle, determine the alterations in the quality of the aquatic macrophytes (Da Silva *et al.* 1994), which are probably perceived by *C. aquaticum* when probing the leaves surface.

Silveira-Guido & Perkins (1975) considered adequate the introduction of *C. aquaticum* in USA for controlling *E. crassipes*, since feeding tests conducted in the laboratory indicate that the probability of this grasshopper to feed on other species in the presence of *E. crassipes* and possibly *P. cordata* would be low. Contrasting results were obtained in our study.

As far as the diet-ovoposition relationship is considered, only a fraction of all acrididae has a narrow range of host plants, but every species that oviposits on host plants has a narrow spectrum (Braker 1989), as in the case of *C. aquaticum*.

In summary, *C. aquaticum* presents oligophagy in the field, feeding on three species and two genera of the same family. Although in the literature *C. aquaticum* is considered specific to the genus *Eichhornia*, this grasshopper species also reproduces on *P. cordata* and feeds on other species in the laboratory. The acceptability of several plant species in the absence of the host plant may indicate that the relative abundance of the host plant in the field is determinant in the amplitude of the diet of *C. aquaticum*. Besides, the selection of *E. azurea* as host plant may be related to a higher protection against predation due to the cryptic coloration of this grasshopper.

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