

The role of the host-specific grasshopper *Cornops aquaticum* (Orthoptera: Acrididae) as consumer of native *Eichhornia crassipes* (Pontederiaceae) floating meadows

María Celeste Franceschini^{1,2}, María Laura De Wysiecki³, Alicia Poi de Neiff^{1,2}, María Eugenia Galassi^{1,2} & Fedra Solange Martínez²

1. Consejo Nacional de Investigaciones Científicas y Técnicas, Centro de Ecología Aplicada del Litoral, Ruta 5, km 2,5 - 3400 - Corrientes, Argentina; celestefranceschini@yahoo.com.ar, guadalupepoi@gmail.com, marugalassi@yahoo.com.ar
2. Universidad Nacional del Nordeste, Cátedra de Limnología, Corrientes, Argentina; fedrasolange@yahoo.com.ar
3. Consejo Nacional de Investigaciones Científicas y Técnicas y Universidad Nacional de La Plata, Centro de Estudios Parasitológicos y de Vectores, Calle 2 N° 584 - 1900 - La Plata, Argentina; mlw@cepave.edu.ar

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Abstract: *Cornops aquaticum* is a widely distributed semiaquatic grasshopper in the Neotropics. The development, feeding and oviposition of *C. aquaticum* take place on Pontederiaceae, especially on species of *Eichhornia*. Several aspects of the feeding of *C. aquaticum* are studied because is one of the most important herbivores of the highly invasive floating *Eichhornia crassipes* in native areas. The aims of this paper were: (1) to quantify the amount of *E. crassipes* consumed by *C. aquaticum*, (2) to determine the growth rate and the conversion efficiency of food ingested by this grasshopper, and (3) to determine the possible effect of consumption on *E. crassipes* productivity. Thirty individuals from each specific age class were used in the experiment: nymphs A, nymphs B, adult males and adult females. Insects were individually confined in plastic pots with a leaf of *E. crassipes*. We estimated feeding by individual, consumption index (CI), relative growth rate (GR) and efficiency of conversion of ingested food to body substance (ECI). The impact of *C. aquaticum* consumption on *E. crassipes* floating meadows was assessed with the abundance of the grasshopper, and the available data on primary production of the host plant at the study site. Food intake of *C. aquaticum* was 11.23% of plant productivity. Food consumption, growth rate and food conversion efficiency of this grasshopper varied according to the specific age classes. Damage caused by *C. aquaticum* is high in comparison with the damage caused by other semiaquatic and grassland grasshoppers, however it is not enough to prevent the growth and coverage of native *E. crassipes* floating meadows because abundance of grasshoppers are relatively low and the growth rate and productivity of the host plant is high. Rev. Biol. Trop. 59 (3): 1407-1418. Epub 2011 September 01.

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Cornops aquaticum Bruner 1906 (Orthoptera: Acrididae: Leptysminae) is widely distributed in the Neotropics, from Southeastern Mexico to central Argentina and Uruguay (Roberts & Carbonell 1979, Lhano 2006, Adis *et al.* 2007). Development, feeding and oviposition of *C. aquaticum* take place on Pontederiaceae, especially on species of *Eichhornia*,

indicating a high specificity of this grasshopper to these host plants (Carbonell 1981).

The water hyacinth, *Eichhornia crassipes* Mart. Solms (Pontederiaceae) is the most common macrophyte in South American rivers and wetlands (Gopal 1987, Blanco-Belmonte *et al.* 1998) and is considered one of the most important pests in natural and artificial water

bodies around the world (Waterhouse & Norris 1987, Julien *et al.* 2001, Center *et al.* 2002). High abundance and coverage of *E. crassipes* constitute one of the most important features of the Paraná River floodplain lakes (Lallana 1980, Neiff 1990, Carignan *et al.* 1994). The seasonal growth pattern is characterized by high biomass in the summer and reduced biomass in the winter (Neiff & Poi de Neiff 1984, Neiff *et al.* 2008). During the high biomass period of *E. crassipes*, abundance of herbivorous population (Casco & Poi de Neiff 1998, Franceschini 2008, Franceschini *et al.* 2008) and leaf biomass removed by herbivory (Franceschini *et al.* 2010) are highest in the Paraná River floodplain lakes.

Quantitative data on the feeding impact and the amount consumed by semiaquatic grasshoppers in their natural habitat are practically non-existent. The only information available is for populations of *C. aquaticum* (Adis & Junk 2003) and *Stenacris fissicauda fissicauda* (Amorim & Adis 1994) in the Amazon floodplain. In contrast, many studies on consumption, preference and feeding impact have been carried out on terrestrial generalist grasshoppers, due to the economic importance of losses of natural grasslands and crops (Haniffa & Periasamy 1981, Ronderos *et al.* 1981, Sánchez & De Wysiecki 1990, De Wysiecki & Sánchez 1992, Pereyra *et al.* 1996, Cigliano & Lange 1998, Abdel-Rahman 2001, Torrusio *et al.* 2005, Franzke *et al.* 2010). Terrestrial acridids feed mainly on highly palatable grasses and thus are an important competitor for cattle (Ronderos *et al.* 1981).

C. aquaticum constitute one of the most important herbivores of native waterhyacinth floating meadows (Adis & Junk 2003, Franceschini 2008, Franceschini *et al.* 2010) and is considered as a biological control agent of this macrophyte in non-native ecosystems (Center *et al.* 2002). For these reasons, several aspects of feeding of this grasshopper are intensely studied in native (Silveira-Guido & Perkins 1975, Ferreira & Vasconcellos-Neto 2001, Adis & Junk 2003, Vieira & Santos 2003, Lhano *et al.* 2005, Franceschini & Capello 2006,

Franceschini 2008, Franceschini *et al.* 2010) and non-native areas (Oberholzer & Hill 2001, Bownes *et al.* 2010).

The aims of this work were: (1) to quantify and compare the amount of *E. crassipes* consumed by nymphs and adults of *C. aquaticum* under outdoor enclosure conditions, (2) to determine the food conversion efficiency and rate of growth of nymphs and adults, and (3) to determine the possible effect of consumption on *E. crassipes* productivity. Our hypothesis is that *C. aquaticum* consumes a low quantity of *E. crassipes* per dry weight of animal, producing scarce effect on the productivity of this macrophyte, and that food consumption, growth rates, and the food conversion efficiency of this grasshopper varies according to the age of individuals.

MATERIAL AND METHODS

In order to assess food consumption, food conversion and growth, individuals of *C. aquaticum* were caught from a boat using an entomological net (70cm diameter), sweeping on the vegetation in a lake of the Paraná River floodplain (El Puente Lake: 27°26'20" S - 58°51'11" W). A total of 120 individual grasshoppers were used in this experiment; development stages of individuals were separated in four specific age class (Franceschini *et al.* 2007, Franceschini 2008, Franceschini *et al.* 2008): nymphs A (stages I and II), nymphs B (stages III to VI), adult males and adult females (with immature and mature ovaries). Thirty individuals from each specific age class of the population were individually confined in transparent 1000mL plastic pots, with moistened cotton at the bottom and covered with plastic film at the top. All pots were kept in a recipient containing water to prevent changes in microclimatic conditions. According to Nunes (1989), this design is the most appropriate to obtain maximum survivorship of semiaquatic grasshoppers and to provide leaves in optimal condition. Experiments were carried out between December 2006 and January 2007 (summer), outside Corrientes, at 7km of the Paraná River (27°29'28" S - 58°

45°33' W). Plastic pots containing the insects were kept in a screened outdoor enclosure exposed to the local climate and without direct sun exposure. During the study period, monthly maximum temperatures ranged from 32.8-36.3°C and monthly minimum temperatures ranged from 19.2-19.9°C. Experiments were carried out in summer because abundance of *C. aquaticum* nymphs and adults (Franceschini *et al.* 2007, Franceschini 2008, Franceschini *et al.* 2008) and leaves biomass, which constitute the food resource (Neiff & Poi de Neiff 1984, Neiff *et al.* 2008), are high in the *E. crassipes* floating meadows.

The fresh weight of each grasshopper was recorded at the beginning of the experiment to obtain the initial animal fresh weight. The feeding ration consisted of a fresh mature leaf of *E. crassipes* per pot. Pilot experiments with different size of leaves were carried out to determine the feeding ration, preventing the excess of food offered (Van Loon 1989). Care was taken to select leaves that were fresh and uniformly green. Leaves were previously weighed to obtain the initial food fresh weight and then offered to the insects for 72 hr. To calculate the dry weight (dw) of leaves used as food at the beginning of the experiment, 50 similar feeding rations were also prepared as a control; their fresh weight was recorded, and then they were dried to 60°C to obtain their dry weight and calculate the conversion factor.

After the period of feeding, the remaining food and the individuals were collected and weighed to measure final animal fresh weight and remaining food fresh weight. Constant dry weight of the food rations and grasshoppers were obtained at 60°C and 100°C, respectively. During weightings, plant and insect materials were stored in a desiccator.

The relationship between final animal fresh weight and final animal dry weight was used to calculate the dry weight of the animal at the beginning of the experiment based on the initial animal fresh weight recorded.

We used the classical gravimetric method of Waldbauer (Waldbauer 1968) because is the most frequently applied technique to quantify

food consumption and fitness of herbivorous insects (Slansky 1993, Fanny *et al.* 1998, Whittaker 1999, Abdel-Rahman 2001, Cohen 2004, Rayapuram & Baldwin 2006, Hwang *et al.* 2008, Strengbom *et al.* 2008, Rao *et al.* 2009, Ruhnke *et al.* 2009, Franzke *et al.* 2010). Despite Waldbauer method may overestimate consumption by neglecting respiration of the leaf material used as a food during the experiment, gravimetric measurements are easy to perform, do not require expensive equipment, and are relatively accurate, which made them widely used by researchers (Van Loon 1989). In the natural feeding situation, the plant will photosynthesize and thus one would expect corrections for an increase in food dry matter instead of decrease for respiration (Whightman 1981).

We assessed the feeding amount by estimating the individual daily consumption (g of food consumed per individual) and calculated the consumption index (CI) proposed by Waldbauer (1968):

$$CI = F/TA$$

where F is the dry weight of food eaten (g), T is the duration of feeding period (days) and A is the mean dry weight of insect during feeding period (g).

According to the longevity of each specific age class of the *C. aquaticum* population (Franceschini 2008), individual cumulative consumption of a specific age class (C_{cum}) was calculated using the criteria of Amorim & Adis (1994):

$$C_{cum} = CI \cdot L \cdot A_c$$

where CI is the consumption index for the specific age class (food consumed (g)/mean weight of insect (g)/day), L is the longevity of individuals in the specific age class (days) and A_c is the mean animal dry weight (g) for the specific age class.

We measured the individual destruction rate (dry weight) by weighting the separated portions of destroyed leaf remained as a consequence of grasshopper consumption (Sánchez & De Wysiecki 1990).

We also assessed growth and food conversion of ingested food using the relative growth index (GR) and conversion efficiency of ingested food to body substance (ECI) from Waldbauer (1968):

$$GR=G/TA$$

where G is the dry weight gain of insect during the feeding period (g), T is the duration of the feeding period (days) and A is the mean dry weight of insect during feeding period (g).

$$ECI=(\text{dry weight gained of the insect} / \text{dry weight of the food ingested}) \cdot 100$$

To analyze the effect of *C. aquaticum* consumption on the productivity of *E. crassipes* we follow the criteria of Adis & Junk (2003). Grasshopper abundance (ind/m²) was estimated on the floating meadows from a boat, with a net of 0.25m² of diameter, trapping all the *E. crassipes* leaves within the boundaries of the net, and counting all the grasshoppers (nymphs and adults) found within this defined area. Daily plant consumption of *C. aquaticum* population in the field per m² was calculated by multiplying grasshopper abundance on *E. crassipes* per m² (nymphs and adults) with the daily consumption by individual nymphs and adults. Net primary production data for *E. crassipes* were calculated from Neiff & Poi de Neiff (1984) and Neiff *et al.* (2008). We estimated height, density and biomass of *E. crassipes* leaves using an aluminium ring of 0.3058m², following to Neiff *et al.* (2008). To calculate biomass, leaves were dried at 105°C.

We compared consumption, destruction, individual dry weight, relative growth rate and efficiency of conversion of ingested food between categories of the *C. aquaticum* population using ANOVA with post hoc Tukey test. In females, comparison of the indices between females with immature (types I and II) and mature (type III) ovaries (Franceschini *et al.* 2007) were analyzed by ANOVA. All these variables were transformed to normalize distributions and stabilize variances. The differences

in abundance of *C. aquaticum* and daily plant consumption per m² between nymphs and adults were assessed with a Wilcoxon test. We considered significant p values of <0.05. Statistical analyses were performed using Infostat Software (version 1.1).

RESULTS

Food consumption of *C. aquaticum*:

Daily consumption by individual varied significantly according to the specific age classes of population structure (ANOVA, p<0.0001); the highest value was found in adult females (0.119±0.03g) and the lowest was found in nymphs A (0.029±0.031g). Daily consumption of *C. aquaticum* was 0.039 and 0.093g of food per day in nymphs and adults, respectively.

The relative consumption index (CI) was significantly different between different specific age classes of individuals (ANOVA, p<0.0001); the highest value was found in nymphs A (11.840±13.749), which consumed more food per unit of body weight. Adults had the lowest CI, with similar values for males (1.260±1.438) and females (1.263±0.279). The CI was not significantly different between females with immature and mature ovaries (ANOVA, p>0.05). Destruction rate was 2.21%, 0.22% and 1.91% of the remaining leaf in adult females, adult males and nymphs B (only stages V and VI), respectively. Of the nymphs, stage I to IV did not produce destruction material as a result of feeding. Destruction values tended to be similar between stage VI nymphs (only females) and adult females. Significant differences were found in destruction rate between adult females, adult males, and nymphs B (ANOVA, p<0.0001).

Individual cumulative consumption (C_{cum}) was significantly different among different specific age classes of the *C. aquaticum* population (ANOVA, p<0.0001); higher and less variable values were found in adult females (24.704±6.039g) than in adult males (17.456±19.315g), whereas the lowest value was observed in nymphs A (0.482±0.517g). Considering total longevity of *C. aquaticum*

individuals, individual cumulative consumption (from stage I nymphs to adults) was also higher in females (27.34g) than in males (20.09g). The application of the post hoc Tukey test to tests for significant differences between different specific age classes of *C. aquaticum* are provided in Table 1.

Growth and efficiency of conversion of ingested food in *C. aquaticum*: Individual dry weight of grasshopper was significantly different between specific age classes of grasshopper population (ANOVA, $p < 0.0001$); highest values were observed in adult females (0.096 ± 0.015 g).

Relative growth index (GR) values were also significantly different between different specific age classes of the population (ANOVA, $p < 0.0001$); post hoc Tukey test identified three groups of individuals: nymphs A with the highest increase in dry weight per day (0.107 ± 0.042), nymphs B (0.065 ± 0.038) and adult females (0.045 ± 0.016) with intermediate growth rates, and adult males with the lowest daily increase in dry weight (0.024 ± 0.014).

Efficiency of conversion of ingested food to insect biomass (ECI) was significantly different between specific age classes of the

C. aquaticum population (ANOVA, $p < 0.0001$); post test separated the adult males, which had the lowest ECI values, from other categories of individuals. GR and ECI were not significantly different between females with immature and mature ovaries (ANOVA, $p > 0.05$). Tukey test to identify significant differences between different specific age classes of *C. aquaticum* are provided in Table 2.

Effect of *C. aquaticum* consumption on the *E. crassipes* plant population: Plants with elongate leaves (large biotype) were dominant at the study site. *E. crassipes* floating meadow had a leaf density of 401 ± 115.5 leaves/m², with a leaf height of 55.9 ± 31.3 cm. Leaf lamina biomass and total leaf biomass were 251.1 ± 92.2 g/m² and 799.6 ± 115.5 g/m², respectively.

Mean total abundance of *C. aquaticum* at the study site was 6.8 individual/m² (± 6.61). Mean abundance of nymphs was 4.8 individual/m² (± 5.74), whereas mean abundance of adults was 2 individual/m² (± 3.39). There was a significant difference between the average abundance of *C. aquaticum* nymphs and adults (Wilcoxon test, $p = 0.015$, $n = 30$). The daily plant consumption (dw) of the *C. aquaticum* population in the field per m² was 0.187 ± 0.224 g

TABLE 1

Mean quantities of *Eichhornia crassipes* (g) eaten by specific age classes of *Cornops aquaticum* population: nymphs A (stages I and II), nymphs B (stages III to VI), adult males and adult females

	Nymphs A	Nymphs B	Adult males	Adult females
Daily consumption by individual	0.029 ^a ± 0.031	0.049 ^b ± 0.033	0.066 ^b ± 0.073	0.119 ^c ± 0.03
CI	11.840 ^c ± 13.749	3.221 ^b ± 3.883	1.260 ^a ± 1.438	1.263 ^{a,b} ± 0.279
Destruction rate	0.00	0.003 ^b ± 0.001	0.000 ^a ± 0.000	0.006 ^c ± 0.002
C_{cum}	0.482 ^a ± 0.517	2.164 ^b ± 1.678	17.456 ^c ± 19.315	24.704 ^d ± 6.039

Daily consumption by individual: g of food eaten by individual; consumption index (CI): g of food eaten per g of animal per day; destruction rate: g of leaf destroyed by individual per day; individual cumulative consumption in each specific age class (C_{cum}): g of food eaten by individual during the longevity of each specific age class.

(\pm) is the standard deviation.

Different letters indicate means statistically differences between population categories of *C. aquaticum* (Tukey's test, $p < 0.05$).

TABLE 2

Growth and food conversion efficiency for specific age class of *C. aquaticum* population: nymphs A (stages I and II), nymphs B (stages III to VI), adult males and adult females

	Nymphs A	Nymphs B	Adult males	Adult females
Individual dry weight	0.003 ^a ±0.001	0.025 ^b ±0.017	0.053 ^c ±0.006	0.096 ^d ±0.015
GR	0.107 ^c ±0.042	0.065 ^b ±0.038	0.024 ^a ±0.014	0.045 ^b ±0.016
ECI (%)	3.489 ^b ±4.294	4.459 ^b ±4.974	0.030 ^a ±0.025	3.607 ^b ±1.375

Individual dry weight: g of animal; growth rate (GR): g of animal biomass gained per g of animal per day; efficiency of conversion of ingested food to insect biomass (ECI): g of animal biomass gained per g of consumed food.

(±) is the standard deviation.

Different letters indicate means statistically differences between population categories of *C. aquaticum* (Tukey's test, $p < 0.05$).

dw for nymphs, 0.186 ± 0.315 g dw for adults, and 0.382 ± 0.400 g dw for all individuals of the population (nymphs+adults). There was no significant differences between the daily plant consumption (dw) of nymph and adult grasshoppers/m² in the field (Wilcoxon test, $p > 0.05$, $n = 30$).

Given a mean daily plant consumption/m² of 0.382 for *C. aquaticum* individuals, and a daily net primary production of 3.4g/m² of *E. crassipes* calculated from Neiff & Poi de Neiff (1984) and Neiff *et al.* (2008) for floating meadows at the study site, the estimated food intake of this grasshopper was 11.23% of the plant productivity.

DISCUSSION

Food consumption of *C. aquaticum*:

Higher daily consumption by individual females is related to a highest mean dry weight and increase in dry weight per individual found in this specific age class of the population. Highest individual consumption in females is also found in semiaquatic (Amorim & Adis 1994) and grassland grasshoppers (Gangwere 1959, Sánchez & De Wysiecki 1990).

In the Amazon floodplain, the relative consumption index (CI) of *C. aquaticum* with *E. crassipes* as a host plant is 0.9g of food

eaten per gram of animal per day (Adis & Junk 2003); given a mean dry weight per individual of 0.058g for adult males and 0.093g for adult females, estimated daily consumption by individual to the Amazonian population is 0.0522g and 0.0837g, respectively; these values are consistent with the results we obtained for the *C. aquaticum* population on the Paraná River floodplain.

The CI of *C. aquaticum* found in our study is higher than the consumption found for other semiaquatic grasshoppers (Thomas 1974, Amorim & Adis 1994). Based on the amount of consumption reported by Amorim & Adis (1994) for *Stenacris fissicauda fissicauda* (Leptysminae), we estimated the CI for the different specific age classes of this Amazonian grasshopper (nymphs A: 0.774, nymphs B: 0.473-0.502 and adults: 0.262). Because the mean individual dry weights of both Leptysminae species are similar, thus, we postulate that *C. aquaticum* has a greater consumption capacity than *S. fissicauda fissicauda*. Differences in consumption between the two Leptysminae species may be related to the leaf characteristics of their host plants; while the leaves of *Eichhornia* have a considerable proportion of aerenchyma and few sclerenchyma cells (González 2002, Boeger & Adis 2007), *Paspalum* leaves have few aerenchyma

and a considerable amount of sclerenchyma associated with the vascular bundles and within the subepidermic layer (Aliscioni 2000). The RCI of *Paulinia acuminata* (Pauliniidae) eating *Salvinia* is 0.19 and estimation was made on the basis of the fresh weight of the animal (Thomas 1974).

The generalist *Dichroplus pratensis*, which is one of the most abundant grassland grasshoppers and has an economic impact in the Argentine pampas, has a CI considerably lower than the values obtained for *C. aquaticum* in our study (Sánchez & De Wysiecki 1990, De Wysiecki & Sánchez 1992). The same trend is observed in other important species of terrestrial grasshoppers (Philippe 1991, Thompson *et al.* 1996, Fanny *et al.* 1998, Abdel-Rahman 2001).

Nymphs A of *C. aquaticum*, which have the lowest values of daily consumption by individual, have higher CI values in comparison with the other categories of the population. This finding is consistent with that of Amorim & Adis (1994) for the semiaquatic *S. fissaicauda fissaicauda*. Greater consumption of food per animal weight in nymphs with respect to adults has also been found in terrestrial grasshopper (Sánchez & De Wysiecki 1990, Pereyra *et al.* 1996).

The CI of *C. aquaticum* adults seems to be similar in females and males, unlike findings for other Acrididae (Gangwere 1959, Sánchez & De Wysiecki 1990). In the current study, the relative consumption index of *C. aquaticum* is not related to ovary maturation. In contrast, Sánchez & De Wysiecki (1990) note that pre-reproductive females of *D. pratensis* engage in more feeding activity than reproductive ones.

Considering the total losses (destruction rate+consumption), the destruction rate of *C. aquaticum* appears to be unimportant in comparison to the high amount of food consumed (Table 1). According to the data provided by Sánchez & De Wysiecki (1990), destruction rates of *D. pratensis* represent between 4.9% and 9.7% of the total losses.

Individual cumulative consumption was higher in adult females than in other age classes

of the population. Although adult males have higher longevity than adult females (Franceschini 2008), the latter have notably greater individual daily consumption values. The same trend was observed in *S. fissaicauda fissaicauda* (Amorim & Adis 1994), with lower values than those found for *C. aquaticum* in our study.

Growth and efficiency of conversion of ingested food in *C. aquaticum*:

The greater relative growth index (GR) values for *C. aquaticum* nymphs when compared to adults is consistent with results obtained for *D. pratensis* by Pereyra *et al.* (1996). The higher growth value for nymphs A with respect to other specific age classes of the *C. aquaticum* population is related to the finding that this specific age class has the highest consumption per gram of animal. The GR of *D. pratensis* nymphs is closely related to the water content of food, and nymphs that eat withered leaves show greater growth values (Pereyra *et al.* 1996). Higher values of GR than *C. aquaticum* are known in adults of terrestrial grasshoppers (Pereyra *et al.* 1996, Abdel-Rahman 2001, Frankze *et al.* 2010).

Adult females of *C. aquaticum* convert the food ingested more efficiently to insect biomass than do adult males; the same trend is also observed in *D. pratensis* (Pereyra *et al.* 1996). ECI found in terrestrial grasshoppers are higher than the values obtained for *C. aquaticum* (Pereyra *et al.* 1996, Fanny *et al.* 1998, Frankze *et al.* 2010); ECI is closely related to the quantity and quality of food consumed (Haniffa & Periasamy 1981, Bernays & Simpson 1990, Pereyra *et al.* 1996). Nymphs A of *C. aquaticum* had a high CI and ECI, and as a consequence, GR of this specific age class was also high. Conversely, adult males of this grasshopper had low values of CI and ECI, moreover GR were also low.

Effect of *C. aquaticum* consumption on the productivity of *E. crassipes*:

Our results show that the effect of *C. aquaticum* on the productivity of *E. crassipes* is high in the floating meadows of the Paraná River floodplain.

At the same study site and season, an impact of 3.78% of *E. crassipes* productivity was previously reported for this grasshopper, calculated on the basis of a population density of 1.95 ind/m²±2.15 (Franceschini 2008); this density value was estimated with the semi-quantitative method, which is widely used for grassland grasshoppers (Sánchez & De Wysiecki 1990). The higher density values obtained in our study suggest that trapping the vegetation and directly counting the number of individuals within the sweep net is the most appropriate method for estimating the abundance of this semiaquatic grasshopper. Abundance of approximately one individual per plant was mentioned for this grasshopper by Silveira-Guido & Perkins (1975) in some sites located along to the Paraná River. Number of waterhyacinth plant per m² seems to vary in our study area, depending of the biotype, size and height of plants, the elasticity of the floodplain system during high and low water phase and, the wind effect that can produce a coefficient of variation of 30% of the plant density at the same day (Neiff *et al.* 2008, Neiff 2009, pers. comm.).

In the Amazon floodplain, the abundance and impact of the *C. aquaticum* population on *E. crassipes* floating meadows is higher than the values that we found for the population of this grasshopper in the Paraná River floodplain. In fact, Adis & Junk (2003) report a density of the *C. aquaticum* population of 21.4 to 33 ind/m², net primary production of *E. crassipes* of 15g/m² per day, and a feeding impact of this grasshopper of 16.7% of the net primary production of the host plant. In the Panama Canal, Sanders *et al.* (1982) report that *C. aquaticum* produces slight to moderate damage on mature leaves of *E. crassipes* collected in situ. In non-native areas, Bownes *et al.* (2010) found that *E. crassipes* decline significantly the competitive performance and biomass as a result of herbivory by *C. aquaticum* adults, using in the experiments the grasshopper abundance reported by Silveira-Guido & Perkins (1975) to native areas.

The effect of the semiaquatic grasshoppers on plant populations was also studied in *Paulinia acuminata* (Pauliniidae) by Vieira & Adis

(1992). According to these authors, the density of this grasshopper in the field is between 12.6 and 43.2 ind/m², and growth of *Pistia stratiotes* and *Salvinia auriculata* is 51% to 64% higher in enclosure experiments.

In terrestrial grasshoppers that have economic impact, a density of 22 ind/m² of *D. pratensis* removes 4.8% of the primary production of the Pampa grasslands, which has a productivity of 5610kg/ha/yr (De Wysiecki & Sánchez 1992). Because the density of *C. aquaticum* is lower and the effect on plant productivity is higher in comparison with *D. pratensis*, the semiaquatic grasshopper can be considered to be a more efficient consumer. A greater effect on the plant population has also been found for the terrestrial grasshopper *Hesperotettix viridis*, which can reduce up to 75% of the biomass of the shrub *Gutierrezia sarothrae* (Compositae) with a density of 5 individuals per plant (Thompson *et al.* 1996).

The food consumption of *C. aquaticum* and other herbivores has not been taken into account in estimations of *E. crassipes* productivity, possibly because invertebrate herbivory of living macrophytes was considered unimportant until recently (Wetzel 1983), whereas in terrestrial systems, damage caused by grasshoppers is included in estimations of grassland productivity (De Wysiecki & Sánchez 1992). Franceschini *et al.* (2010) found that the lamina biomass removed in *E. crassipes* by *C. aquaticum* and other herbivorous invertebrates is high (13% to 26% of the lamina biomass/m²), pointing that damage due to herbivory must be taken into account in biomass and productivity estimations of this macrophyte.

C. aquaticum consumes a higher amount of food per dry weight of animal in comparison with other semiaquatic and terrestrial Acrididae yet, although damage to *E. crassipes* productivity is considerable, it is not enough to prevent the growth and coverage of this macrophyte in the study site. This may be explained by the relatively low abundance of grasshopper population and the high growth rate, biomass and productivity of the host plant (Neiff & Poide Neiff 1984, Neiff 1990, Neiff *et al.* 2008).

Thus, our first hypothesis, that *C. aquaticum* consumes a low quantity of *E. crassipes* per dry weight of animal, producing a scarce effect on the productivity of this macrophyte, must be partially accepted. Because there were important differences in consumption, growth, and food conversion efficiency between different specific age classes of the population, we also accept the second hypothesis that the food consumption, growth rate and food conversion efficiency of this grasshopper vary according to the age of individuals.

Our study was conducted during a period of prolonged hydrological isolation of the Paraná River floodplain lakes (low water). According to Poi de Neiff *et al.* (1977) and Poi de Neiff & Casco (2003), grasshopper abundance under these conditions is noticeably higher than the abundance observed during periods of a prolonged hydrological connection of the floodplain lakes (high water).

This study also highlight the need to consider estimations of abundance (with an adequate method for semiaquatic grasshopper) and the composition of the specific age classes in the population structure (especially from long-term studies) in order to assess consumption and impact of *C. aquaticum* on *E. crassipes* populations. Finally, we suggest that information about population and feeding impact of herbivores from native areas are crucial in species that have been considered as biological control agent of *E. crassipes* in non-native areas. Moreover, we suggest including herbivorous damage in estimations of macrophyte productivity and biomass.

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RESUMEN

Cornops aquaticum es una tucura semiacuática Neotropical que vive asociada a las Pontederiaceae y constituye uno de los más importantes herbívoros de *Eichhornia crassipes* en áreas nativas. Los objetivos de este trabajo son: (1) cuantificar el consumo de *C. aquaticum* (2) determinar la tasa de crecimiento y la eficiencia de conversión del alimento ingerido de esta tucura, y (3) determinar el efecto del consumo en la productividad de *E. crassipes*. De cada categoría de edades de la población se utilizaron 30 individuos: ninfas A, ninfas B, adultos machos y hembras. Los insectos fueron confinados individualmente en recipientes con hojas de *E. crassipes*. Luego, se estimó el consumo por individuo, la tasa de consumo (CI), tasa de crecimiento (GR) y la eficiencia de conversión del alimento (ECI). La abundancia de *C. aquaticum* se determinó en verano y con los datos de productividad de la planta se calculó el efecto del consumo sobre *E. crassipes*. La tasa de consumo, tasa de crecimiento y la eficiencia de conversión del alimento varió entre las distintas categorías de edades de la población. *C. aquaticum* consume el 11% de la productividad primaria de *E. crassipes*. Si bien el consumo es alto, el daño no produce mermas importantes en los camalotales debido a la abundancia relativamente baja de *C. aquaticum* y la alta productividad de la planta huésped.

Palabras clave: consumo, *Cornops aquaticum*, *Eichhornia crassipes*, herbivoría, planicie de inundación, productividad de macrófitas, tucuras.

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