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ORIGINAL ARTICLE

Trophic interactions among plains vizcacha (*Lagostomus maximus*), greater rhea (*Rhea americana*), and cattle in a wetland of the Paraná River Delta Region, Argentina

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The plains vizcacha (*Lagostomus maximus*) and the greater rhea (*Rhea americana*) are considered to compete for forage with cattle in agroecosystems of South America. The aims of this research were to analyze the diet diversity and the trophic niche breadth of these three herbivores where they share a wetland area in Argentina, and to assess the extent of food niche overlap throughout the year. The three species all showed relatively narrow trophic niches in all seasons, which defines them as selective feeders. Vizcacha and cattle showed the highest (54.8%) mean food niche overlap throughout the year. A low overlap was observed between greater rhea and the other two herbivores, except in Winter (61.2% greater rhea and cattle). Vizcacha showed the highest mean diet diversity, and diet diversity was similar, but lower, in greater rhea and cattle. According to the results, if livestock raising increases and a scenario of competition is considered, the vizcacha is likely be the most affected species, because its foraging areas are restricted to the surroundings of its fixed burrows. On the other hand, greater rheas have an opportunistic foraging behavior and can move into areas where cattle are absent.

Keywords: Argentina; *Lagostomus maximus*; niche breadth and overlap; Paraná River Delta; *Rhea americana*; wetlands

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Introduction

Animal usage of food resources and the trophic interaction among community members play an important role for an understanding of species ecology, conservation and management. Native sympatric herbivores tend to exploit the habitat in different ways, and this determines the structure of their community. Over evolutionary time, herbivores have developed feeding adaptations to reduce interspecific competition (Bell 1970; Owen-Smith 1988; Voeten & Prins 1999).

Domestic livestock were introduced into South America in the early 1500s and by grazing and trampling have severely altered the vegetation of Argentine natural areas, together with other human activities (Noton-Ramírez 1995). Domestic herbivores usually use similar food resources to those consumed by native wild herbivores (e.g. Kufner et al. 1992; Quintana et al. 1998; Bontti et al. 1999; Quintana 2002; Pereira et al. 2003) and thus have influenced the trophic niches of native herbivores in rangeland landscapes (Voeten & Prins 1999; Quintana 2002).

The plains vizcacha, *Lagostomus maximus* Desmarest, 1817 (Rodentia, Chinchillidae), and the greater rhea, *Rhea americana* Linnaeus, 1758 (Struthioniformes, Rheidae), are native species that often coexist with cattle in farming ecosystems in Argentina. The plains vizcacha is the largest species of the family Chinchillidae (Branch 1993), and it lives in communal burrow systems (''vizcacheras'') in groups composed of several adult females, young, and one or more adult males (Branch 1993). Members of a social group share a common foraging area around the communal burrow system (Branch & Sosa 1994; Arias et al. 2003), and feed on a variety of grasses and forbs, occasionally browsing on low shrubs (Giulietti & Jackson 1986; Kufner et al. 1992; Branch et al. 1994; Puig et al. 1997; Bontti et al. 1999; Pereira et al. 2003). Greater rheas live in polygamous social clusters, and are generally associated with farming and cleared fields where native vegetation has been replaced by improved pastures (Martella et al. 1996; Reboreda & Fernández 1997). These birds feed on leaves, seeds, fruits, arthropods, lizards, toads, and small mammals (Raikow 1968; Bruning 1974; Martella et al. 1996; Pereira et al. 2003).

Both these native species were considered to ''compete'' with domestic stock for forage, and are often hunted as agricultural pests because they cause losses in the yield of crops such as corn, soybean, pastures, and horticultural species (Rendel 1990; Martella et al. 1996; Navarro et al. 1997; Bertonatti

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1997). Wildlife conservation agencies are worried about the survival of these two wild native herbivores because current hunting and agriculture activities have severely reduced their populations in the wild (Redford & Eisenberg 1992; Bertonatti 1997). In spite of this, very few studies have examined trophic relations between the plains vizcacha and cattle (Giulietti & Jackson 1986; Kufner et al. 1992; Bontti et al. 1999), and between the greater rhea and cattle (Martella et al. 1996).

More recently, as a part of our study (Pereira et al. 2003), we described and compared diet composition of vizcacha, greater rhea, and cattle living in sympatry at the Paraná River Delta Region, Argentina. In that work we pointed out that vizcachas and cattle fed exclusively on plant leaves whereas greater rheas also fed on *Prosopis nigra* pods and some arthropods. This study also showed that diet composition of vizcachas and cattle were relatively constant along the year, whereas the diet of greater rheas was different among seasons, according to the availability of *P. nigra* pods. As for the comparison of diet composition among herbivores, vizcachas and cattle showed a similar diet; inversely, vizcacha and greater rhea diets did not show significant associations. In addition, diet composition of cattle and rheas were negatively correlated. According to those results, differences and similarities in foraging patterns were evidenced in both seasonal comparisons of each herbivore species and among the three species in each season. The question is how these differences can affect foraging niche characteristics of the native herbivores when they are sharing a wetland habitat with cattle. This fact is important because large wetland habitats are rapidly being converted into cattle-raising areas in Argentina due to the expansion of soybean crops in the formerly livestock fields. In consequence, native herbivore species are now facing new interactions with cattle. Therefore, baseline studies focusing on the interactions between native herbivores and cattle are needed to improve conservation strategies in these areas.

In this context, the aims of the present study were to analyze the seasonal effects on trophic niche breadth and diet diversity of plains vizcacha, greater rhea and cattle sharing a wetland area in the Paraná River Delta, and to assess the extent of food niche overlap throughout the year.

Materials and methods

Our analysis was based on the diets, assessed by fecal samples, of plains vizcachas, greater rheas and cattle performed between November 1996 and August 1998. For detailed description of methods and previous results about the diet analysis, botanical composition of herbivore diets, and their seasonal variations, see Pereira et al. (2003).

We calculated the trophic niche breadth by applying the standardized Levins' index, B_A (Hurlbert 1978; Krebs 1999). We used a Bootstrap technique to estimate breadths and their associated variances (Jaksic & Medel 1987). We assessed differences in breadth values between seasons and species using a one-way Kruskal–Wallis test, followed by Tukey Multiple Comparison Test when significant differences ($\alpha=0.05$) were found (Zar 1996). We measured diet overlap among the three species through the proportional similarity (PS) or Schoener's measure (Krebs 1999). We calculated diet diversity using the Shannon–Wiener index (Colwell & Futuyma 1971), and we used the Hutcheson test (Zar 1996) to determine seasonal differences in diet diversity for the same species and differences in diet diversity for different species in the same season. We averaged data over the two years in order to compare the plains vizcacha and cattle diets between them in each season and each herbivore diet among seasons.

Results

Trophic niche breadth

During the two-year study, the number of food items in the diets of plains vizcacha, greater rhea and cattle ranged from 17 to 39 (Table 1). The highest trophic niche breadth for the plains vizcacha was found in Spring, for cattle in Fall, and for greater rhea in Spring and Winter, whereas the lowest niche breadth for the plains vizcacha occurred in Fall and, for the other two herbivores, in Summer (Table 1).

The trophic niche breadth varied among the three herbivore species when comparing both seasonal patterns for a single species and those of different species in the same season (Kruskal–Wallis test, Table 2). The exceptions were greater rhea between Spring and Winter, its values being similar (Tukey test, $q=1.31$, $P<0.05$, Table 3), and the comparison between vizcacha and greater rhea in Spring and Fall (Tukey test, $q=0.76$, $P<0.05$ and $q=0.28$, $P<0.05$, respectively, Table 4).

Trophic niche overlap

The plains vizcacha and cattle showed the highest mean food niche overlap throughout the year (54.8%), ranging from 50.7% in Winter to 58.0% in Fall (Figure 1). Low overlap was observed during

Table 1. Number of food items, diet diversity and trophic niche breadth of plains vizcacha (PV), greater rhea (GR) and cattle (CA) in the Paraná River Delta.

	Spring			Summer			Fall			Winter		
	PV	GR	CA	PV	GR	CA	PV	GR	CA	PV	GR	CA
Number of food items	28	17	21	36	22	21	39	22	23	39	19	18
Diet diversity	1.21	0.97	1.02	1.25	0.88	0.96	1.14	0.93	1.14	1.19	1.07	0.97
Trophic niche breadth	0.41	0.40	0.31	0.32	0.19	0.26	0.21	0.21	0.47	0.25	0.43	0.29

Table 2. Kruskal–Wallis test (H) among the trophic niche breadths of (a) different seasons for the same herbivore species and (b) different herbivore species for the same season in the Paraná River Delta.

	H
(a)	
Plains vizcacha	200.00
Greater rhea	200.00
Cattle	114.47
(b)	
Spring	73.67
Summer	96.16
Fall	92.48
Winter	100.00

All the comparisons showed significant differences in trophic niche breadth at $P<0.01$.

Table 3. Tukey Multiple Comparisons (TMC, q) and Hutcheson test (HT) between different seasons for the same herbivore species in the Paraná River Delta.

	TMC	*HT*	
Comparison	*q*	*t*	df
Plain vizcacha			
Spring–Summer	4.17	−0.39	98
Spring–Fall	12.50	0.80	93
Spring–Winter	8.34	0.24	95
Summer–Fall	8.33	1.10	98
Summer–Winter	4.17	0.58	99
Fall–Winter	4.17	−0.53	100
Greater rhea			
Spring–Summer	9.45	1.51	95
Spring–Fall	6.52	0.51	91
Spring–Winter	1.31*	−1.34	100
Summer–Fall	2.93	−0.83	99
Summer–Winter	10.77	−2.66	96
Fall–Winter	7.83	−1.63	93
Cattle			
Spring–Summer	7.50	0.57	99
Spring–Fall	4.94	−1.73	97
Spring–Winter	2.93	0.55	100
Summer–Fall	12.44	−2.26	94
Summer–Winter	4.57	−0.03	100
Fall–Winter	7.87	2.27**	95

Critical q value (0.05; $K=4$; ∞)=2.63; *similar trophic niche breadth; **significant differences ($P<0.05$).

Spring and Summer between greater rhea and the other two herbivores, but overlap values increased in the remaining seasons reaching the highest value in this study in Winter (61.2% with cattle, Figure 1).

Diet diversity

The plains vizcacha showed the highest mean diet diversity throughout the year ($H'=1.19$, Table 1), and the difference with the diet diversity of the other two herbivores was significant, except in Fall with cattle ($t=-0.13$, $P>0.05$) and in Winter with greater rhea ($t=1.42$, $P>0.05$, Table 4). Between greater rhea and cattle, diet diversity showed no significant differences throughout the year (Table 4). The diet diversity of each herbivore species showed no significant differences throughout the year, except for cattle between Fall and Winter ($t=2.27$, $P>0.05$, Table 3).

Table 4. Tukey Multiple Comparisons (TMC, q) and Hutcheson test (HT) between different herbivore species for the same season in the Paraná River Delta.

	TMC	*HT*	
Comparison	*q*	*t*	df
Spring			
Plains vizcacha–Greater rhea	0.76*	3.24**	100
Plains vizcacha–Cattle	8.25	2.43**	98
Greater rhea–Cattle	9.01	−0.55	97
Summer			
Plains vizcacha–Greater rhea	11.39	4.43**	99
Plains vizcacha–Cattle	5.87	3.12**	100
Greater rhea–Cattle	5.52	−1.28	100
Fall			
Plains vizcacha–Greater rhea	0.28*	2.12**	100
Plains vizcacha–Cattle	8.77	−0.13	90
Greater rhea–Cattle	8.49	−2.58	90
Winter			
Plains vizcacha–Greater rhea	11.21	1.42	95
Plains vizcacha–Cattle	5.84	2.44**	100
Greater rhea–Cattle	5.36	1.25**	97

Critical q value (0.05; $K=3$; ∞)=3.31; *different trophic niche breadth; **significant differences ($P<0.05$).

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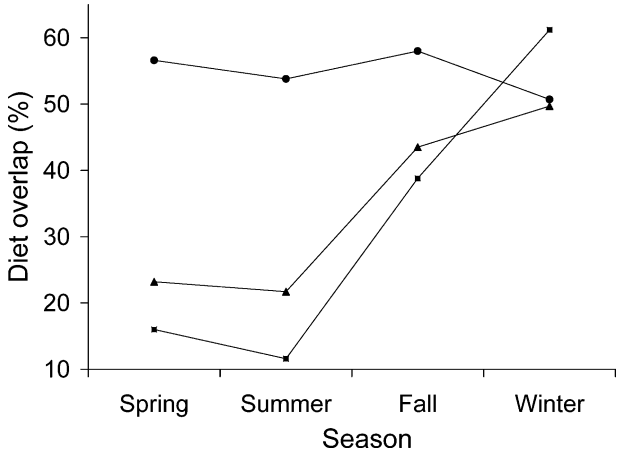

Figure 1. Diet overlap among cattle–plains vizcacha (●), cattle–greater rhea (■) and plains vizcacha–greater rhea (▲) in the Paraná River Delta.

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Discussion

Trophic niche breadth

Plains vizcachas, greater rheas, and cattle consumed a wide variety of plants (Pereira et al. 2003); however, the values obtained for niche breadths suggest a trend towards forage selectivity for each of the three species. In addition, seasonal variations in their trophic niche breadths are the result of changes in foraging patterns along the year. In this sense, several authors have pointed out that temporal heterogeneity is one of the factors influencing plant–herbivore relationships, since it determines the type and magnitude of phenological changes in vegetation and subsequent changes in species foraging patterns (Westoby 1978; Schwartz & Ellis 1981; Crawley 1983). Vizcachas showed a more generalistic foraging behavior in Spring and Summer, coincidently with the greater abundance of grasses (Arias et al. 2005), the main food items of this rodent (Pereira et al. 2003). Greater rhea showed a more specialized foraging behavior in Summer and Fall, and a more generalized behavior in the other seasons. These selectivity patterns are the result of the low number of food items comprising the staple diet of rhea in both seasons (Pereira et al. 2003). The greater niche breadth observed in Fall for cattle might be interpreted as resulting from the differential inclusion of less represented items, considering that the most important food items were constant in the diet. In contrast to that observed in vizcachas, cattle niche breadth was narrower in Spring and Summer with respect to the other seasons. It might be due to the wider range of movement of cattle as compared to that of the rodents.

Trophic niche overlap

The moderate (though constant) diet overlap between vizcachas and cattle was due to the shared consumption of grasses by these herbivores. A similar observation was made for both of these species during Winter and Spring by Bontti et al. (1999), who nevertheless observed a marked decrease of dietary overlap in the other seasons, due to a high consumption of *Prosopis caldenia* pods by cattle. Previous studies on diet overlap between these two herbivores have shown widely varying results, from less than 40% overlap in areas of natural grassland (Giulietti & Jackson 1986) to 75% overlap in semiarid areas (Bontti et al. 1999).

We found that the niche overlap between greater rhea and the other two herbivores was smallest in Spring and Summer, due to the differential consumption of a few food items, mainly *Prosopis nigra* pods and some broad-leaved species by the rheas. In the other seasons, the decrease or lack of these items in the diet was associated with an increased consumption of grasses also consumed by vizcachas and cattle and a consequent increase in trophic niche overlap.

When exotic herbivores like cattle are introduced into a natural system, a high overlap in resource use between them and the resident herbivores can occur and may be indicative of competition (Pulliam 1986; Dawson & Ellis 1994; Voeten & Prins 1999; Bagchi 2006). However, Wiens (1989) stated that a high niche overlap involves competition only when resources are scarce. Considering that vizcachas restrict their grazing to the area next to their burrows (Arias et al. 2005) and that they exhibit a similar forage pattern to that of cattle along the year (Pereira et al. 2003), the observed dietary overlap with cattle may result in an asymmetric increase of the effects of competition, especially detrimental for this rodent. As for greater rheas, niche overlap might indicate competition between these birds and the other two species in Fall and Winter. However, the ability of the birds to move to neighboring fields where cattle are absent (which we observed in four of the eight seasons sampled) might allow greater rhea to exhibit a seasonal exploitation of available resources in different areas and thus decrease its trophic interaction with cattle.

Diet diversity

According to Hansen & Reid (1975), a greater dietary diversity is indicative of a higher potential adaptability for selecting the foraging resources available in the habitat, which is shown in a greater inclusion of new items during the same season. Compared to the other two species, the vizcachas showed the greatest mean dietary diversity throughout the year, probably

reflecting a longer adaptive history to the resources provided by the environments of the region due to their condition of native species. These results are coincident with the findings of Branch et al. (1994) and Puig et al. (1997) in other areas.

Conclusions

The vizcachas from the Paraná Delta showed a feeding behavior opposite to the diet selection pattern predicted by the optimal foraging theory (Stephens & Krebs 1986), because they exhibited a greater dietary selectivity during Fall and Winter. According to Quintana (1996), these seasons (mainly Winter) might be considered as the critical period concerning abundance and quality of forage in the Paraná River Delta because of low temperatures and less rainfall. In contrast, such foraging behavior would be consistent with the selective quality hypothesis (Weekerly & Kennedy 1992), which predicts that herbivores will be more selective in times of scarcity due to the reduced availability of palatable or acceptable diet components (Branch et al. 1994). However, since we did not determine the relative availability of food, this idea should be considered as a hypothesis. In addition, the niche overlap between vizcachas and cattle might be a negative factor for the vizcachas populations remaining in the area if there are changes in the availability of forage species used by both herbivores, whether they are due to environmental factors or to an increase of cattle density.

In short, the trophic niche features of the three species suggest a negative impact of cattle on vizcachas. Competition between cattle and greater rhea appears restricted to only a part of the year, but the greater mobility of these birds might decrease their foraging interference with cattle.

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