Ecol Res (2014) 29: 191–201
DOI 10.1007/s11284-013-1113-2

ORIGINAL ARTICLE

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Patterns of habitat use and selection by the capybara (*Hydrochoerus hydrochaeris*): a landscape-scale analysis

Received: 18 January 2013 / Accepted: 28 November 2013 / Published online: 21 December 2013

Abstract Habitat selection analysis provides useful information on how animals become distributed in response to spatial heterogeneity. Here, we analyze the habitat use and selection of different water bodies (marsh, swamps and round shallow lakes) by capybaras (*Hydrochoerus hydrochaeris*) and their relation to environmental variables during contrasting climate-hydrological seasons in the Esteros del Iberá (Corrientes, Argentina). We evaluated the intensity of use by capybaras through the total number of individuals (abundance) in each water body, the number and mean size of social groups, and the physical and vegetation characteristics of the environment. The capybaras used marsh and swamps according to availability in both seasons, while they used rounded shallow lakes less than their available would suggest in summer. The use intensity of different rounded shallow lakes estimated based on group size did not show significant differences. In contrast, significant differences were observed when evaluated by the number of individuals in each rounded shallow lake. Different intensity of use was closely associated with environmental and vegetation characteristics. The results show that habitat suitability for capybaras is associated with vegetation cover and "embalsados" in the low-lying area rather than with the morphometry of the rounded shallow lakes. The pattern of habitat selection may depend on forage quality, water availability for thermoregulation and mating, and presence of shelter and resting sites. On the other hand, the present study shows how the size, shape and the abundance of different types of water bodies affect population abundance and density.

Keywords Argentina · Habitat selection · *Hydrochoerus hydrochaeris* · Spatial heterogeneity · Wetlands

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Introduction

Habitat selection analysis provides useful information on how animals become distributed in response to spatial heterogeneity. On this basis, processes associated with habitat selection are of crucial importance to landscape ecology (Morris and Brown 1992). Spatial heterogeneity is a feature of the landscape, and can be viewed as mosaics or patches of environments differing in species composition, structure (shape and distribution) and quality of the vegetation (Hanski and Gilpin 1991; Sanderson and Harris 2000). These factors affect behavior at the individual, population and community levels (Romero and Morláns 2007). Such patches and their arrangement can be defined only in relation to the habitat and the spatial requirements of different species (Bowers and Matter 1997). Therefore, the landscape scale may be on the scale of tens of meters or hundreds of kilometers, depending on the species considered (Turner et al. 2001). The physical and biological characteristics of the different habitat types greatly affect the density of animal populations and habitat selection by individuals, as well as their pattern of resource use (Wiens 1992). Resource abundance and distribution are primary factors determining habitat selection. In this context, it is important to understand why a species selects a particular area and/or any of its components as feeding, refuge and reproduction sites, which may differ in productivity and relative suitability (Johnson 1980). Consequently, landscape structure affects both the distribution of environments and of the individuals using them (Wiens et al. 1993; Ritchie 1997; Barrett and Peles 1999).

The capybara (*Hydrochoerus hydrochaeris*) uses different habitat types such as marshes, swamps, shallow lakes, rivers and streams. In each habitat type, it uses environments adjacent to water bodies, such as alluvial plains, grasslands, river banks and riverine forests (Ojasti 1973; Jorgenson 1986; Quintana and Rabinovich 1993; Soini 1993; Corriale 2010). The proportion of suitable environments for this species in the area depends on basic requirements such as the availability of water, and foraging, resting and refuge sites (Ojasti and Sosa Burgos 1985; Corriale 2010). The spatial arrangement of landscape elements is a key factor in determining species distribution because capybaras usually use the water–land interface, avoiding areas distant to this ecotone, or near the center of large water bodies (Quintana 1996; Corriale et al. 2013a).

The capybara has high productivity and high-quality meat and leather, thereby emerging as a wildlife resource of great social and economic value in many areas within its distribution range in Argentina (Ojasti 1991; Quintana et al. 1994; Bolkovic et al. 2006). Capybara populations have experienced a drastic population decline due to heavy hunting pressure by subsistence and commercial poachers (Martin et al. 1981; Gruss and Waller 1988; Kravetz 1991; Alvarez and Kravetz 2002). In recent years, however, changes in the original landscape by the development of human activities and an increase in the intensity of land use led to range expansion in South America (Ferraz et al. 2003; 2007; 2009; Campos-Krauer and Wisely 2011); in many places, capybara is considered to be harmful and even a pest (Ojasti 1973; Escobar and Gónzalez-Jiménez 1976; Quintana et al. 1998a; Ferraz et al. 2007). It is known to compete with livestock for forage (Quintana et al. 1998a), to damage crops (Ferraz et al. 2003, 2009) and has the potential to transmit zoonotic diseases (Pereira and Labruna 1998; Labruna et al. 2001, 2004).

The ecoregion of the Iberá Macrosystem is a freshwater wetland ecosystem (Neiff 2004) consisting of a vast mosaic of sandy plains, gentle slopes and an intricate complex of marshes, swamps, "embalsados" (floating soil) and shallow lakes. The habitat diversity, spatial heterogeneity and landscape structure of the Iberá Macrosystem lead to environments that satisfy the bio-ecological requirements of capybaras (Canziani et al. 2003). However, there is little information on variations in habitat suitability in this ecoregion. On the other hand, ongoing anthropogenic activities are causing hydrologic changes, the replacement of natural vegetation with tree plantations and use of fire in cattle raising and agriculture, all of which affect the landscape and, consequently, wildlife (Neiff 2004). In this regard, analysis of habitat use at the landscape scale by an ecologically and economically important species such as *H. hydrochaeris* is of major interest to prevent or reduce the negative impact of environmental alterations on capybara populations.

Based on the considerations mentioned above, the objective of this work was to analyze habitat use and selection by capybaras at the landscape scale in relation to environmental variables during contrasting climate-hydrological seasons in the Esteros del Iberá (Corrientes, Argentina). We evaluated the intensity of use by capybaras of different water bodies through the total number of individuals (abundance) in each water body, the number and mean size of the social groups, and the physico-chemical and vegetation characteristics of the environment. Information on the population dynamics of this species in its natural environment will contribute to the design of sustainable management measures compatible with traditional productive activities.

Materials and methods

Study area

The study was conducted in the Park Guayaibí (28°00 S 57°18 W)—a former livestock farm located to the north of central Iberá wetland macrosystem, in Los Campos District (Carnevali 2003), Corrientes province, Argentina. It covers an area of about 750 ha corresponding to a sandy ridge bordered by marshes and swamps. The sandy ridge includes five rounded shallow lakes of wind-pseudokarstic origin (Carnevali 2003; CLT 2006; Fig. 1). The landscape is dominated by "paja colorada" grassland, represented mainly by *Andropogon lateralis*, *Axonopus fissifolius* and *Rhynchospora barrosiana* (Carnevali 2003; Corriale et al. 2013b). The rounded shallow lakes—also called deflation basins—have a well-defined surface area, and contain water almost permanently. Some temporary ponds filled with water only during the rainy season (spring–summer) and occasional periods of prolonged or heavy rainfall are also present on the sandy ridge. The area corresponds to a private ecological reserve under low grazing pressure, where grassland areas are subject to low-intensity burns during autumn and winter (Corriale et al. 2013b).

Climate is subtropical humid, with hydric and thermal seasonality. Rainfall occurs in all seasons but it is heavier in spring (21 September to 20 December) and summer (21 December to 20 March). In summer, average and maximum temperatures are 27 and 44 °C, respectively, and in winter average temperature is 16 °C, with the historical record of minimum temperature over the past 50 years being −2 °C. The average annual rainfall reaches 1,800 mm (Neiff and Poi de Neiff 2005).

Habitat use

Taking into account ready access and the relative abundance of the different habitats, we surveyed 3 km of the marsh perimeter along the western margin of the sandy ridge, 3.16 km of the swamps perimeter along the eastern margins of the sandy ridge, and four of the five rounded shallow lakes, corresponding to 81.5 % of the habitats available for capybaras in the study area (Fig. 1). To estimate the intensity of use for each habitat

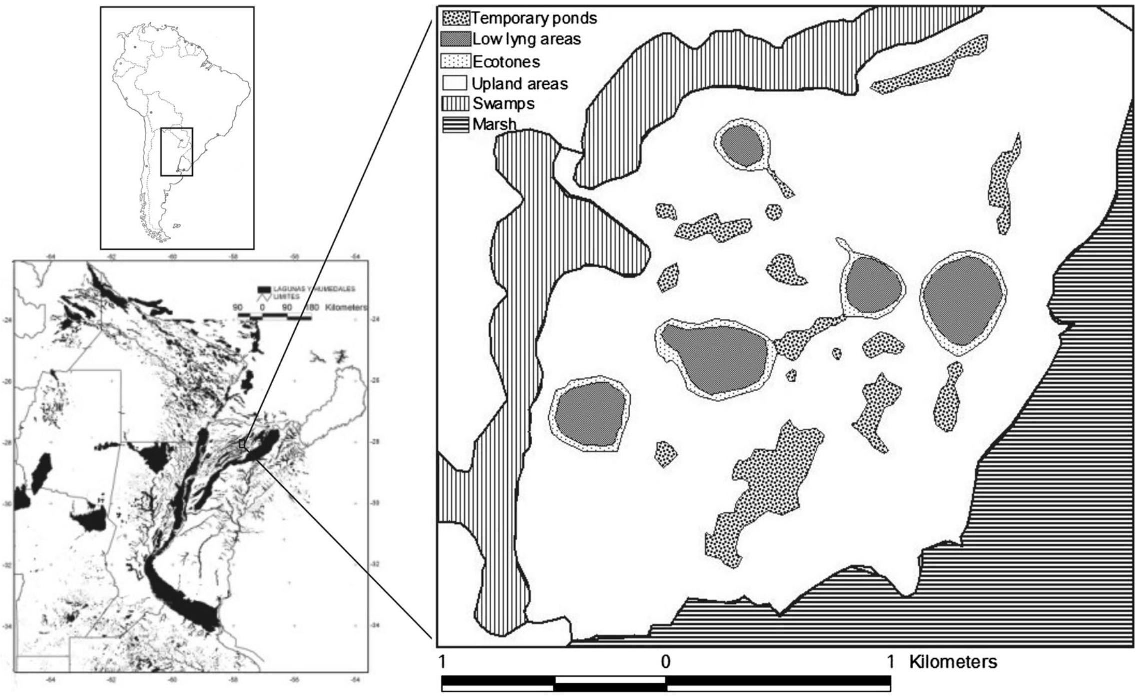

Fig. 1 Study area and thematic map of environments in the study area obtained from the interpretation of aerial photographs (1:20,000 scale) and satellite imagery (Landsat 2001; Google Earth 2011), with further field validation

type we performed an analysis of habitat selection or use versus availability of resources and then applied a study design I (Marcum and Loftgaarden 1980; Thomas and Taylor 1990, 2006; Manly et al. 1993, 2002), with all measurements being made at the population level.

The number of capybara groups observed in each type of habitat (marsh, swamps and rounded shallow lakes) was compared with that expected according to their availability. The estimators of availability were the perimeter and surface area of each water body, and the number of expected groups was calculated using the following formula: GNe = perimeter or area of the type of water body under consideration * frequency of use/total perimeter or area considering all the types of water bodies); where frequency of use is the number of individuals or number of groups in the type of water body under consideration.

The χ^2 homogeneity test was used to test for significant differences between the frequency of resource use and its frequency of occurrence (availability). When there were significant differences, multiple comparisons were made with simultaneous confidence intervals (IC: Neu et al. 1974; Randall Byers and Steinhorst 1984). Habitat use intensity was assumed to be higher if the habitat was used more than in proportion to its availability, otherwise it was considered to be lower; non-significant differences indicated use in proportion to availability (Johnson 1980).

We obtained the number of capybara groups on foot or horseback along the shoreline of the marsh, the swamps and the rounded shallow lakes in the morning and evening, and while they were grazing or resting in open areas close to the water (Ojasti 1973; Cordero and Ojasti 1981; Herrera 1986; Jorgenson 1986; Alho et al. 1989; Mourão and Campos 1995; Campos Krauer 2009). We estimated the number of capybaras in the rounded shallow lakes during 2 days in each season by instantaneous scan sampling at 15-min intervals and at a distance of 100–250 m from each group to prevent movement of individuals. We used a Bushnell Spacemaster telescope 15–45 × 60 mm and Tasco binoculars 8 × 20 × 50. The survey was conducted during the first 4 h after sunrise (from 7:00 a.m. to 10:30 a.m.) and the last 4 h before sunset (from 4:00 p.m. to 6:30 p.m.); the number of observations recorded during 2 days in each season for each group was 52, the mode was used as an estimate of the number of individuals of each social group. The size of all the social groups present in the rounded shallow lakes and the size of 18 randomly selected social groups inhabiting the marsh were analyzed with the Kruskal-Wallis non-parametric ANOVA. In the swamps, the characteristics of the vegetation prevented us from determining the size of capybara groups. A social group was defined as being composed of at least two individuals and solitary males were excluded from the analysis. The study was conducted over 2 years during contrasting climate-hydrological seasons (summer and winter).

Environmental variables

A preliminary identification of the different water bodies and habitats in the study area was made through the interpretation of aerial photographs (1:20,000 scale) and satellite imagery (Landsat 2001; Google Earth 2011). Data were imported into a Geographic Information System (ArcView 3.2) to generate a thematic map of environments. Results were further validated in the field (Fig. 1).

We characterized the different environments in the rounded shallow lakes to evaluate an association between habitat use intensity and environmental variables. These were measured during summer 2007–2008 and winter 2007–2008. The surface area, perimeter, percentage of low-lying areas and percentage of land–water interface were mapped in the field using a positioner system. The remaining variables were estimated seasonally from aerial photographs (1:20,000 scale), aerial photographs taken seasonally from a small plane at an approximate scale of 1:5,000 and through a stratified random sampling (Corriale et al. 2013b). A total of 120 plots were selected randomly in proportion to the area of each environment type during the two seasons. Because of the vegetation structure, plots of 1 × 1 m were used in all environment types except in the "embalsados" where plots of 5 × 5 m were used for presenting a upper stratum of woody shrubs (Corriale et al. 2013b). The shape of the rounded shallow lakes was determined using Patton's Diversity Index (Patton 1975), as follows: $R = P/2\sqrt{\pi}A$, where P is the perimeter and A is the area of the water body; R ranges between 1 and infinity and is classified into shape categories from round ($R < 1.25$) to irregular or amorphous ($R > 2$) (Henao 1988).

Canonical correspondence analysis (CCA) was applied to analyze the relationship between patterns of shallow lake selection and their environmental and physical characteristics (ter Braak 1987a; Palmer 1993); CCA was conducted with CANOCO software (ter Braak 1987b).

Results

Use intensity of the marsh, swamps and rounded shallow lakes

The number of social groups was larger in the marsh than in the other water bodies for winter and summer, but capybaras used the different water bodies according to availability in winter ($\chi^2 = 1.585$, df = 2, $P = 0.453$ for winter 2007; $\chi^2 = 5.602$, df = 2, $P = 0.061$ for winter 2008), while they used the rounded shallow lakes less than available and the marsh and swamps according to availability in summer ($\chi^2 = 6.218$, df = 2; $P = 0.045$ for summer 2007; $\chi^2 = 8.656$, df = 2; $P = 0.013$ for summer 2008; Table 1).

Group size of capybaras in the marsh and rounded shallow lakes

The sizes of capybara groups were relatively large both in the marsh and in the rounded shallow lakes; group sizes were highest and similar during both summers and lowest and similar during both winters in all water bodies. No significant seasonal differences in size group were found among the rounded shallow lakes (Kruskal–Wallis, $H = 6.82$, df = 3, $P = 0.07$ for summer 2007; $H = 3.17$, df = 3, $P = 0.161$ for summer 2008; $H = 095$, df = 3, $P = 0.913$ for winter 2007; $H = 1.49$, df = 3, $P = 0.681$ for winter 2008). There were significant differences in size group between rounded shallow lakes and the marsh during summer 2007, 2008 and winter 2008, with lower values for the latter in all the studied seasons (Table 2).

Use intensity of rounded shallow lakes

Use intensity of rounded shallow lakes estimated based on group size showed a similar pattern over time. No significant differences were observed when habitat availability was based on the area (summer 2007: $\chi^2 = 1.513$, df = 3, $P < 0.679$; winter 2007: $\chi^2 = 1.328$, df = 3, $P < 0.722$; summer 2008: $\chi^2 = 2.104$, df = 3, $P < 0.551$; winter 2008: $\chi^2 = 2.104$, df = 3, $P < 0.551$), the perimeter (summer 2007: $\chi^2 = 0.679$, df = 3, $P < 0.878$; winter 2007: $\chi^2 = 0.865$, df = 3, $P < 0.834$; summer 2008: $\chi^2 = 0.686$, df = 3, $P < 0.876$; winter 2008: $\chi^2 = 0.686$, df = 3, $P < 0.876$).

In contrast, habitat use intensity differed significantly when evaluated by the number of individuals in each rounded shallow lake; this result was obtained

Table 1 Simultaneous confidence intervals for the proportion of use of the habitats (H) marsh (M), rounded shallow lakes (L) and swamps (S)

	H	P	NGo	NGe	EP	OP	CI	IU[a]
Summer 2007	M	3,011.7	24	16.9	0.269	0.371	0.234–0.508	=
	L	5,017.0	19	28.2	0.448	0.306	0.175–0.438	–
	S	3,169.0	20	17.8	0.283	0.323	0.190–0.456	=
Summer 2008	M	3,011.7	26	17.2	0.269	0.406	0.269–0.544	=
	L	5,017.0	18	28.7	0.448	0.281	0.155–0.407	–
	S	3,169.0	20	18.1	0.283	0.313	0.183–0.442	=

P Perimeter, *NGo* number of groups observed, *NGe* number of groups expected, *EP* proportion expected according to the perimeter available, *OP* observed proportion, *CI* confidence interval for OP, *IU* Habitat use intensity

[a] = Used according to availability, + selected, – used less than available

Table 2 Results of the *t* test comparing the size of capybara groups (TG) in the marsh (M) and the rounded shallow lakes (L) for the different seasons studied

	n (M)	*n* (L)	TG (M) ± SD	TG (L) ± SD	*T*	*P*
Summer 2007	18	18	26.82 ± 4.65	31.56 ± 6.29	−2.74	0.009
Winter 2007	18	19	23.36 ± 5.72	25.26 ± 6.09	−1.03	0.310
Summer 2008	18	18	26.82 ± 5.07	31.44 ± 8.38	−2.11	0.045
Winter 2008	18	18	23.36 ± 6.88	29.61 ± 7.62	−2.72	0.010

Table 3 χ^2 homogeneity test for comparing the observed (NIo) and expected (NIe) number of individuals based on the area (A) of each shallow lake (L)

L	A (ha)	EP	Summer 2007					Winter 2007				
			NIo	NIe	OP	CI	IU[a]	NIo	NIe	OP	CI	IU[a]
L. 1	4.76	0.125	66	71.2	0.116	0.073–0.159	=	77	60.5	0.159	0.106–0.213	–
L. 2	6.59	0.174	165	98.6	0.290	0.229–0.352	+	146	83.8	0.302	0.235–0.369	+
L. 3	12.70	0.334	131	190.0	0.231	0.174–0.288	–	108	161.6	0.224	0.163–0.285	–
L. 4	13.92	0.367	206	208.2	0.363	0.298–0.428	=	152	177.1	0.315	0.247–0.383	=
T	37.97	1.000	568	568	1			483	483.0	1.000		

EP Expected proportion according to the area available, *OP* observed proportion, *CI* confidence interval for OP, *IU* Habitat use intensity
[a] = Used according to availability, + selected, − used less than available

Table 4 χ^2 homogeneity test for comparing the observed (NIo) and expected number of individuals (NIe) based on the area (A) of each shallow lake (L)

L	A (ha)	EP	Summer 2008					Winter 2008				
			NIo	NIe	OP	CI	IU[a]	NIo	NIe	OP	CI	IU[a]
L. 1	4.76	0.125	71	71.5	0.125	0.080–0.169	=	79	64.7	0.153	0.102–0.204	=
L. 2	6.59	0.174	160	98.9	0.281	0.220–0.341	+	131	89.6	0.254	0.192–0.316	+
L. 3	12.7	0.334	133	190.7	0.233	0.176–0.290	–	120	172.6	0.233	0.173–0.292	–
L. 4	13.92	0.367	206	209.0	0.361	0.297–0.426	=	186	189.2	0.360	0.292–0.429	=
T	37.97	1.000	570	570	1			516	516.0	1.000		

EP Expected proportion according to the area available, *OP* observed proportion, *CI* confidence interval for OP, *IU* habitat use intensity
[a] = Used according to availability, + selected, − used less than available

for all seasons using the area (summer 2007: $\chi^2 = 63.466$, df = 3, $P < 0.0001$; winter 2007: $\chi^2 = 71.879$, df = 3, $P < 0.0001$; summer 2008: $\chi^2 = 55.180$, df = 3, $P < 0.0001$; winter 2008: $\chi^2 = 38.423$, df = 3, $P < 0.0001$) or the perimeter as estimators of availability. In considering the area, capybaras selected the shallow lake 2, while they used the shallow lake 3 less intensively (Tables 3, 4), with this pattern being observed in all seasons.

Rounded shallow lakes also showed significant differences when using the perimeter to estimate availability (summer 2007: $\chi^2 = 51.685$, df = 3, $P < 0.0001$; winter 2007: $\chi^2 = 25.350$, df = 3, $P < 0.0001$; summer 2008: $\chi^2 = 43.708$, df = 3, $P < 0.0001$; winter 2008: $\chi^2 = 22.783$, df = 3, $P < 0.0001$. In all seasons, the shallow lake was used less intensively, the shallow lake 3 was used according to availability, and the shallow lake 4 was used more intensively during summer (2007 and 2008) and according to availability during winter (2007 and 2008) (Tables 5, 6).

Association between use intensity of the rounded shallow lakes and environmental characteristics

The values of the environmental variables are shown in Appendix I. The CCA analysis showed that the first two axes explain 63.6 % of the variance in the relationship between the patterns of use and the environmental variables (Table 7). Monte Carlo test indicates that all axes are significant ($F = 4.749$; $P = 0.002$). The first axis of the CCA, which explains 34.8 % of the variance, is related to the characteristics of the vegetation in the water bodies (Monte Carlo test, $F = 3.202$, $P = 0.002$). The second axis of the CCA, which explains 28.8 % of the variance, is related mainly to the physical and morphometric characteristics of the rounded shallow lakes (Fig. 2). On the other hand, the first axis explains the different levels of habitat use intensity by capybaras. The more intensively used rounded shallow lakes were associated with a high percentage of graminoid and cyperacean cover

Table 5 χ^2 homogeneity test for comparing the observed (NIo) and expected number of individuals (NIe) based on the perimeter (P) of each shallow lake (L)

L	P (m)	EP	Summer 2007					Winter 2007				
			NIo	NIe	OP	CI	IU[a]	NIo	NIe	OP	CI	IU[a]
L. 1	1,125.7	0.224	66	127.4	0.116	0.073–0.159	–	77	108.4	0.159	0.106–0.213	–
L. 2	1,121.7	0.224	165	127.0	0.290	0.229–0.352	+	146	108.0	0.302	0.235–0.369	+
L. 3	1,293.6	0.258	131	146.5	0.231	0.174–0.288	=	108	124.5	0.224	0.163–0.285	=
L. 4	1,476	0.294	206	167.1	0.363	0.298–0.428	+	152	142.1	0.315	0.247–0.383	=
T	5,017	1.000	568	568	1			483	483.0	1.000		

EP Expected proportion according to the perimeter available, *OP* observed proportion, *CI* confidence interval for OP, *IU* habitat use intensity
[a] = Used according to availability, + selected, – used less than available

Table 6 χ^2 homogeneity test for comparing the observed (NIo) and expected number of individuals (NIe) based on the perimeter (P) of each shallow lake (L)

L	P (m)	EP	Summer 2008					Winter 2008				
			NIo	NIe	OP	CI	IU[a]	NIo	NIe	OP	CI	IU[a]
L. 1	1,125.7	0.224	71	127.9	0.125	0.080–0.169	–	79	115.8	0.153	0.102–0.204	–
L. 2	1,121.7	0.224	160	127.4	0.281	0.220–0.341	=	131	115.4	0.254	0.192–0.316	=
L. 3	1,293.6	0.258	133	147.0	0.233	0.176–0.290	=	120	133.1	0.233	0.173–0.292	=
L. 4	1,476	0.294	206	167.7	0.361	0.297–0.426	+	186	151.8	0.360	0.292–0.429	=
T	5,017	1.000	570	570	1			516	516.0	1.000		

EP Expected proportion according to the perimeter available, *OP* observed proportion, *CI* confidence interval for OP, *IU* habitat use intensity
[a] = Used according to availability, + selected, – used less than available

Table 7 Results of canonical correspondence analysis (CCA) relating the pattern of use of the rounded shallow lakes by capybaras and environmental variables

Variables	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.696	0.576	0.282	0.199	2.000
Correlations pattern of use—environmental variables	0.991	0.963	0.967	0.735	
Explained variance	34.8	63.6	77.7	87.7	
Explained variance (pattern of use—environmental variables)	39.7	72.5	88.6	100.0	
Correlations environmental variables—axes					
A	−0.226	−0.225			
P	−0.148	0.115			
B	0.033	−0.664			
I	−0.033	0.664			
AB	−0.224	−0.307			
EB	0.674	0.078			
ALB	−0.044	0.095			
SA	−0.770	−0.141			
R	0.112	0.624			
SV	−0.706	−0.052			
GCBNE	0.598	−0.004			
GCE	−0.242	0.512			
GCI	0.441	0.130			

in the land–water interface and in the low-lying area without "embalsado", and a high percentage of "embalsado" in the low-lying area (positive end of axis 1). The rounded shallow lakes that were used less intensively were associated with a high percentage of waterlogged, vegetation-free soil (negative end of axis 1). The rounded shallow lakes that were used according to availability show values around 0 (Fig. 2).

Discussion

In the present paper, capybaras showed a low degree of selection for the different types of water bodies, thus helping to understand the wide diversity of habitats they occupy throughout their distribution range (Krieg 1929; Ojasti 1973; Macdonald 1981a; Jorgenson 1986; Quin-

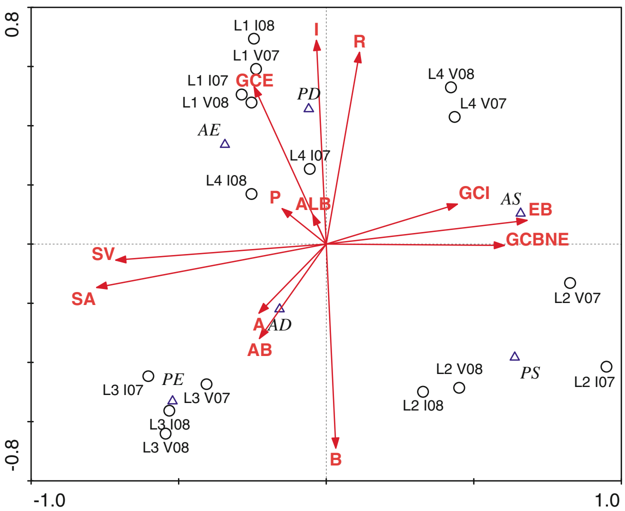

Fig. 2 Ordination diagram of the first two axes of canonical correspondence analysis (CCA) for patterns of use (*triangles*) and environmental variables (*arrows*) in the different rounded shallow lakes (*circles*) during summer 2007 and 2008 (V07 and V08, respectively) and winter 2007 and 2008 (I07 and I08, respectively). *L1* Shallow lake1, *L2* shallow lake 2, *L3* shallow lake 3, *L4* shallow lake 4. *P* Result of the study of habitat selection using the perimeter of the rounded shallow lakes as estimator of availability, *A* result of the study of habitat selection using the area of the rounded shallow lakes as estimator of availability, *S* higher use intensity, *E* lower use intensity, *D* used according to availability. See Table 8 for definitions of abbreviations of variables

Table 8 Physical and biological variables used in canonical correspondence analysis for the four rounded shallow lakes studied

Variable (unit)	Symbol
Water body area (ha)	A
Perimeter (m)	P
Low-lying area	AB
Patton's diversity index	R
Percentage of low-lying area (%)	B
Percentage of land–water interface (%)	I
Percentage of "embalsado" in the low-lying area (%)	EB
Percentage of vegetation-free water surface in the low-lying area (%)	ALB
Percentage of waterlogged, vegetation-free soil in the low-lying area (%)	SA
Percentage of vegetation-free soil in the land–water interface (bare ground and/or vegetation-free water surface) (%)	SV
Percentage of graminoid and cyperacean cover in the low-lying area (without "embalsado") (%)	GCE
Percentage of graminoid and cyperacean cover in the "embalsado" (%)	GCBE
Percentage of graminoid and cyperacean cover in the land–water interface (%)	%GCI

tana and Rabinovich 1993). The three types of water bodies studied by us may adequately fulfill the main requirements of the species (Ojasti and Sosa Burgos 1985) throughout the year.

Survival and reproduction are limited by food supply and the abundance and predictability of resources over time, which affect the spatial distribution of the population (McLoughlin et al. 2000). On this basis, the more stable characteristics of the marsh in terms of vegetation, water permanence and percentage of "embalsado", mainly in summer when evapotranspiration is higher (Neiff 2004) and water bodies tend to dry up, may have led to an increase in the number of capybara groups, at the expense of a less intensive use of the rounded shallow lakes in this season. It is likely that the increase in the number of groups resulted from the splitting of pre-existing groups. Ojasti (2011) indicates that at the beginning of the rainy season, the groups break off into smaller groups and then grow in size though reproduction without disintegrating during the season.

On the other hand, the home range is inversely proportional to resource availability because the area occupied by an animal should be large enough to satisfy its requirements (Schoener 1974; Berstein 1982). In line with this, with higher availability of forage and refuge in the marsh (water and "embalsados"), capybaras probably decreased their home range (Corriale et al. 2013a) and thus allow a larger number of groups, supporting the resource dispersion hypothesis (Macdonald 1981b, 1983; Carr and Macdonald 1986; Johnson et al. 2001). According to this hypothesis, the home range of a social group increases with increasing dispersion of limiting resources, while the size of the group is determined by resource richness or abundance, regardless of the home range area. Taking into account the temporal variations, our results from the marsh and rounded shallow lakes support this hypothesis, since group size was higher in summer, when home ranges were smaller and resource abundance, in terms of food and refuge, was higher (Corriale et al. 2013a). However, group size was smaller in the marsh than in the rounded shallow lakes, which is contrary to that expected. It is likely that the poor forage quality and the low hiding cover along the shoreline would have forced large groups of capybaras to move toward the center of the shallow lake or to travel longer distances, thus increasing their home range (Sekulic 1982; Stallings et al. 1989). Previous studies of capybaras have found a relationship between home range and group size (Herrera and Macdonald 1989). In the marsh, the reduced home ranges could have resulted in more but smaller groups and this, together with a trend toward a higher intensity of use, suggest that it is a highly suitable habitat. This possibly determined extensive home range overlap among the coexisting groups with relatively low competition (McLoughlin et al. 2000).

In regard to the different patterns of use of the rounded shallow lakes by capybaras, habitat suitability was reflected in groups with more individuals rather than in more groups. The estimates of habitat suitability showed different patterns but not opposite tendencies. On the basis of the importance of the low-lying area for capybaras and the fact that the water-land interface is the most intensively used environment (Corriale 2010), both estimators should be considered to draw well-grounded conclusions.

The intensity of use of the rounded shallow lakes would be closely associated with their environmental and vegetation characteristics. The presence of vegetation in the low-lying area without "embalsado", the high forage availability in the land–water interface and the high percentage of "embalsado" cover could support a larger number of individuals making a more intensive use of resources. The rounded shallow lakes in the low-lying area without "embalsado" show a high percentage of vegetation cover during all four seasons and hold water permanently (Neiff 2004). These water bodies are used for bathing, thermoregulation, mating and as a refuge from predators (Alho et al. 1989; Herrera and Macdonald 1989). In turn, the presence of the "embalsado" in the low-lying area would provide dry and safe sites for parturition and the high percentages of graminoid and cyperacean cover in the land–water interface provide capybaras with an adequate supply of forage (Escobar and Gónzalez-Jiménez 1976; Quintana et al. 1994, 1998a, b; Corriale 2010). On the other hand, capybaras avoided shallow lakes associated with low values of these variables and high percentages of waterlogged, vegetation-free soil, which indicates low availability of water in the low-lying area. In this environment, water depth and water-level variations may strongly affect habitat selection by capybaras. Although we could not measure this variable, it can be inferred from the percentages of vegetation-free water surface, waterlogged soil and vegetation in the low-lying area without "embalsado". Deeper lakes exhibit less water–level variation and are more permanent, thus favoring the development of aquatic plants and rich vegetation cover (Neiff 2004).

At a landscape scale, our results show that habitat suitability for capybaras is associated with the cover of the vegetation and "embalsados" in the low-lying area rather than with the morphometry of the rounded shallow lakes in the study area. The pattern of habitat selection may depend on forage quality, water availability for thermoregulation and mating, and presence of shelter and resting sites (Ojasti and Sosa Burgos 1985). On the other hand, the present study shows how the size, shape and the abundance of different types of water bodies affect social group number and group size and consequently population abundance and density (Schmid 1998; Bowers and Matter 1997). Landscapes with a predominance of rounded shallow lakes or swamps are characterized by a larger number of land–water ecotones, allowing the establishment of more capybaras. Such landscapes are more heterogeneous than those with swamps, providing capybaras with a variety of resources. Since *H. hydrochaeris* needs a combination of environments to meet life requirements (Herrera and Macdonald 1989; Quintana 1999; Campos Krauer 2009; Corriale 2010) by landscapes with a predominance of rounded shallow lakes or swamps may support higher population abundances and densities like in the Apure State (Venezuela) where a density of 1 capybara/ha within the home range was estimated (Herrera and Macdonald 1987). In Argentina, the largest capybara populations are found in the Iberá Macrosystem (Bolkovic et al. 2006). In the study area 1.8 capybaras/ha within the home range were estimated Corriale et al. (2013a) estimated. The Iberá Macrosystem is characterized by high environmental diversity and considered as of high habitat suitability for this rodent (Adámoli et al. 1988; Alvarez 2002). Our work sheds light on the differential use of landscape elements by capybaras in some typical environments of the Iberá Macrosystem. It also offers new clues as to how higher environmental heterogeneity, in terms of an increased availability of land–water interface caused by a larger number of smaller water bodies, might affect the behavior and population structure of capybaras. This would be reflected in large-sized groups and higher densities in the area.

Numerous landscape ecological studies of wildlife populations have dealt with the effect of spatial patterns on the distribution, movements and persistence of the species, but most have focused on how these parameters are affected by changes in landscape structure (e.g., due to anthropogenic habitat fragmentation) (Turner 1989). In particular, habitat selection studies are usually performed in landscapes degraded or highly fragmented by human activities (e.g., Hodara 1998; Busch et al. 2001; Pépin and Angibault 2007; Buenestado et al. 2008; Campos Krauer 2009; Desbiez et al. 2009; Hodara and Busch 2010; among others). In contrast, this work provides ecological information on capybaras from moderately disturbed areas with potentially high habitat suitability (Adámoli et al. 1988; Alvarez 2002). It also illustrates the ecological plasticity of the species, which is able to colonize different types of water bodies (Ojasti 1973; Quintana and Rabinovich 1993). This fact, together with a high reproductive efficiency (González-Jiménez 1995; Cueto 1999; Alvarez and Kravetz 2002), the presence of only a few predators that attack mainly juveniles (*Cerdocyon thous, Caiman yacaré,* and *Coragyps atratus*) and high forage heterogeneity and availability (Corriale 2010) all year-round, may account for the success and high densities of *H. hydrochaeris* in the study area.

Acknowledgments The authors thank the Conservation Land Trust and Mr Salvador Sotelo and his family for their help and support during this study. Research was partially funded by grant X-481 (UBACyT) from the University of Buenos Aires.

Appendix I

See Table 9.

Table 9 Environmental and vegetation variables measured on four rounded shallow lakes during summer 2007–2008 (V07 and V08, respectively) and winter 2007–2008 (I07 and I08, respectively)

Shallow lake	Season	A	P	LL	R	% LL	% E	% EB	% VFL	% SA	% SV	% GCLL	% GCE	% GCI
L1	I07	4.76	1,125.7	2.42	1.5	0.51	0.49	30	45	20	65	5	45	27
	I08							20	20	20	40	5	43	28
	V07							45	20	25	45	18	55	36
	V08							60	0	40	40	12	52	31
L2	I07	6.59	1,121.69	4.45	1.2	67.5	32.5	45	40	0	40	10	23	30
	I08							60	5	5	10	22	21	27
	V07							70	10	5	15	25	29	45
	V08							60	5	30	35	21	25	42
L3	I07	12.7	1,293.64	9.6	1.0	75.6	24.4	30	35	25	60	5	26	32
	I08							35	15	50	65	0	28	33
	V07							45	20	25	45	10	35	30
	V08							20	15	40	55	16	41	36
L4	I07	13.92	1,476.01	9.93	1.1	71.3	28.7	40	30	30	60	0	16	38
	I08							45	15	40	55	0	14	36
	V07							55	30	5	35	25	42	48
	V08							70	10	5	15	23	39	44

A Area (ha), *P* perimeter (m), *LA* low-lying area (ha), *R* Patton's diversity index, *% LL* % of low-lying area, *% E* % of water-land ecotone, *% EB* % of "embalsado" in the low-lying area, *% VFL* % of vegetation-free water surface in the low-lying area, *% SA* % of waterlogged, vegetation-free soil in the low-lying area, *% SV* % of vegetation-free soil in the water-land ecotone, *% GCLL* % GCE, *% GCI* % of graminoid and cyperacean cover in the low-lying area (without "embalsado"), the "embalsado" and in the water-land ecotone, respectively

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