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Age Structure and Feeding of the Neotropical Grasshopper *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae) on Water Hyacinth

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Abstract

We aimed to evaluate the variation in the age structure of *Cornops aquaticum* (Bruner) population and its relation to the host plant biomass and the feeding of the different age classes of this grasshopper on the water hyacinth *Eichhornia crassipes* along 2 years, in a Paraná River floodplain lake (Chaco, Argentina). Individuals of *C. aquaticum* were captured with a 70-cm diameter sweep and separated in nymphs A (instars I and II), nymphs B (instars III to VI), adult females, and adult males; host plant biomass was sampled using a ring with a 0.30-m² diameter. Relative daily feeding of *C. aquaticum* population was calculated by multiplying the number of individuals captured per minute by the daily consumption by individual obtained in each age classes. We found that the age structure and the relative daily feeding of *C. aquaticum* varied between seasons and years. The highest values of grasshopper abundance, leaf biomass, and relative daily feeding of *C. aquaticum* population were observed in summer 2006. Plant biomass was directly correlated with nymph abundance and not correlated with adult abundance. Plant biomass available as refuge (leaves), food (laminae), and oviposition site (petioles) to *C. aquaticum* represented up to 62% of the total plant biomass. The results obtained in *C. aquaticum* show the importance of considering total plant biomass and plant biomass available for herbivores separately. Our study highlights the need to find an adequate method to estimate the density of *C. aquaticum* and other semiaquatic grasshoppers in the Paraná River floodplain involving different seasons, years, and water phases (rising and falling).

Introduction

Cornops aquaticum (Bruner) is a semiaquatic grasshopper which originated in the Amazon Basin (Amedegnato 1977) and widely distributed from Southeastern Mexico to the center of Argentina and Uruguay (Lhano 2006, Adis *et al* 2007). This grasshopper lays the egg-pods inside the petioles of Pontederiaceae plants, especially *Eichhornia* spp. (Center *et al* 2002), and nymphs and imagines feed on its

leaf laminae (Carbonell 1981), suggesting a high specificity to these host plants. The water hyacinth *Eichhornia crassipes* is one of the most typical macrophytes of floating meadows in large rivers and wetlands in South America (Blanco Belmonte *et al* 1998) and is considered an important weed of natural and artificial wetlands around the world (Center *et al* 2002).

Data on population age structure and feeding of semiaquatic oligophagous grasshoppers are scarce. The information

available in general includes each aspect separately and is related to grasshopper populations closely associated with macrophytes that are invasive around the world (Nunes *et al* 1992, Nunes & Adis 1994, Adis & Junk 2003, Capello *et al* 2004, Franceschini *et al* 2007, Silva *et al* 2010a, b, Franceschini *et al* 2011a, b, Braga *et al* 2012). In contrast, most studies on grasshopper populations have been carried out in terrestrial generalist grasshoppers due to the economic importance of losses on natural grasslands and crops (Cigliano *et al* 2000, Skinner & Child 2000, Gardner & Thompson 2001, Quesada Moraga & Alvarez 2001, Sánchez *et al* 2001, Torrusio *et al* 2002, Squitier & Capinera 2002, O'Neill *et al* 2003, Gardiner *et al* 2005, Messi *et al* 2006, Powell *et al* 2007, Jannot *et al* 2009).

Cornops aquaticum is of special interest in South American wetlands because this grasshopper constitutes one of the most abundant herbivores of *E. crassipes* floating meadows and its feeding behavior causes damage on the leaf biomass and productivity of this host plant (Adis & Junk 2003, Franceschini *et al* 2010, 2011a). In non-native ecosystems, this grasshopper is also a potential biological control agent of the water hyacinth (Silveira Guido & Perkins 1975, Center *et al* 2002). Estimations of age structure and abundance of *C. aquaticum* populations across the seasons, especially long-term studies, are useful because different age classes have different consumption levels of the host plant and daily consumption by individual is highest in adult females and lowest in first and second instars (Franceschini *et al* 2011a). In addition, variations in the biomass of green leaves during the phenology of *E. crassipes* determine that the herbivorous damage causes different effects on the period of maximum biomass, the end of the growth period, and the decay period (Franceschini *et al* 2010).

Seasonal variations in *C. aquaticum* populations have been studied in many sites over its distribution range (Medeiros 1984, Franceschini *et al* 2007, Capello *et al* 2004, Silva *et al* 2010a, b, Franceschini *et al* 2011b, Braga *et al* 2012), where temperature and insolation vary greatly (Adis *et al* 2004). However, it remains unclear whether the abundance and the feeding of different age classes of *C. aquaticum* vary in different years and what is the relation between the age structure of this grasshopper and the biomass of the host plant. Here, we aimed to evaluate the variation in the age structure of *C. aquaticum* population and its relation to the host plant biomass and the feeding of different age classes of this grasshopper on *E. crassipes* floating meadows along 2 years, in the Paraná River floodplain.

Our hypotheses were that the grasshopper age structure is related to the host plant biomass and that the feeding of *C. aquaticum* population varies between seasons and years.

Material and Methods

Study site

Samplings were conducted in an oxbow lake of the Paraná River floodplain (27°26'S, 58°51'W), within the RAMSAR Site of the Chaco Wetlands, Argentina. Due to the difficulties to distinguish nymphs of different species of *Cornops*, we selected this oxbow lake after many exploratory studies that allowed us to confirm that *C. aquaticum* was the only species of this genus occurring in this lake. The lake is small (200×2,000 m), shallow (0.4–2 m), and surrounded by a gallery forest. During the sampling period, from February 2004 to April 2006, there was a prolonged isolation phase and the lake was connected to the river for only a very short time. The climate of this area is classified as subtropical, summers and springs are warm and prolonged, whereas winters are shorter and mild, with a frequency of frost days of 0.25 days/year (Bruniard 1981, 1996).

Sampling procedure

Age structure. Samplings were carried out monthly from February 2004 to April 2006, in a day, from 9:00 to 13:00 hours, avoiding cloudy and rainy days. Individuals of *C. aquaticum* on *E. crassipes* floating meadows were captured from a boat using a sweep net with a diameter of 70 cm and a depth of 1 m. In June and August 2004 and May to July 2005, samplings were also carried out on the edge of the lake, on dry land, walking and waving the network on dry *E. crassipes* plants due to the presence of individuals in this sector. Following Johnson (1989) and the criteria established by the "Host-Insect Coevolution on Waterhyacinth" project (Adis *et al* 2004, Brede *et al* 2007), a preset number of grasshoppers (50 individuals) was captured at random in different zones of the *E. crassipes* floating meadows. On each sampling date, we recorded the required time to reach the preset number of individuals. In the laboratory, individuals were separated in different age classes following the criteria of Franceschini *et al* (2007): nymphs A (instars I and II), nymphs B (instars III to VI), adult females, and adult males. Instars were determined using the length of the hind femora (Franceschini *et al* 2005). Abundance was expressed as the proportion of the different age classes in the population and the number of individuals of each age class captured per minute.

Host plant biomass and leaf density. Seasonal samplings were carried out from autumn 2005 to summer 2006. Our sampling unit consisted of an aluminum ring with a 0.30-m² diameter. Three replicates were performed on each sampling date on the *E. crassipes* floating meadows.

All green leaves and roots within the boundaries of the ring were cut off, separated, and dried at 105°C. The leaf density was estimated following Neiff et al (2008). We considered leaf biomass, petiole biomass, and lamina biomass separately because *C. aquaticum* uses each of them as refuge (leaves), oviposition site (petioles), and food (lamina), respectively. Root biomass and total plant biomass were also estimated to calculate the percentage of the plant biomass that is available for *C. aquaticum* population as refuge, food, and oviposition site.

Relative daily feeding of the grasshopper population

Daily consumption by individual of different development stages was estimated following Franceschini et al (2011a). Relative daily feeding of *C. aquaticum* population on *E. crassipes* floating meadows from February 2004 to April 2006 was calculated by multiplying the number of nymphs A, nymphs B, and adults captured per minute by the daily consumption by age class obtained previously by Franceschini et al (2011a).

Statistical analyses

Spearman's coefficient was used to assess the relation between the abundance of the age classes of *C. aquaticum* population. To corroborate synchrony between the occurrence of peaks of nymphs A and the subsequent peaks of nymphs B, the abundance of nymphs A of 1 month was correlated with the abundance of nymphs B of the following 1, 2, and 3 months later; for example, correlation coefficients were computed between the monthly abundance of nymphs A in February 2004 and the abundance of nymphs B in March, April, and May 2004. Using the same comparison criterion, we also corroborated the occurrence of synchrony between abundance of nymphs B with the abundance of adults. The differences in leaf density and plant biomass between seasons were assessed with ANOVA with post hoc Tukey tests, transforming the data to log₁₀. We used Spearman's coefficient to assess the relation between grasshopper age structure and the biomass of the host plant. We correlated the relative abundance of the four age classes (individuals captured per minute) from autumn 2005 to summer 2006 with the values of leaf density and the plant biomass of the same period. The relation between daily feeding by individuals on the host plant and the different development stages of *C. aquaticum* (from instar I to adults) was assessed with Spearman's coefficient. Differences in relative daily feeding of the *C. aquaticum* population during the sampling period were assessed with the Kruskal–Wallis test. We considered 5% significance levels. Statistical analyses were performed using Infostat software (version 1.1) (2002).

Results

Age structure of *C. aquaticum* population and the host plant biomass dynamics

During the sampling period, we recorded a total of 1,192 individuals of *C. aquaticum* (748 nymphs and 444 adults). Nymphs were more abundant in spring and summer, whereas adults were more abundant in winter and at the beginning of spring. Nymphs A, mainly first instar, showed three peaks of high proportion in each year, with the peaks observed in spring being most important (Fig 1a, b). We corroborated synchrony between the abundance of nymphs A of each month with the abundance of nymphs B of the following one ($r_s=0.53$; $p<0.01$, $N=26$ sampling dates) and 2 months later ($r_s=0.44$; $p<0.03$, $N=25$ sampling dates); there was no synchrony between the abundance of nymphs A of 1 month with the abundance of nymphs B of the following 3 months ($r_s=-0.04$; $p>0.05$, $N=24$ sampling dates). Higher abundance of nymphs B did not generate subsequent peaks of adults in the population (Fig 1a, b). No synchrony was observed between the abundance of nymphs B of 1 month and the abundance of the adults of the following 1, 2, and 3 months ($r_s=0.67$, 0.31 , 0.1 ; $p>0.05$, $N=24$ – 26 sampling dates). Peaks of individuals captured per minute were observed in March–April 2004 (5 individuals captured per minute), November 2004–April 2005 (4–14 individuals captured per minute), and from September 2005 to April 2006 (8–61 individuals captured per minute) (Fig 1c).

Eichhornia crassipes presented similar coverage during the sampling period and was the most abundant macrophyte, occupying near 80% of the lake. Plants of *E. crassipes* with elongated leaves (large biotype) were dominant. Highest values of leaf density and plant biomass were recorded in spring and summer (Fig 2). However, significant differences between seasons were only found in leaf density (ANOVA, $p=0.046$), leaf biomass (ANOVA, $p=0.004$), and lamina biomass (ANOVA, $p=0.008$). No significant differences were observed between seasons in petiole biomass, root biomass, and total plant biomass (ANOVA, $p>0.05$). Plant biomass available as refuge (leaves), food (lamina), and oviposition site (petioles) to *C. aquaticum* population represented between 51.8% and 62% of the total plant biomass during the sampling dates.

Plant biomass was related to the age structure of *C. aquaticum*, whereas no correlation was found between leaf density and the grasshopper age structure. Nymphs A captured per minute were highly correlated with leaf biomass ($r_s=0.72$; $p=0.02$), lamina biomass ($r_s=0.78$; $p=0.01$), and total plant biomass ($r_s=0.65$; $p=0.03$). Nymphs B captured per minute were highly correlated with leaf biomass ($r_s=0.62$; $p=0.04$) and lamina biomass ($r_s=0.67$; $p=0.03$). No correlation was obtained between the number of adults

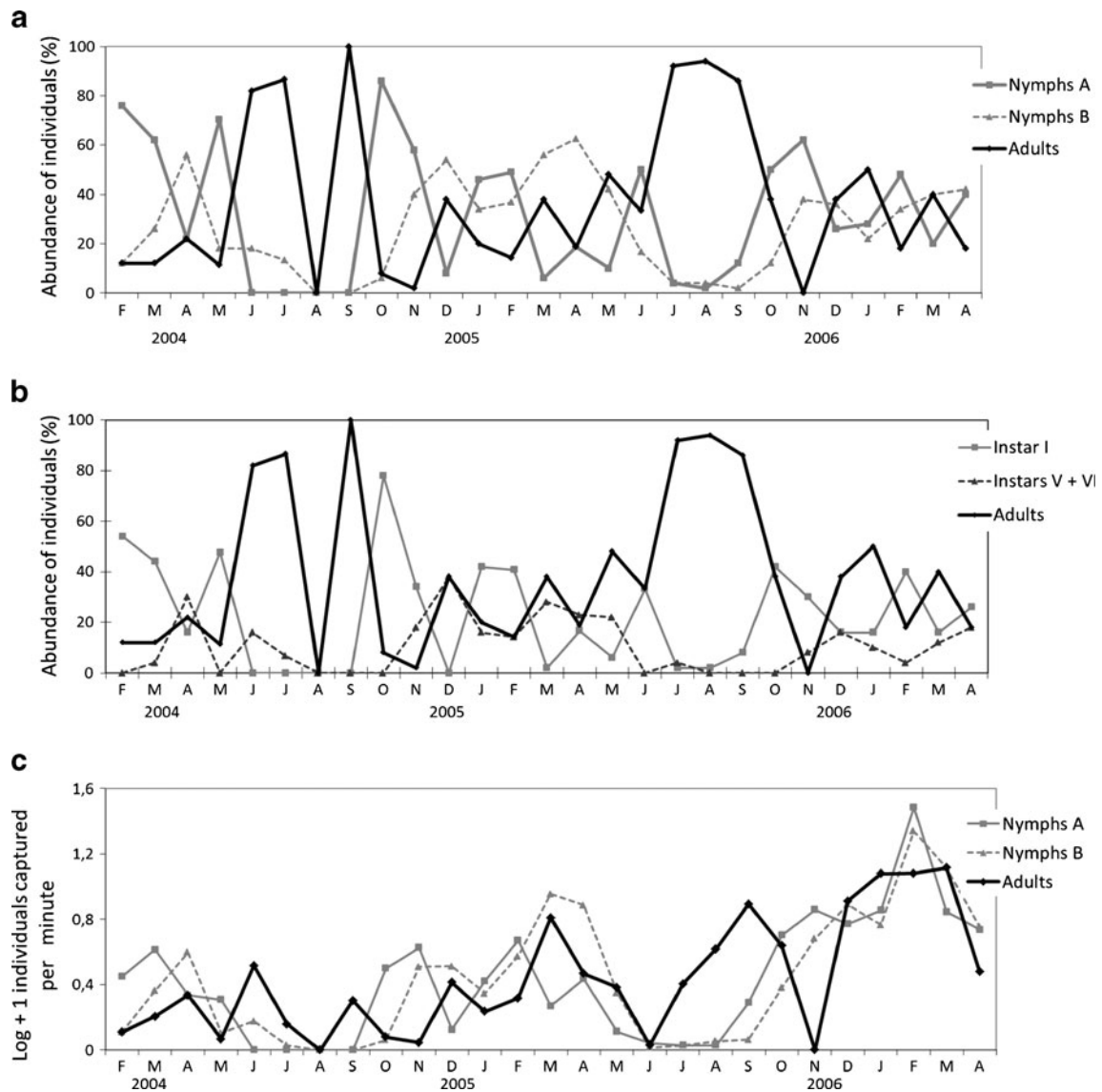


Fig 1 Age structure and abundance of *Cornops aquaticum* population on the *Eichhornia crassipes* floating meadow. **a** Proportion of nymphs A (instars I and II), nymphs B (instars III to VI), and adults. **b** Proportion of instars I, last instar nymphs (V + VI), and adults. **c** Nymphs A, nymphs B, and adults. Abundance is expressed as \log_{+1} of individuals captured per minute. Winter is from June 21 to September 21 and summer from December 21 to March 21.

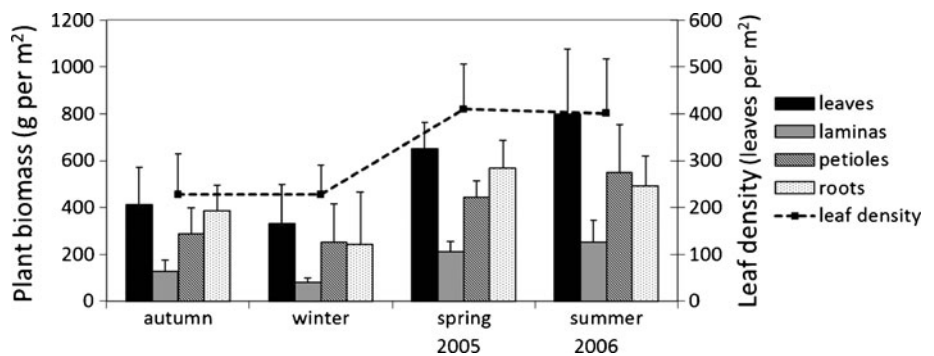


Fig 2 Seasonal variation of plant biomass and leaf density of the host plant *Eichhornia crassipes*, from autumn 2005 to summer 2006. Winter is from June 21 to September 21 and summer from December 21 to March 21.

captured per minute and plant biomass. The total number of individuals of *C. aquaticum* captured per minute was highly correlated with leaf biomass ($r_s=0.72$; $p=0.02$), lamina biomass ($r_s=0.69$; $p=0.02$), petiole biomass ($r_s=0.61$; $p=0.04$), and total plant biomass ($r_s=0.63$; $p=0.04$). No correlation was found between the root biomass and the age structure of *C. aquaticum*.

Relative daily feeding of *C. aquaticum* population

Daily consumption by individual was low in first and second instars (instar I, 8 ± 5 mg; instar II, 37 ± 34 mg), intermediate from third to sixth instars (instar III, 39 ± 27 mg; instar IV, 35 ± 26 mg; instar V, 48 ± 36 mg; instar VI, 66 ± 39 mg), and high in adults (93 ± 61 mg). We found a high correlation between daily consumption by individual on the host plant and the different development stages of *C. aquaticum* ($r_s=0.59$; $p<0.0001$).

Relative daily feeding of *C. aquaticum* population varied significantly across the seasons and years (Kruskal–Wallis test, $p<0.05$); the highest values of relative daily feeding of grasshopper population were observed in summer 2006, which reached up to 2.9 g of the host plant per day, with a grasshopper abundance of 61 individuals captured per minute. Adults and nymphs B presented the highest values of relative daily feeding of *C. aquaticum* population during the sampling period (Fig 3). Relative daily feeding of grasshopper population increased during spring and summer, when the leaf biomass and the grasshopper abundance were high (Figs 1c and 3).

Discussion

Cornops aquaticum population and the host plant biomass

The nymphs A present during most of the study period showed that the *C. aquaticum* population on *E. crassipes*

has several reproduction periods across the year. The same trend has been observed in another *C. aquaticum* population with *Eichhornia azurea* as the host plant (Franceschini et al 2005, 2011b). Our results are different from those found in *C. aquaticum* populations of the Pantanal of Mato Grosso and Amazonia, which show continuous reproduction and nymphs A during the whole year (Silva et al 2010a, Braga et al 2012). Contrasting to the pulse regime of Pantanal and Amazonia, the hydrological regime of the Paraná River is irregular with floods of different recurrences and amplitudes (Neiff 1990). Our results showing three peaks of nymphs A across the year and the occurrence of nymphs and adults during winter differ from the results found for this grasshopper in other sites of Argentina (Silveira Guido & Perkins 1975, Capello et al 2004). Nymphs B were recruited as adults, but the fact that adults were notably more abundant than the nymphs B and that there was no correlation between abundance of both age classes indicate overlapping of generations.

The seasonal growth pattern of the host plant biomass found in this study is similar to those reported by Neiff et al (2008) in the same site between August 1999 and December 2001.

Data of variation in the host plant biomass are scarcely included in monitoring of grasshopper populations (Nunes et al 1992, Nunes & Adis 1994). The results obtained in *C. aquaticum* show the importance of considering total plant biomass and plant biomass available for herbivores separately, discriminating the biomass available as food, oviposition site, and refuge; the fact that only 62% of the plant biomass was available for this grasshopper and root biomass did not correlate with any of the age classes supports this statement.

The high correlation of nymphs A with leaf biomass, lamina biomass, and total plant biomass indicates that higher amounts of biomass in the host plant represent more food available to the newly hatched nymphs. Adults of *C. aquaticum* are strong fliers and can disperse when

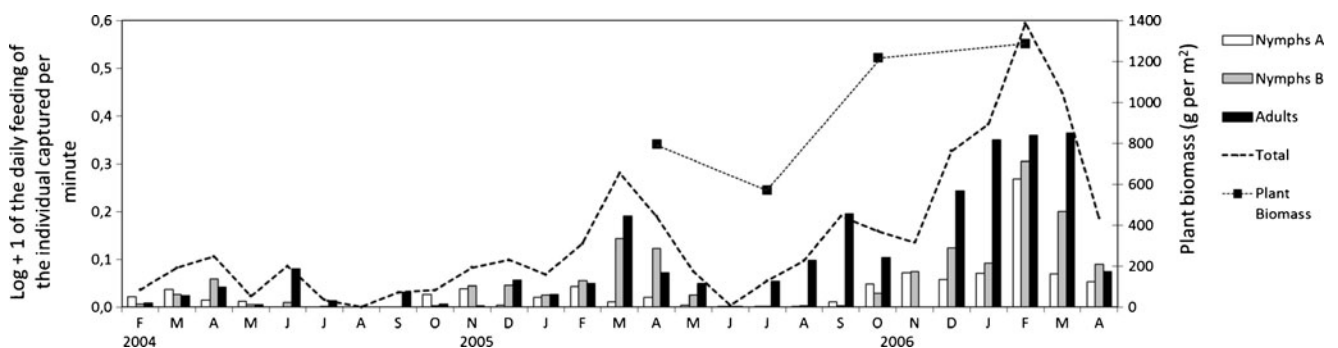


Fig 3 Relative daily feeding of nymphs A (instars I and II), nymphs B (instars III to VI), and adults of *Cornops aquaticum* and total biomass of *Eichhornia crassipes*. Relative daily feeding was transformed to $\log+1$. Winter is from June 21 to September 21 and summer from December 21 to March 21.

food becomes scarce, which can contribute to explaining the lack of correlation of this age class with the plant biomass. The correlation between plant biomass and nymph abundance and the lack of correlation with adult abundance have also been mentioned for other semiaquatic grasshoppers in the Amazonian floodplain (Nunes *et al* 1992, Nunes & Adis 1994).

Relative daily feeding of C. aquaticum population on E. crassipes floating meadows

The high correlation between consumption by individual and development stages of *C. aquaticum* shows that the age structure should be also taken into account to evaluate the feeding of herbivore populations.

High relative daily feeding of *C. aquaticum* population in spring and summer was related to the high number of individuals captured per minute (mainly nymphs) and high leaf biomass of *E. crassipes*. In the Amazonian floodplain, the highest daily feeding of *C. aquaticum* population is found in spring, when adults are notably more abundant than the nymphs (Adis & Junk 2003).

Our results about the relative daily feeding of *C. aquaticum* population are coincident with those previously found for invertebrate herbivores of *E. crassipes* at the same site. In fact, cumulative damage recorded in the field is highest in summer and at the beginning of autumn, and herbivores including *C. aquaticum* remove up to 24% of the lamina biomass per square meter (Franceschini *et al* 2010). The lower feeding of the *C. aquaticum* population and the lower plant biomass available as food during winter may be overcompensated by the higher nitrogen content of *E. crassipes* leaves found in this season (Franceschini *et al* 2010).

Conversely to our estimations, daily feeding of *C. aquaticum* populations was calculated on the basis of the density of individuals in the Amazonian floodplain (Adis & Junk 2003). We were not able to estimate grasshopper density due to the high above-water height of *E. crassipes* leaves in the High Paraná floodplain (leaf up to 120 cm long) in comparison to the Amazonian floodplain (Neiff *et al* 2008, Adis *personal communication*).

We found that the age structure and the relative daily feeding of *C. aquaticum* population varied between seasons and years. Thus, our first hypothesis that the age structure and feeding of *C. aquaticum* populations vary between seasons and years must be accepted. Because plant biomass, specifically leaf biomass, was only related to the abundance of nymphs A and nymphs B, the second hypothesis that age structure is related to biomass of the host plant must be also partially accepted.

Our study highlights the need to find an adequate method to estimate the density of *C. aquaticum* and other grasshoppers associated with *E. crassipes* in the Paraná

River floodplain. We recommended that estimations of *C. aquaticum* abundance and feeding from long-term studies involving different seasons, years, and water phases (rising and falling), taking into account also the number of individuals per area and per plant biomass, should be carried out.

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