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Determinants of capybara presence in afforestations of the lower delta of the Paraná river, Argentina

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The delta of the Paraná River in Argentina represents the southernmost stronghold for capybaras (*Hydrochoerus hydrochaeris*), but this area is highly modified due to commercial afforestations with Salicaceae. Water management (e.g. drainage of marshes) and land protections (e.g. polders) are carried out to improve field conditions for developing afforestations. To assess determinants of capybara presence within polder afforestations, its presence was surveyed in 2011–2013 along with 35 habitat and human-related variables at two spatial scales, in 53 watercourse-side sites. Using logistic regression, a habitat model was developed. Capybaras were present in 52.8% of sites. Water depth at the center of the watercourse had the strongest positive effect on capybara presence, followed by cover of reed marshes and cover of grass bush on the banks. Cover of adult poplar plantations showed a significant negative effect on capybara presence. Watercourses within polder afforestations can provide habitat for capybaras, although their use by these rodents depends on factors interacting at different scales.

Keywords: *Hydrochoerus hydrochaeris*; polder afforestation; predictive model; restoration; Salicaceae; sustainable forestry production

Introduction

Capybaras (*Hydrochoerus hydrochaeris*) are large (ca. 50 kg), gregarious rodents widely distributed in South America. Adapted to the amphibian life, they can be found in different habitat types such as marshes, swamps, rivers, estuaries, and streams, avoiding areas distant to the water–land interface (Mones & Ojasti 1986). Capybaras depend on water for thermo-regulation, mating, and as a refuge from predators, whereas feeding and resting occur on land (Schaller 1976). Thus, the spatial arrangement of water bodies and vegetation in adjacent areas are key factors in determining species presence (Herrera & Macdonald 1989; Quintana 1999; Corriale 2010).

Capybaras are currently common in agroecosystems and anthropogenic lands (Verdade & Ferraz 2006; Ferraz et al. 2009; Campos-Krauer et al. 2014). Although they are considered to be harmful in many places because of crop damage (Ferraz et al. 2003), food competition with cattle (Ojasti 1973; Escobar & González-Jiménez 1976), and zoonotic diseases transmission (Labruna et al. 2004), they also constitute an important source of protein and fur for local people (Ojasti 1991; Bolkovic et al.

2006). Consequently, some local populations of capybaras have been eliminated and large internal markets exist for their products (Mones & Ojasti 1986; Bolkovic et al. 2006). Nevertheless, the species is considered as “Least Concern” at global scale (Queirolo et al. 2008).

The Paraná River Delta, one of the largest wetlands in South America, represents the southernmost stronghold for capybaras, since the remaining southward populations of the species are small and isolated (Gómez-Villafañe et al. 2005). The lower portion of this delta (i.e. where this wetland ends into the Rio de la Plata) has experienced a large-scale transformation process during the last 150 years, first with the introduction of permanent human settlements and fruit cultivation, and more recently with commercial afforestations with Salicaceae (*Populus* sp. and *Salix* sp.) and intensive silvopastoral systems (Borodowski & Suárez 2004; Galafassi 2004). To improve field conditions for developing these activities, water management (e.g. drainage of freshwater marshes, construction of channels) and land protections (e.g. ditches, polders) are carried out to regulate or

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impede the entry of water into plantation areas (see Study Area for details). As a result, the hydrological regime and morphology of watercourses have been altered within plantations, affecting both the associated plant and animal assemblages (Bó et al. 2010; Fracassi 2012) and the dynamics of biogeochemical processes (Ceballos et al. 2013). The construction of channels in “open-ditch plantations”, with the resulting reticulate pattern that creates more land–water interfaces, appear to have positive effects on habitat suitability for amphibious species such as Southern river otter (*Lontra longicaudis*) and capybara (Quintana & Kalesnik 2007). Conversely, in large “polder afforestations” (those totally surrounded by ditches and levees, and where water management implies the drainage of watercourses) capybaras have low occupancy rates, suggesting that this activity could considerably diminish the habitat aptitude for this rodent (Quintana 1999; Fracassi 2012). In this context, Quintana and Kalesnik (2007) suggested that once afforestation exceeds a certain threshold in terms of intensity or impact on original landscape structure, this activity may become incompatible with the very existence of capybaras.

Facing this situation, stakeholders involved in the Paraná Delta development (e.g. governmental institutions, forestry companies, environmental NGOs) are concerned about minimizing or mitigating impacts related to polder afforestations, improving the sustainability of the current production model by including biodiversity conservation into the process (e.g. Fracassi et al. 2014). As one of the most typical and emblematic vertebrates of the Paraná Delta, conservation of capybaras within forestry establishments is one of the main targets of these initiatives. However, an idea of which landscape elements must be preserved or restored to enhance the conservation of capybaras is required (Quintana & Kalesnik 2007). Due to its association with the land–water interface, new protocols concerning management of watercourses and riparian habitats are probably needed, but supporting data to guide the development of these protocols is lacking.

To assess determinants of capybara presence in watercourses within polder afforestations of the Lower Paraná River Delta, habitat features and human activities that affect this rodent’s presence were evaluated at two spatial scales (local and landscape levels). Furthermore, a habitat model for capybaras in afforestations was developed. Guidelines for forest landscape planning are proposed to make compatible this activity with the presence of capybaras.

Materials and methods

Study area

Located at the end of the Paraná River and in the upper portion of the Rio de la Plata estuary, Argentina, the lower delta of the Paraná River (33°48′ to 34°26′S, 59°00′ to 58°31′ W; hereafter, “lower Delta”) has an extension of *ca.* 3200 km² with the typical deltaic morphology (numerous islands surrounded by an intricate net of watercourses; Kandus & Malvárez 2004). The presence of different landscape patterns determines a marked environmental heterogeneity (Kandus et al. 2003). The original riparian forests of the peripheral levees of the islands have been mostly replaced by commercial plantations, hamlets, and forestry infrastructure; whereas the central areas of the islands are freshwater marshes with low species richness and the dominance of graminoids such as *Scirpus giganteus* and “ceibo” (*Erythrina crista-galli*, Fabaceae) forests (Kandus et al. 2003).

Afforestation with Salicaceae, mainly poplar (*Populus* spp.) and willow (*Salix* spp.), is the principal economic activity in the lower Delta, occupying *ca.* 840 km² (MAGyP 2011). Afforestation areas are not homogeneously distributed throughout the delta, and the largest concentration of plantations is located in the so-called “forest nucleus” (f. INTA – Delta del Paraná), with *ca.* 500 km². Willow is used due to its rapid growth and tolerance to waterlogged conditions, whereas poplar requires dryer conditions and it is planted on natural levees and inside polders (Latinoconsult 1972).

The hydrological regime of the region is dominated by floods from the Paraná River combined with floods from Gualeguay and Uruguay rivers, tidal and storm surges from the Rio de la Plata estuary, and local rainfall events (Baigún et al. 2008). To avoid prolonged waterlogged conditions within plantations, two water-management modalities are practiced by producers of the lower Delta (Latinoconsult 1972). On one hand, small producers follow the “open-ditch” modality, involving the construction of a network of ditches and drainage channels to eliminate excess water and guide it rapidly to main streams and rivers. This practice increases the percentage of land–water interfaces and the presence of patches of freshwater marshes. On the other hand, large companies follow a “polder afforestation” model by totally surrounding plantations with levees to protect trees from floodwaters. Consequently, the area behind the dam is drained and original marshes are mostly eliminated. The total area of the lower Delta currently under water protection by polders and ditches is *ca.* 1250 km² (Blanco & Méndez

2010). As a form of productive diversification in polder afforestations, livestock rising under silvopastoral systems is expanding in the lower Delta, also affecting soil properties and the native flora and fauna (Baigún et al. 2008; Quintana et al. 2014).

Sampling design

To assess how habitat, landscape pattern, and human activities influence the presence of capybaras in polder afforestations of the lower Delta, the presence/absence of the species was surveyed along with several habitat variables at two spatial scales in 53 watercourse-side sites randomly selected within 15 forestry establishments in the lower Delta (Figure 1). Each sampling site consisted of a 50 m long transect parallel to the watercourse flow, and extending for 5 m upslope from the watercourse border. A complete survey of this plot was performed, searching for any evidence of the presence of the species (tracks, feces, beds, wallows, plants browsed with distinctive marks).

As an additional method to assess capybara presence, a 30-day survey with an analogical camera trap (Leaf Rivers Trail Scan Model C-1, Vibra Shine, Taylorsville, MS, USA) was performed. The camera-trap was located near the center of the transect, at a height of 0.50 m from the ground and up to

4 m away from the watercourse border, pointing toward the land–water interface. Cameras were active 24 h a day and were checked once every 15 days to replace batteries or film. Cameras were used only in 38 of the sampling sites (72%) due to security issues (i.e. some places were highly vulnerable to vandalism) or camera availability. Although the recording rate of capybaras in cameras was low (see results), we recognize that the absence of cameras in some sampling sites produced different sampling efforts, probably biasing our results. To further increase the chances of detecting capybara presence in a sampling site, a third method was considered. Unstructured interviews were carried out with laborers and producers working on properties containing sampling sites, selecting the most appropriate candidates (i.e. those responsible for the area under investigation or with better knowledge about wildlife in the property) based on workers' advice. Interviewees were asked about capybara presence in the exact position of the sampling sites or in immediate adjacent areas, considering an extension of up to 200 m from the center of each sampling site. We consider that, collectively, the three methods to assess capybara presence (field survey, camera trapping, and interviews) were complementary and minimized the chances of considering the species absent if it was present in a sampling site.

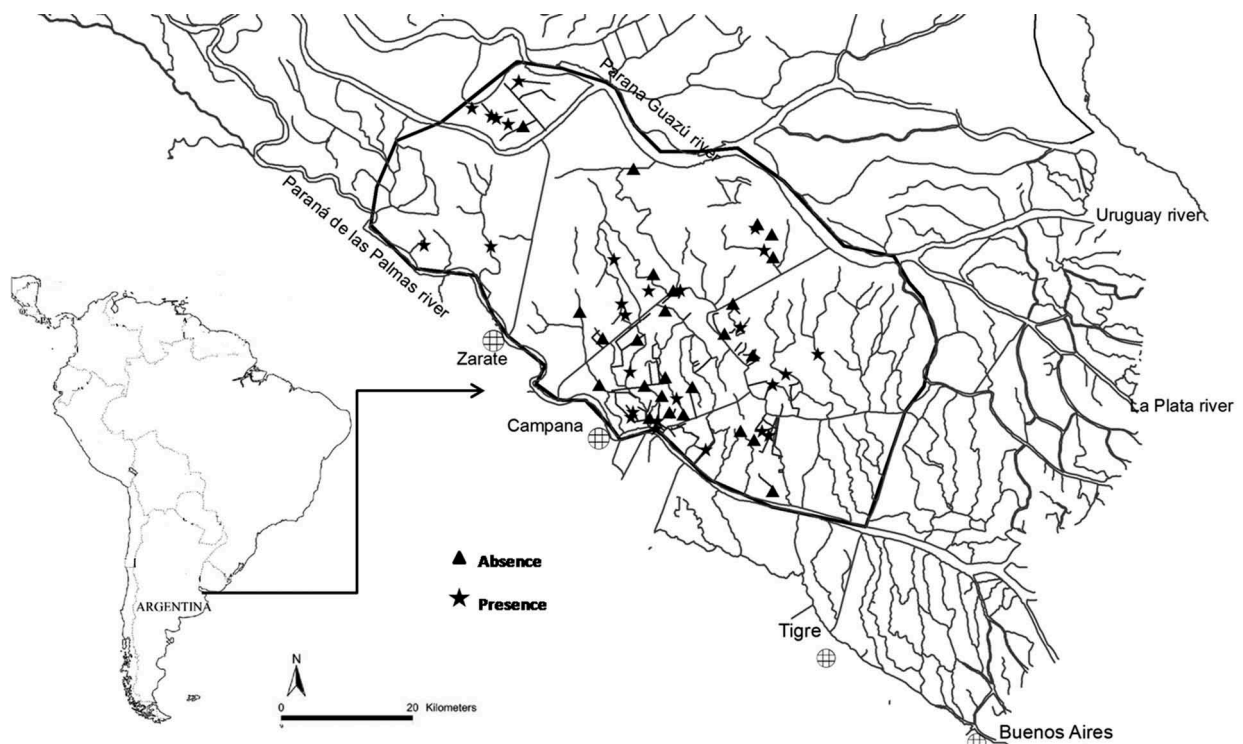


Figure 1. Sampling sites at watercourses within the “forest nucleus” of the lower Delta of the Paraná River, Argentina.

Territory size of capybaras, which is positively correlated with group size, varies from 5 to 16 ha (Herrera & Macdonald 1989) whereas daily movements rarely exceed 500 m (Azcárate 1980; Macdonald 1981). Following these studies, and considering that only small capybara groups are present in the lower Delta (Quintana 1999), adjacent sampling sites were separated by at least 500 m (although distance was usually much greater) to ensure independence between sites. Field sampling was concentrated during late spring and summer (November–March) of 2011–2012 and 2012–2013, diminishing inter-site bias in measured variables due to differences in climate or plant phenology throughout the year.

At each sampling site, habitat and anthropogenic variables potentially important for capybaras for feeding, thermoregulation or protection (following Herrera & Macdonald 1989; Quintana et al. 1994; Quintana 1999; Ferraz et al. 2007, 2009; see Table 1) were measured. These variables were recorded as presence/absence, categorical (high, medium, low, none) or continuous scales (e.g. distances in m, degrees of slope) considering two spatial scales. First, at site scale, variables regarding morphology and dynamics of the watercourse, and vegetation in the border (see Table 1) were measured within the same plot used to determine capybara presence, extending it to the watercourse. To assess habitat

Table 1. Habitat features (measured at site and landscape scales) and anthropogenic variables evaluated to model capybara presence in polder afforestations in the lower Delta of the Paraná River, Argentina.

Variable	Units or categories
<i>(a) Habitat variables at site scale¹</i>	
Type of watercourse	Stream or channel
Watercourse active ² at the moment of the survey?	Yes or no
Temporal dynamics of the watercourse	Permanent or sporadic
Width of the watercourse	In meters
Water depth at the center of the watercourse	In meters
Cover of floating vegetation	In percentage
Cover of rooted vegetation in the watercourse	In percentage
Cover of herbaceous in the border	In percentage
Cover of grass bush (<i>Cortaderia selloana</i>) in the border	In percentage
Cover of shrubs in the border	In percentage
Cover of trees in the border	In percentage
Cover of bare soil in the border	In percentage
Exposed roots in the border	Yes or no
Border slope	In degrees
<i>(b) Habitat variables at landscape scale³</i>	
Cover of adult willow plantations	In percentage
Cover of young willow plantations	In percentage
Cover of adult poplar plantations	In percentage
Cover of young poplar plantations	In percentage
Cover of riparian forests	In percentage
Cover of cortadera (<i>Scirpus giganteus</i>) marshes	In percentage
Cover of grasslands	In percentage
Cover of reed (<i>Schenoplectus californicus</i>) marshes	In percentage
Cover of other water bodies	In percentage
Width of the nearest road	In meters
Distance to the nearest road	In meters
Distance to the nearest principal road	In meters
Distance to the nearest river	In meters
Distance to the nearest cortadera marsh patch	In meters
Distance to the nearest riparian forest patch	In meters
Distance to the nearest hamlet, town or city	In meters
<i>(c) Anthropogenic variables</i>	
Main activity of the property	Afforestation, cattle rising or both
Presence of cattle	Yes or no
Time-in-production of the property	In years
Transit level (by vehicles and pedestrians)	High (>8/day), medium, low (<2/day) or none
Hunting pressure	High (≥4 hunters/month), medium, low (≤1 hunter/month) or none

¹Measured within plots of 500 m²

²Water is running through the watercourse

³Measured within a 450 m radius plot centered in the center of the transect

variables at the landscape scale, a supervised classification of a Landsat 7 TM satellite image (CONAE, Buenos Aires, Argentina; bands 4, 5, and 7; November 2010) was performed using the maximum-likelihood decision rule (Lillesand & Kiefer 1994) in Erdas Imagine 9.1 software. Using ArcView 3.2, a 450 m radius buffer centered in the middle of each transect was superimposed over the classified image. Variables assessed at this scale included cover of different habitat patches and distances to several landscape elements with potential impact on capybara presence (Table 1). Finally, anthropogenic variables related to human activities and land use (Table 1) were obtained by interviewing managers and laborers of each property.

Data analysis

A probabilistic model based on 35 predictor variables (Table 1) was performed, considering “presence” or “absence” of capybaras as the response variable. A three-step chained analysis was conducted using SPSS software (version 16.0). First, to determine which variables were significantly correlated with the response variable, a correlation analysis between each predictor variable and the response variable was carried out. A chi square (Pearson χ^2) test was used for categorical variables whereas a Mann–Whitney test was used for continuous variables (Zar 1999). Those variables significantly correlated ($p < 0.05$) with the presence of capybaras were retained in the analysis. Second, to prevent overparametrization of the prediction model, multicollinearity of explanatory variables retained in the previous step was tested by calculating Spearman’s correlation coefficients (rho) for variables. Groups of correlated variables were defined using a stringent rho threshold-value of 0.4 to get a simple model with only few variables. Just one variable per group was retained, namely the variable that was most significantly correlated to the presence of capybaras. The variable “Distance to the nearest hamlet, town or city”, however, was retained in the analysis in spite of its significant correlation with variables “Cover of young willow plantation” and “Cover of adult poplar plantation” (see Results) since the interpretation of these relationships was not ecologically logical. Finally, a predictive model for capybara presence was built using a logistic regression analysis. Logistic regression evaluates the functional relationship between the binomial response variable and the independent explanatory variables, constituting a way to identify the spatial environmental determinants that affect species presence (Trexler & Travis 1993; Pearce & Ferrier 2000). The predictive model was obtained

by sequentially running the logistic regression, eliminating in each successive iteration the variable with the highest p -value until finding a combination of variables in which all variables have a p -value < 0.05 . Finally, the goodness of fit of the obtained model was assessed through a Hosmer–Lemeshow test (Hosmer & Lemeshow 2000) whereas its predictive performance was evaluated considering model reliability or calibration (the agreement between predicted probabilities of occurrence and observed proportions of sites occupied; Pearce & Ferrier 2000).

Results

Sampling sites at the lower Delta corresponded to borders of 34 human-made channels and 19 natural streams. Presence of capybaras was confirmed in 28 out of 53 (52.8%) sites (Figure 1). Sign survey was the most effective method of recording capybara presence, but camera trapping provided the unique confirmation source in two sampling sites. Capybaras were recorded in eight sampling sites through interviews, but these sites were also positive during sign surveys.

From the original set of pre-candidate explanatory variables (Table 1), only four (two at the local scale and two at the landscape scale; Table 2) were retained in the logistic regression model after taking into account correlation with capybara presence and collinearities. Water depth at the center of the watercourse had the strongest positive effect on the response variable, followed by cover of reed marshes and cover of grass bush in the border; cover of adult poplar plantations, on the contrary, showed a significant negative effect on capybara presence (Table 2). The Hosmer–Lemeshow goodness of fit test indicated a good fit of the model ($\chi^2 = 13.003$; $df = 8$; $p = 0.112$). The performance of the model is shown in Figure 2; the range of predicted probability of sites with capybara presence was 0.15–0.99 (mean = 0.75; median = 0.89;

Table 2. Parameters of the logistic regression model showing coefficients (B), standard errors (SE), Wald estimates, and significance values (p) derived from the Wald chi-square test ($df = 1$).

Variable	B	SE	Wald	p
Intercept	-2.760	1.106	6.231	0.013
Water depth at the center of the watercourse	1.731	0.756	5.242	0.022
Cover of grass bush in the border	0.085	0.031	7.601	0.006
Cover of reed marshes	0.443	0.271	4.148	0.042
Cover of adult poplar plantations	-0.027	0.015	3.254	0.071

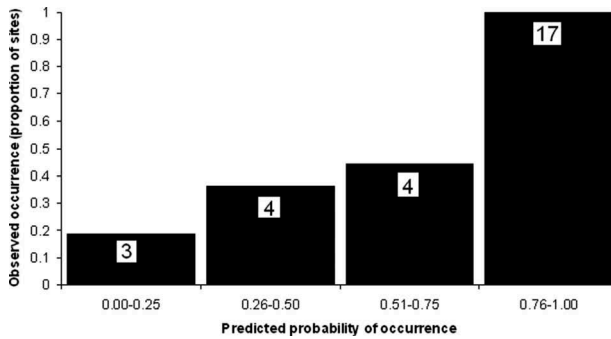


Figure 2. Performance of the obtained model for capybara (*Hydrochoerus hydrochaeris*) presence in the lower Delta of the Paraná River, Argentina. Values on bars are numbers of sites where capybaras were present.

Table 3. Means, medians, and coefficients of variation (CV) of the four variables significantly related to the capybara (*Hydrochoerus hydrochaeris*) habitat model, measured at sites with and without the species in the lower Delta of the Paraná River, Argentina.

Variable	Sites with capybaras (n = 28)			Sites without capybaras (n = 25)		
	Mean	Median	CV	Mean	Median	CV
Water depth at the center of the watercourse	1.3	1.2	0.69	0.9	0.8	0.67
Cover of grass bush in the border	21.6	20.0	0.95	8.1	5.0	1.52
Cover of reed marshes	3.4	0	1.53	0.2	0	5.00
Cover of adult poplar plantations	12.4	0	2.01	34.6	30.0	0.81

SD = 0.29; $n = 28$). Considering a threshold of 0.5 for predicted probability of occurrence (i.e. probabilities above 0.5 imply that capybaras are present), the model correctly predicted 75% of the sites with capybara presence and 80% of the sites without capybaras. Descriptive statistics of the independent variables correlated with the presence/absence of capybaras in watercourses are presented in Table 3.

Discussion

Habitat model for capybaras in afforestations

Watercourses within polder afforestations of the lower Delta of the Paraná River can provide habitat for capybaras, although their use by these rodents depends on several factors interacting at different scales. At the site scale, characteristics of the watercourse (water depth) and of the vegetation in the

border (cover of grass bushes) were significant predictors of capybara presence, whereas at the landscape scale, cover of reed marshes and cover of adult poplar plantations affected the species presence.

Our model indicated that water depth was the only variable associated with watercourses with a significant effect on capybara presence. Neither the type of watercourse (natural stream or artificial channel) nor their widths were important variables. Water depth is central for capybaras since they use water primarily as a place of refuge: when alarmed on land, they rapidly run toward the nearest water body entering diving head-first and remaining submerged for a time (Schaller & Crawshaw 1981; Murphey et al. 1985). On the other hand, water depth in our model was also related to the presence or absence of water in the watercourse; a water depth of zero implies that the watercourse was inactive (i.e. it was drained). Water depth is thus reflecting a critical requirement for this amphibian rodent (Ojasti 1973; Herrera & Macdonald 1989). In addition, high cover of grass bushes (*Cortaderia selloana*) on the banks of watercourses may also be related to protection and shelter for this species, as do patches of dense vegetation (Alho et al. 1987; Ferraz et al. 2007; Quintana et al. 2012). Capybaras have been historically subjected to hunting by humans in the Paraná Delta, either for subsistence, trade, or sports (Quintana et al. 1992; Bó & Quintana 1999). Where capybaras are subjected to persecution, they usually remain hidden during daylight hours in patches of dense vegetation, moving to more open areas toward the sunset or night (Moreira & Macdonald 1997). Thus, the significant predictor value of these habitat features associated with refuge and protection for capybaras in the lower Delta is expected. At the same time, watercourses and riparian vegetation provide abundant palatable species for this rodent, being good food sources (Escobar & González-Jiménez 1976; Schaller & Crawshaw 1981; Quintana et al. 1994).

Considering the landscape matrix, capybara presence was affected by cover of patches of reed marsh, a community locally dominated by giant bulrush (*Schenoplectus californicus*). This sedge has tall, thin stems and can form high-density stands. As freshwater marshes with good cover, reed marshes are commonly used by capybaras as refuge, grazing, and thermoregulation areas (Quintana 1999), and they probably constitute corridor paths between watercourses. Frequency of occurrence of capybaras in freshwater marshes (as those dominated by *Scirpus giganteus* in other areas of this delta) is high in comparison with other habitats in the lower Delta

(Quintana 1999). In this context, conservation of reed marshes should be warranted as an important habitat element at the landscape level and, since they are not subjected to periodic management practices as plantations, they could be considered as stable and predictable refuges for capybaras.

Higher covers of adult poplar plantation, by contrast, negatively affected capybara presence. A similar pattern was observed by Quintana et al. (2012) in open-ditch afforestations of the lower Delta. Due to management practices associated with poplar plantations (e.g. high tree density, mechanical weeding), they typically have only sparse and short understory, mostly of small herbaceous plants, and little vertical structure. These plantations usually extend until the border of the watercourses, promoting the elimination of the riparian vegetation (Fracassi 2012). Additionally, poplar plantations are a common substrate for silvopastoral systems, and thus cattle browsing and trampling may further contribute to the loss of herbaceous and shrubby covers. Although adult poplar plantations can provide good forage for capybaras, since they contain several of the most-preferred plant species for this rodent, such as *Carex riparia* or *Panicum grumosum* (Quintana et al. 1994, 2005), these plantations may fail in providing adequate refuge sites, lowering habitat suitability for capybaras. An opposite situation occurs in willow and young poplar plantations, where a different management scheme allows the development of a rich herbaceous carpet and a dense shrubby cover (Quintana et al. 2005), characteristics that favor the presence of this rodent (Quintana 1999; Fracassi 2012). Our sample design did not allow evaluation of the threshold value of adult poplar plantation cover that determines a change in habitat suitability for capybaras, thus this could be an interesting research line to perform in the future.

Afforestation planning and capybara conservation

The open-ditch plantation modality employed in other areas of the lower Delta, in opposition to polder afforestations, implies the construction of drainage channels which increase the aquatic network and create more land–water interfaces. This afforestation modality appears to improve habitat suitability for capybaras, as new water corridors enable their access to different resource patches (Quintana 1999; Quintana & Kalesnik 2007). In polder afforestations, conversely, the areas behind the polder are drained and the original marshes are replaced by plantations. Although Quintana and Kalesnik (2007) suggested that habitat within polder afforestations becomes unsuitable for capybaras under current management

practices, we found that the existence of particular key-habitat elements allows the presence of capybaras on these properties. Nevertheless, measures to improve large-scale habitat conditions for this rodent are strongly dependent on the goodwill and attitude of producers and forestry managers. Landscape changes in anthropogenic areas (e.g. plantations) are usually more dynamic than those in non-disturbed sites, but capybaras have a strong capacity to adapt to a wide variety of situations (Quintana et al. 1994; Verdade & Ferraz 2006). Thus, new afforestation protocols (e.g. Fracassi et al. 2014) should include habitat improvements (e.g. rehabilitation of drained channels, use of floodgates to manage water level in channels and streams, restoration of riparian vegetation) as a tool to contribute to the sustainability of the afforestation activity.

Our model is useful to prioritize habitat restoration measures to enhance capybara presence in polder afforestations and it could be also employed for predicting the likely distribution of the species in the “forest nucleus”, assisting in the designing of connectivity paths among different capybara subpopulations. Afforestation and territory planning in the lower Delta should include the promotion of habitat heterogeneity, combining active watercourses (rivers, streams or artificial channels), retention of riparian vegetation, maintenance of patches of reed marshes, and the alternation of poplar plantations of different ages. In addition, restoration and habitat-improvement measures should be complemented with anti-poaching activities (e.g. law enforcement, producers’ awareness) since hunting pressure seems to be an important factor in determining capybara density in different habitat types, irrespective of habitat quality (Quintana & Rabinovich 1993). A key point to assure sustainability of the afforestation activity is to design and support management actions to make production compatible with biodiversity conservation, integrating ecosystem conservation and socioeconomic activities. This could be particularly important in the Paraná River Delta, one of the least-disturbed deltaic systems in the world (Baigún et al. 2008).

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