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ORIGINAL ARTICLE

Effects of coypu (*Myocastor coypus*) abundances and diet selection on a wetland of the Patagonian steppe

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We assessed diet selection, impact on vegetation, and explored habitat relationships with marsh birds of coypus (*Myocastor coypus*) in a steppe lagoon in Argentinean Patagonia. In two consecutive springs, abundance and spatial use of the coypus and nesting marsh birds were estimated by direct counts. The coypu was a selective consumer with seasonal variations in food items, and *Myriophyllum* sp. and *Schoenoplectus californicus* dominated its diet. Coypus and marsh birds showed a differential spatial use when rushes cover was high. However, when rushes cover decreased by coypu browsing, there was a similar use of space, and marsh birds were displaced to nest on the open water and other poorly protected areas of the rushes. Our results suggest that high abundances of coypu can have a detrimental effect on wetland ecosystems. Systematic monitoring and evaluation of their effects on wetlands in recently colonized areas is recommended.

Keywords: diet selection; coypu impact; invasive species; pest; marsh birds; Argentina; wetland

Introduction

Coypus (*Myocastor coypus*), also known as nutrias, are aquatic herbivores, native to southern South America, and widely distributed in Argentina (Parera 2002). They are tolerant to different climatic and hydrological conditions and have a high capability of dispersion and colonization (Carter & Leonard 2002; Bertolino et al. 2005). Their reproductive rate is high with 2–3 reproductive periods per year and a mean litter size of 5 at birth (Parera 2002). Coypus build resting and feeding platforms of compacted vegetation, form trails through edge vegetation, dig burrows, and also create grooming areas (Witmer & Lewis 2001; Carter & Leonard 2002; Guichón 2003). The diet of coypus in the Pampas plains of Argentina consists of hygrophilic and aquatic plants and they feed near the water (< 10 m), and generally do not affect agricultural crops (Borgnia et al. 2000; D'Adamo et al. 2000; Guichón et al. 2003). However, in many countries the introduction of coypus caused severe economic damage and they were considered a pest because they negatively affected crops, flora, fauna, and drainage systems (Witmer & Lewis 2001; Carter & Leonard 2002; Bertolino et al. 2005; Bertolino & Viterbi 2010). These characteristics make coypus one of the world's 100 most invasive species (Carter & Leonard 2002; Bertolino 2009).

The coypus' impact on wetlands through feeding on aquatic vegetation can be severe because they have selective feeding habits, cause massive reduction of vegetation, and eliminate or reduce native plant species (Witmer & Lewis 2001; Bertolino & Genovesi 2007). In the USA, the species has been implicated in muskrat (*Ondatra zibethicus*) population declines, probably due to competitive exclusion (Witmer & Lewis 2001). Unfortunately, little information is available about the direct or indirect impacts of coypus on vegetation and fauna within their native range. The coypus are patchily distributed throughout their historic range, although the current distribution was expanded associated with artificial water bodies such as canals and dams (Parera 2002) and probably the presence in the Patagonian steppe was a result of human introduction (Lessa et al. 2008). In this region, the subspecies *M. c. bonariensis* inhabits water bodies with low vegetation cover and its densities are lower than in the rest of the country (Parera 2002).

Wetlands are ecosystems of priority in conservation biology, since they are subject to major disturbances that have led to significant losses of biodiversity (Abell 2002; Battisti et al. 2008). In semi-arid and arid regions, high evapotranspiration, and low rainfall make these few places essential for a large number of species (Hollis 1990). In the extra-Andean

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Patagonia, wetlands are environments of high conservation value because they support many wildlife species, some of which are included on priority conservation lists (Perotti et al. 2005). Although the current understanding of Patagonian wetlands is fragmentary, some studies indicate that the use of the land and introduction of exotic species represent the factors of greatest impact on Patagonian wetland communities (Bonvissuto et al. 1992; Bertiller & Bisigato 1998; Bonvissuto & Somlo 1998; Macchi et al. 1999; Perotti et al. 2005).

Most biological invasions are caused by the introduction of species from elsewhere, although some native species have become invasive in recently occupied habitats (Carrete et al. 2010; Simberloff 2010). The coypu has the typical characteristics of an invasive vertebrate species: a high reproductive potential, wide distribution, and the ability to live in a wide range of environmental conditions (Ehrlich 1989; Bertolino & Genovesi 2007). The feeding behavior of coypus and their impact on vegetation has been extensively studied in countries where they have been introduced (Towns et al. 2003; Johnson & Foote 2005). In Patagonia, there are no studies of the changes in abundances and the effects of this species on wetland communities of plants and vertebrates. The aims of this work were to determine coypus' feeding behavior and to evaluate their possible impact on vegetation. We hypothesized that a high consumption of hygrophilic vegetation by the coypus will modify vegetative structure. We also conducted preliminary observations and explored the habitat use by coypus and nesting pairs of marsh birds in this Patagonian wetland.

Materials and methods

Study area

The study was carried out at a lagoon, in a steppe area of NW Patagonia, inside a protected area named "Wildlife refuge Laguna los Juncos" (41°03′38″ S, 71°00′38″ W). This is an endorheic wetland of 7 ha with a maximum depth of 1.5 m and periods of desiccation (Perez et al. 2005). It is located at an elevation of 910 m. The mean annual temperature in this area is 8°C, with a mean annual precipitation of *c.*600 mm and the largest amounts of precipitation (as rain or snow) in autumn and winter (Bustos 1996).

The vegetation surrounding the lagoon corresponds to the western district of the Patagonian phytogeographic province, characterized as a grassy, shrub steppe of *Mulinum spinosum* (Apiaceae) and *Stipa speciosa* (Poaceae), accompanied by *Festuca pallescens* (Poaceae), *Poa* spp. (Poaceae), *Bromus* spp. (Poaceae), and the shrubs *Senecio* spp.(Asteraceae) (León et al. 1998). The lagoon has emergent vegetation of rushes (*Schoenoplectus californicus*, Cyperaceae) and the aquatic watermilfoil (*Myriophyllum* sp., Haloragaceae). Along the shoreline there are meadows of hygrophilic vegetation characterized by *Juncus* spp. and *Carex* spp. (Cyperaceae) and exotic trees: *Salix nigra* (Salicaceae), *Betula pendula* (Betulaceae), and *Malus domestica* (Rosaceae) (Perez et al. 2005).

In this wetland a small number of 3–4 coypus were observed during monitoring of fauna performed annually from 1996 to 2008 (Galende unpublished data), and a previous study reported that their presence was scarce (Perez et al. 2005). Perez et al. (2005) recorded 87 species of resident and migratory birds, 30 of which are dependent on the existence of water and shoreline environments. The rushes and aquatic vegetation are used mainly by the Silvery Grebe (*Podiceps occipitalis*, Podicipedidae), and coots (*Fulica leucoptera*, *F. armillata*, *F. rufifrons*, Rallidae), for protection and support of their nests (Canevari et al. 1991; De la Peña 1999).

The lagoon is fenced and activities are restricted to bird watching. Hunting and navigation are not allowed. However, the land surrounding the lagoon is used for livestock grazing in low quantities but only during the non-breeding season of birds. The study site is one of the few Patagonian wetlands in arid zones with high diversity of birds; therefore, it represents special interest for wildlife conservation (Perez et al. 2005).

Vegetation study

Surveys of vegetation and coypu feces were performed in spring 2009 (December) and winter 2010 (August), to examine the preferences of coypu feeding habits. We estimated composition and cover of terrestrial plants near the edge of the lagoon, since the feeding behavior of coypus is concentrated within 5 m from the edge (Borgnia et al. 2000; Guichón et al. 2003). In order to estimate availability every 50 m around the perimeter of the lagoon, we established two sampling quadrants (50 × 50 cm), one on the ground (at 3 m from the shoreline), and the other on the water (5 m from the shoreline) following Guichón et al. (2003), totaling 42 plots per season. These distances included the most important areas of rush cover. The cover of aquatic plants (%) was visually estimated using panoramic photos. For each quadrant, we estimated the percentage of vegetative cover for each species and expressed data as means (± SE) for each habitat type: terrestrial, waterlogged soil and aquatic. Plants were grouped into four categories corresponding to the three habitat types: (1) terrestrial monocotyledons, (2) terrestrial dicotyledons, (3) hygrophilic monocotyledons, and (4) hygrophilic dicotyledons.

The effect of browsing by coypus was estimated by differences in height and size in the 10 patches of rushes in spring 2009, winter 2010, and spring 2010. As an indicator of browsing by coypus, we measured the maximum and minimum heights in two points at each patch of rushes. The size of each patch of rushes was estimated by the maximum width and overall length of the patch. Browsing by coypus was easily distinguishable because they produce a diagonal cut on the stem. Based on this foraging behavior characteristic, no browsing by other species was detected in the rushes.

Fecal collection and diet analysis

In spring 2009 and winter 2010 (during the last 10 days of each season) we collected fresh coypu fecal pellets within 5 m of the shoreline of the pond, where most coypus' activities take place (D'Adamo et al. 2000; Guichón et al. 2003). In each season 25 fresh fecal samples were collected, and five pellets from each one were selected randomly for the microhistological analysis. Pellets were dried at 60°C and milled to a size of 1 mm, to reduce variation. All the material was cleared with 90% ethanol followed by a treatment with 50% sodium hypochlorite, and stained with safranin. Finally, the sample was mounted in glycerin jelly on slides for microscopic observation (Latour & Pelliza de Sbriller 1981). We also sampled plant species near the pond and similarly prepared them, to make a microhistological reference collection. Plant fragments were identified in 100 microscopic fields per fecal sample at 100× magnification (Sparks & Malechek 1968; Holechek et al. 1982). Presence of food items was recorded for each field, and its percentage of occurrence was determined for each sample (Holechek et al. 1982). Data are given as means (± SE). We identified plant material found in the fecal pellets to species level whenever possible.

Use of rush patches by coypus and nesting birds

In two consecutive breeding seasons (December 2009 and December 2010), we performed direct counts of the total number of coypus (juveniles and adults) and nesting pairs of marsh birds to explore relationships in habitat use. During two days in each spring, two observers walked the entire perimeter of the lagoon at different times of day, and recorded the number of nesting pairs of these marsh birds and the location of their nests. Observations were performed with 12 × 50 binoculars at the time of highest diurnal activity of coypus, between 09:30 h and 16:00 h (Galende personal observation). Two counts, spaced by one hour, were conducted during the morning, and two in the afternoon, totaling four counts per season. We expressed the data as means (± SD) of the four counts for each season.

Statistical analysis

Seasonal differences in terrestrial plant species that cover >5% of the area, and differences in height, and size of the rushes were tested by the Wilcoxon test for dependent samples (Zar 1999). The proportions of plant groups in the diet were assessed by the Kruskal–Wallis ANOVA and a posterior multiple comparisons test. Seasonal differences in consumption of plant groups, and species (in proportions >5%) were evaluated by the Wilcoxon test.

Diet selection by functional groups and plant species (consumed in proportions >5%) in relation to their availability was calculated by using simultaneous confidence intervals of Bonferroni. These intervals determine the actual proportion of use (Pu) for each vegetative group in the following way (Neu et al. 1974; Byers et al. 1984):

$$\begin{aligned} \bar{pi} - Z\,(\alpha/2k)\sqrt{\bar{pi}\left(1-\bar{pi}/n\right)} &\le Pu \\ &\le \bar{pi} + Z\,(\alpha/2k)\sqrt{\bar{pi}\left(1-\bar{pi}/n\right)}, \end{aligned} \tag{1}$$

where $\bar{pi}$ is the proportion observed of use, $Z\,(\alpha/2)$ the upper standard normal table value corresponding to a probability tail area of $(\alpha/2)$, k the number of dietary categories, and n the total observations in diet. We then compared Pu with the expected proportion of use (Pe), which is calculated as the relative plant cover by observed diet frequency (Neu et al. 1974; Byers et al. 1984). Plant use was qualified as: selected, proportional, or avoided depending on whether the expected proportion was located below, within or above the confidence interval of the dietary frequency.

Microhabitat preferences of coypus for the rushes were evaluated in two consecutive springs. We considered the relations between the maximum number of coypus, height, and size of the rush patches, and applied the Spearman correlation coefficient. This coefficient was also used to test for correlation between the number of bird breeding pairs that use the rushes and the number of coypus in two breeding seasons. In all cases we used a significance level of $p < 0.05$ (Zar 1999).

Results

Vegetation composition

The vegetation adjacent to the lagoon consisted of 20 terrestrial species, and the hygrophilic vegetation was dominated by *S. californicus* and *Myriophyllum* sp. (Table 1). There were significant seasonal changes (spring and winter) in the cover of main terrestrial plants (in proportions >5%, $Z = 2.31$, $p < 0.05$,

Table 1. Comparison between the availability of plants and their occurrence in the diet of coypus at the wildlife refuge "Laguna los Juncos" in the Patagonian steppe, Argentina, during spring 2009 and winter 2010. Availability was measured as plant cover in 50 × 50 cm plots ($n = 42$) in the terrestrial and waterlogged habitats and by direct visual observation of cover in the aquatic habitat; occurrence in diet was assessed by fecal analysis. The results are expressed as mean percentage (± SE) for each habitat type (waterlogged soil, terrestrial, aquatic). In parentheses: plant species preferred (S), avoided (A) or used with indifference (P) calculated by Bonferroni confidence intervals. $n = 5$ composite samples by season. Total percentage of a vegetation type (Total) is the mean total cover of this vegetation in the correspondent habitat. The difference to 100% corresponds to water and/or soil.

Habitat type		Spring		Winter		
		Plant cover	Occurrence in diet	Plant cover	Occurrence in diet	Average in diet (%)
Waterlogged soil	Hygrophilic monocots					
	Schoenoplectus californicus	29 ± 7.6	18.4 ± 4.4 (P)	18 ± 5.9	13.3 ± 2.3 (P)	15.8 ± 2.5
	Juncus spp.	14.2 ± 3.7	11.1 ± 2.2 (S)	13.8 ± 2.7	2 ± 0.4 (A)	6.5 ± 4.5
	Poa spp.	19.2 ± 5.9	10.5 ± 2.7 (P)	15 ± 2.5	7.6 ± 0.8 (A)	9.1 ± 1.4
	Carex sp.	1 ± 0.4	6.7 ± 1.1 (S)	1 ± 0.5	1 ± 0.2 (A)	3.9 ± 2.8
	Eleocharis sp.	7.3 ± 3.1	9.4 ± 1.4 (S)	7.1 ± 2.9	4.1 ± 0.2 (P)	6.8 ± 2.6
	Total	71.3 ± 5.1	56.1 ± 4.2 (S)	54.9 ± 2.9	28 ± 3.0 (A)	42 ± 14
Aquatic	Hygrophilic dicots					
	Salix nigra	—	2.4 ± 1.7	—	10.7 ± 1.5	6.5 ± 2.6
	Myriophyllum sp.	70	22.4 ± 2.1 (A)	60	46 ± 1.9 (S)	34.2 ± 11.8
	Total	70	24.8 ± 3.6 (A)	60	56.5 ± 2.9 (S)	40.7 ± 15.9
Terrestrial	Monocots					
	Hordeum murinum	6.9 ± 3.7	1.8 ± 0.7	3 ± 1.2	3.8 ± 0.7	2.8 ± 1
	Holcus lanatus	0.5 ± 0.4	2.9 ± 1.1	0.2 ± 0.2	4.2	3.6 ± 0.6
	Bromus tectorum	13.3 ± 3.9	9.5 ± 2.6 (S)	3.3 ± 2.1	4.7 ± 1.8 (S)	7.1 ± 2.4
	Stipa speciosa	2.9 ± 1.2	—	2.9 ± 1.2	—	—
	Total	23.6 ± 3.4	14.2 ± 2.4 (S)	9.4 ± 1.8	12.7 ± 2.4 (S)	13.4 ± 0.7
	Dicots					
	Rumex crispus	0.1 ± 0.1	—	—	—	—
	Veronica spp.	0.1 ± 0.1	—	—	—	—
	Myosotis sp.	1.7 ± 1.7	—	—	—	—
	Taraxacum officinale	0.1 ± 0.1	0.4 ± 0.4	2.2 ± 1	—	0.2 ± 0.2
	Rumex acetocela	0.1 ± 0.1	0.1 ± 0.1	—	—	0.05 ± 0.05
	Erodium cicutarum	0.8 ± 0.5	—	—	—	—
	Conium maculatum	0.5 ± 0.2	—	—	—	—
	Montia perfoliata	0.5 ± 0.4	—	—	—	—
	Berberis heterophylla	1.6 ± 1.6	1.6 ± 0.92	1 ± 1	0.2 ± 0.2	0.9 ± 0.7
	Acaena pinnatifida	0.1 ± 0.1	—	—	—	—
	Plantago lanceolata	11.5 ± 4.4	—	7.2 ± 2.6	1.5 ± 0.6	0.7 ± 0.7
	Trifolium repens	9.1 ± 3.2	2.5 ± 1.0	9.6 ± 1.9	1.1 ± 0.7	1.8 ± 0.7
	Undet. plant matter	—	0.4	—	0.1	0.13 ± 0.1
	Total	26.1 ± 1.2	4.6 ± 1.7 (A)	20 ± 1.6	2.8 ± 1.4 (A)	3.7 ± 0.9

Table 2. Variation in height and size of 10 rush patches in a Patagonian steppe lagoon in spring 2009, winter 2010 and spring 2010. Heights of the rush patches correspond to minimum and maximum values in cm.

	Spring 2009		Winter 2010		Spring 2010	
Rush patch	Area(m^2)	Height range (cm)	Area(m^2)	Height range (cm)	Area(m^2)	Height range (cm)
1	40	90–150	15	40–80	20	30–70
2	60	90–150	10	80–90	10	40–60
3	450	110–130	300	90–100	300	85–95
4	75	60–100	75	65–80	50	5–15
5	150	100–100	50	20–40	40	20–40
6	640	100–120	420	30–50	280	20–30
7	340	60–100	280	40–70	252	30–70
8	24	50–90	9	20–45	6	20–40
9	60	60–80	30	20–50	29	20–40
10	200	90–110	100	25–55	80	25–55
Mean ± SD	203.9 ± 65.7		128.9 ± 46.9		106.7 ± 37.9	

Wilcoxon test), and in the height and size of 10 patches of rushes (Table 2).

Between spring 2009 and winter 2010, the browsing by coypus significantly decreased the height of the tallest ($n = 10$, $Z = 2.80$, $p < 0.01$, Wilcoxon test) as well as the lowest rushes ($n = 10$, $Z = 2.70$, $p < 0.01$). In this period, the average total area covered by rushes also decreased significantly ($n = 10$, $Z = 2.66$, $p < 0.01$; Table 2). Comparing throughout an annual cycle from spring 2009 to spring 2010, the tallest ($n = 10$, $Z = 2.80$, $p < 0.01$) and the lowest rushes ($n = 10$, $Z = 2.80$, $p < 0.01$) decreased significantly in height, as well as the patch size ($n = 10$, $Z = 2.80$, $p < 0.01$; Table 2).

Diet selection

The diet of the coypus comprised 15 food items, and was dominated by hygrophilic vegetation (annual average 83%). The main species in the diet were *Myriophyllum* sp. and *S. californicus* (Table 1).

In spring, the coypus showed a differential consumption of the four plant groups (Kruskal–Wallis test $H_{3,20} = 15.75$; $p < 0.001$), and the hygrophilic monocots were consumed in higher proportion than terrestrial plants ($p < 0.05$, posterior multiple comparisons test). Three dietary items, *Myriophyllum* sp. (22%), *Juncus* spp. (11%), and *S. californicus* (18%) represented over 50% of the diet (Table 1). In winter, there were also differences in the consumption between the groups of plants ($H_{3,20} = 16.14$, $p < 0.001$). However, the hygrophilic dicots were dominant and showed a significant increase compared to spring ($Z = 2.02$, $p < 0.05$), while the hygrophilic monocots decreased in the diet ($Z = 2.02$, $p < 0.05$). The proportion of terrestrial monocots ($Z = 0.13$, $p > 0.05$) and dicots ($Z = 0.40$, $p > 0.05$) showed no changes in winter (Table 1). The consumption of *Myriophyllum* sp. ($Z = 2.02$, $p < 0.05$) and *Salix nigra* ($Z = 2.02$, $p < 0.05$) increased compared to spring, whereas *Juncus* spp. ($Z = 0.02$, $p < 0.05$) and *Carex* sp. ($Z = 2.02$, $p < 0.05$; Table 1) significantly decreased. The coypus showed selective feeding behavior, since some food plants were consumed in a higher proportion than their availability, with variations depending

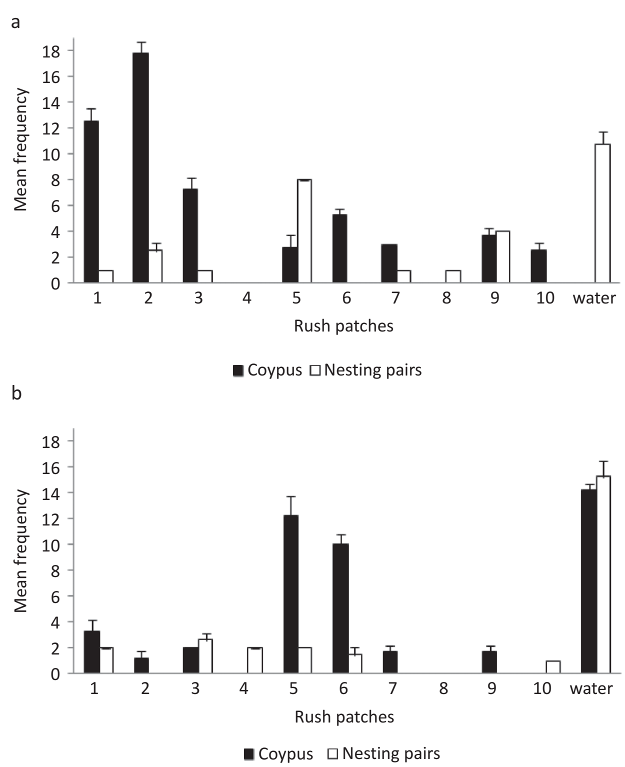

Figure 1. Use of rush patches ($n = 10$) by coypus and nesting pairs of coots (*Fulica* spp.) and silvery grebes (*Podiceps occipitalis*) in two consecutive years: a, spring 2009; and b, spring 2010. The number of individuals in the four counts per season is expressed as mean ± SD.

on the season (spring $X^2 = 210.7$, $p < 0.001$, winter $X^2 = 193.4$, $p < 0.001$). In spring, the hygrophilic monocots were selected, because the expected proportion of use (Pe = 0.3732) was lower than the proportion of actual use (Pu = 0.5025–0.5703). A similar relationship was observed for the terrestrial monocots: 0.1235 (0.1246–0.1729). In contrast, the terrestrial dicots 0.1366 (0.0384–0.0697) and the hygrophilic dicots 0.3664 (0.2306–0.2902) were avoided. In this season four species were selected, two consumed proportionally, and one avoided (Table 3).

In winter, the hygrophilic dicots 0.0415 (0.4692–0.5514) and the terrestrial monocots 0.065 (0.1150–0.1728) were selected. In contrast, hygrophilic monocots 0.3804 (0.2759–0.3522) and terrestrial dicots 0.1386 (0.0172–0.0460) were avoided. Three food items were selected, and two consumed proportionally (Table 3).

Coypu abundances and use of rushes

In four censuses conducted in spring 2009, we counted approximately 55 coypus (52–57, including adults and juveniles; Figure 1a). The number of individuals was positively correlated with the height of rushes ($R = 0.74$, $p = 0.01$, $n = 10$; Figure 1a, Table 2); however there was no correlation with the size of the rush patches (R = 0.07, $p = 0.82$, $n = 10$; Figure 1a, Table 2). In spring 2010, when height and size of rushes decreased (Table 2), the coypus switched to other rush patches in the lagoon (Figure 1). In this season the abundance of the approximately 46 coypus (45–48, Figure 1b) was no longer correlated with the height ($R = 0.21$, $p = 0.54$, $n = 10$; Table 2) nor the size of rush patches ($R = 0.25$, $p = 0.47$, $n = 10$; Table 2).

Table 3. Plant species selected (S), avoided (A) or used proportionally (P) by the coypus in spring 2009 and winter 2010 in the northwestern Patagonia. Proportion expected of use in diet (relative cover by the frequency in diet), and actual proportion of use calculated by Bonferroni confidence intervals.

	Proportion expected use	Proportion actual use
Spring		
Schoenoplectus californicus	0.1876	0.1588–0.2194 P
Eleocharis sp.	0.0472	0.0760–0.1222 S
Juncus sp.	0.0918	0.0961–0.1466 S
Poa spp.	0.1281	0.0916–0.1412 P
Carex sp.	0.0065	0.0497–0.0890 S
Bromus tectorum	0.0860	0.0909–0.1403 S
Myriophyllum sp.	0.4528	0.2540–0.3241 E
Winter		
Schoenoplectus californicus	0.1869	0.1513–0.2231 P
Poa spp.	0.1558	0.0794–0.1365 E
Myriophyllum sp.	0.6231	0.5952–0.6835 P
Bromus tectorum	0.0343	0.0428–0.0884 S

Coypu and bird associations

The numbers of coypus and the total number of bird pairs (grebes plus coots) remained almost unchanged between the censuses performed in each season (23 pairs of coots and seven of grebes in spring 2009; 26 pairs of coots and one of grebes in spring 2010). In spring 2009, the numbers of coypus (juveniles and adults) and nesting bird pairs in the rushes were not correlated ($R = 0.05$, $p = 0.87$, $n = 10$), and they showed a differential spatial use (Figure 1a). However, in spring 2010, when the vegetation was reduced, we found a positive association between the number of coypus and nesting pairs of birds ($R = 0.60$, $p = 0.04$, $n = 10$; Figure 1b) that suggest a spatial overlap. In the 10 rush patches monitored in spring 2009 and 2010, we observed changes in the distribution of silvery grebes and coot nests (Figure 1). In 2009 we counted 30 nesting pairs, 19 of which were in the rushes (grebes: 7, coots: 12). In spring 2010 we counted 27 bird pairs 11 of which were in the rushes (grebes: 1, coots: 10). The most important change was observed in rushes number five, where seven pairs of silvery grebes were nesting in 2009, but only one pair and four abandoned nests were found in 2010 (Figure 1). In addition, in other rushes, eggs from two coot nests were lost when they rolled out of the nest because the coypus used their nests as resting platforms.

Discussion

Feeding behavior

Coypus' feeding habits greatly reduced the coverage of vegetation, particularly on rushes, and produced changes in the ecological structure of the lagoon. This was due to their dramatically increased population since 2009. Coypus consume 1200–1700 g of food daily (Parera 2002), and at high densities they can reduce emergent vegetation and impact communities (Woods et al. 1992; Taylor & Grace 1995). We are confident that the observed differences in the structure of this wetland were due to browsing by coypus and not due to phenological changes of the rushes, because the diagonal shape of the clippings could clearly be attributed to coypus. Also, in other regions, similar plant species were selected by coypus and represented high percentages of their diet (Willner et al. 1979; Johnson & Foote 1997, 2005). This feeding behavior strongly reduced the stem density, height, and productivity of rushes (Johnson & Foote 1997, 2005), and changed the structure and abundance of native plants (Johnson & Foote 1997, 2005; Towns et al.

2003). In Italy, the coypus severely affected wetland vegetation, leading to the start of a control program. Subsequent studies indicated that vegetation recovery is possible when coypus occur at low densities (Bertolino et al. 2005).

Seasonal changes in diet

The diet of the coypus was dominated by hygrophilic vegetation, and only two species (*Myriophyllum* sp. and *S. californicus*) constituted half of the diet, accompanied by terrestrial monocots and dicots in lower proportions. Similar results were obtained in studies conducted in Argentina (Borgnia et al. 2000; Guichón et al. 2003), the USA (Wilsey et al. 1991), and Italy (Prigioni et al. 2005). In this study the coypus showed a selective feeding behavior with variations between food items according to the season. These results agree with other studies that documented seasonal variations according to environmental characteristics (D'Adamo et al. 2000; Guichón et al. 2003; Towns et al. 2003; Prigioni et al. 2005). The seasonal changes in the diet could be due to the phenology of the plant species and to the browsing by coypus, which modified availability and structure of the vegetation.

Rushes use by coypus and breeding birds

The spatial use of the coypus in two consecutive springs varied according to the structure of the rush patches. In spring 2009, they used the tallest rushes, but in the following spring, when the height of rushes had decreased by the coypus' browsing, they showed no preference in the use of the rush patches. These changes could be related to the decrease in the rushes cover since they are used by the coypus for protection and resting platforms (Guichón 2003).

The negative impact on aquatic vegetation by the coypus could directly affect the nesting potential of marsh birds (silvery grebes and coots). When patches of rushes had the highest values for cover (i.e., during low browsing activity), coypus and coots did not overlap in spatial use. In contrast, when the rushes cover declined, they tended to use the same places. At the end of the study, we found some coot and grebe eggs floating adrift, possibly indicating a lower quality of the nests due to a decrease in abundance and size of rushes and the watermilfoil used to hold the nests. In addition, coypus also directly affected bird nesting as they used coot nests as resting platforms, spoiling the reproductive effort of the birds. Similar damage caused by coypus on nests of the duck *Anas platyrhynchos* (Battisti et al. 2008) suggested that they could provoke a decrease of suitable nesting sites, affecting local populations of specialized birds or species of conservation concern (Bertolino & Genovesi 2007; Marini et al. 2011).

Implications for conservation

The population of coypus can quickly increase and cause impacts on vegetation. This makes coypus a species of particular interest as a modifier of ecosystem structures in areas important for conservation, such as wetlands. The modifications produced by coypus must be considered when planning conservation management of a wetland or a species inhabiting these areas. Therefore, it is important to start systematic monitoring of coypu populations, and to evaluate the factors that produce changes in the abundances of this herbivore, to increase our understanding of their patterns of invasiveness and the possible effects of the invasion.

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