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Building large-scale spatially explicit models to predict the distribution of suitable habitat patches for the Greater rhea (*Rhea americana*), a near-threatened species

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ABSTRACT

We developed large-scale spatially explicit models to predict the distribution of suitable habitat patches for the Greater rhea (*Rhea americana*), a near-threatened species, in two areas of central Argentina with different land use: a grassland area (ca. 4943 km^2) mainly devoted to cattle grazing and an agro-ecosystem area (ca. 4006 km^2) mostly used for crop production. The models were developed using logistic regression and were based on current records of Greater rhea occurrence coupled with remote sensing data, including land cover and human presence variables. The habitat suitability maps generated were used to predict the suitable habitat patch structure for wild rhea populations in each area. Fifty-one percent of the total grassland area was suitable for the species, being represented by a single large patch that included 62% of the individual locations. In the agro-ecosystem, only 28% of the total area was suitable, which was distributed among four patches. Seventy percent of rhea observations were in suitable habitat, with all rheas grouped in the largest patch. Conservation efforts for preserving wild rhea populations should be focused on maintaining habitats similar to grasslands, which are less profitable for landowners at present. Consequently, the protection of the pampas grasslands, a key habitat for this species as well as for others with similar habitat requirements, will demand strong conservation actions through the reconciliation of interests between producers and conservationists, since the proportion of croplands is increasing.

1. Introduction

Conversion of native habitat to human-dominated uses is currently the main driver of global biodiversity loss. Specifically, the change in agricultural land-use pattern has been identified as the main factor affecting species abundance and distribution at local and regional levels (Pereira et al., 2004; Anzures-Dadda and Manson, 2007; Holzkämper and Seppelt, 2007). Wildlife conservation in agricultural landscapes is a challenging issue because land-use changes reduce the amount and quality of native habitat, threatening the persistence of populations of many species inhabiting those modified landscapes (Bretagnolle and Inchausti, 2005; Maron and Fitzsimons, 2007; Pita et al., 2007).

The long-term persistence of populations in modified habitats is influenced by landscape features, such as the number, size, and isolation of suitable habitat patches (Hanski and Gaggiotti, 2004). Consequently, determining the amount and spatial distribution of those patches for a given target species is imperative to design effective conservation programs (Holzkämper and Seppelt, 2007; Pita et al., 2007).

Patch identification is quite straightforward in some species that have habitat requirements with sharp boundaries in the landscape. However, other species may respond to more than one habitat variable simultaneously, and the boundaries of suitable habitat patches are defined by the interaction of several variables (Akçakaya, 2001). This may be the case for the Greater rhea (*Rhea americana*), a near-threatened (IUCN, 2008) flightless bird endemic to South America that inhabits grassy plains and open bush areas.

In Argentina, Greater rheas are typically associated with the pampas grasslands (Folch, 1992), one of the most human-modified habitats in the country (Bilenca and Miñarro, 2004; Brown et al., 2005). Modification of the pampas region began by the first half of the 16th century, with the arrival of Europeans in the region; the pampas underwent little change until the 1870s, however, when a tide of immigration flowed into the country, generating a transformation process that is still ongoing (Guerschman and Paruelo, 2005; Baldi et al., 2006). The original grassland was transformed into an agricultural mosaic, where mixed cropping (i.e., cattle grazing alternated with winter and summer crops) was the dominant land use. However, in the last two decades, agriculture

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has become more profitable than cattle raising, and the grazing-agriculture rotation system is being replaced by double-cropping (Ghersa et al., 2002; Baldi et al., 2006). Consequently, most wild Greater rhea populations currently occur in agricultural landscapes.

Rheas forage mainly on wild and planted dicots (Martella et al., 1996; Pereira et al., 2003) and build their nests in grasslands as well as in pastures (Bellis et al., 2004b). However, the increasing expansion of annual crops leads to a reduction in the extent and, probably, in the quality of these breeding and foraging habitats. These land-use changes have been suggested as a possible cause of recent declines in free-ranging Greater rhea populations (Di Giacomo and Krapovickas, 2005; Martella and Navarro, 2006). For instance, Greater rhea density was found to be significantly lower in an agricultural area than in a grazing-dominated area (Giordano et al., 2008). Hence, habitat conservation will unfailingly lead to the protection not only of this emblematic bird but also of other typical grassland species.

Models predicting species distribution by combining known occurrence records with digital layers of environmental variables have great potential for application in conservation (Pearson, 2007). Recently, numerous works that predict the presence/absence or abundance of a particular species in a specific geographical area have examined species-habitat relationships at a large spatial scale by combining the use of Geographic Information Systems (GIS) and statistical procedures (Franco and Sutherland, 2004; Gibson et al., 2004; Posillico et al., 2004; Balbotín, 2005). For presence/absence data, logistic regression methods are the most commonly used statistical procedures (Akçakaya, 2001, 2005; Franco and Sutherland, 2004; Anzures-Dadda and Manson, 2007; Pita et al., 2007).

We constructed habitat suitability models using GIS and stepwise logistic regression for the Greater rhea in two study areas: a grassland area (ca. 4943 km^2) mainly devoted to cattle grazing and an agro-ecosystem area (ca. 4006 km^2) mostly used for crop production. These models were used to develop large-scale spatially explicit maps to predict the number, size, location of and distances between patches of suitable habitat for the Greater rhea in the Argentine pampas region.

Because of the continuous advance of the agricultural frontier from the humid east of the pampas to the semi-arid west, the challenging task of defining actions that make land use compatible with the persistence of several grassland species becomes imperative. Therefore, our models will help to identify critical areas not only for wild rhea populations but also for other endangered pampas species with similar habitat requirements (e.g., the pampas deer *Ozotoceros bezoarticus celer*).

2. Materials and methods

2.1. Study areas

Although almost the entire Argentine pampas region has been transformed into agro-ecosystems, 3.4% of the grasslands still persist in areas where particular edaphic or climatic conditions hindered the expansion of agriculture (Miñarro et al., 2005). This low percentage of natural grasslands is mainly distributed in two areas: one situated in the eastern Flooding pampa, where a large proportion of halomorphic soils made tillage difficult, and the other located at the semi-arid westernmost portion of the Inland pampa (Guerschman et al., 2003a; Viglizzo et al., 2004; Miñarro et al., 2005) (Fig. 1).

Presence–absence data on Greater rhea and habitat variables were collected from two areas of the pampas region, each located in the sub-region known as Inland pampa. The study locations were selected on the basis of their conservation status: a semi-natural grassland area located in the south-central portion of San Luis province (ca. 4943 km^2, upper left coordinate: 33°54′59.93″S; 66°16′51.69″W), which still resembles the natural habitat of rheas, and an agro-ecosystem close to the grassland area (south-western Córdoba province, ca. 4006 km^2, upper left coordinate: 33°24′59.92″S; 65°5′0.67″W). The San Luis study area covered almost all the grassland where habitat conversion has been less extensive, in the westernmost portion of the pampas, and is the last relict of semi-arid grassland (Demaría et al., 2004). As there is no other grassland site in the Inland pampa sub-region that meets exactly the same conditions and extent as the area surveyed in the present study, there are no replicates available.

The major difference between the study areas is their average annual rainfall, which decreases westwards from 900 mm in Córdoba to 500 mm in San Luis (Ghersa et al., 2002; Sierra and Pérez, 2006). Rainfall is concentrated between October and April in both areas. The selected grassland area is characterized by sandy soils and rolling hills with fixed and moving dunes (Anderson et al., 1970). Maximum summer temperatures can peak 43 °C, whereas winter temperatures can be as low as −15 °C. Vegetation is mostly composed of native grasses (*Sorghastrum pellitum*, *Elyomurus muticus*, *Bothriochloa springfieldii*, *Chloris retusa*, *Schizachyrium plumigerum*, *Eragrostis lugens*, *Sporobolus subinclusus*, *Aristida spegazzini*, *Poa ligularis*, and *Poa lanuginosa*), with small tree patches of *Geoffrea decorticans*, *Prosopis caldenia*, and *Prosopis alpataco* (Anderson et al., 1970; Anderson, 1973). Exotic grass species, such as *Eragrostis curvula* and *Digitaria eriantha*, were introduced to increase carrying capacity for livestock on ranches (Demaría et al., 2003). Land is mostly used for cattle grazing and is only sporadically devoted to crop production because of the low annual rainfall, which in turn has contributed to maintaining its natural physiognomy (Guerschman et al., 2003b).

Unlike the neighboring grassland study area, the agro-ecosystem has been severely transformed by agriculture and cattle raising over the past 150 years (Díaz-Zorita et al., 2002; Viglizzo et al., 2005). Climate is temperate, with mean temperatures of 33 °C in summer and 1.6 °C in winter. The area is characterized by flat to gently rolling dunes. The vegetation was originally composed of grasslands and forests, but is currently dominated by crops (*Zea mays, Triticum aestivum*, *Glycine max*, *Helianthus annus, Arachis hypogea*), followed by pastures (*Medicago sativa*, *Festuca arundinacea*, *Eragrostis* sp., *Agropyron* sp., *Bromus* sp.) (Díaz-Zorita et al., 2002; Guerschman and Paruelo, 2005).

2.2. Habitat variable data

We performed an extensive bibliographic search to identify the main habitat variables that may be relevant to the Greater rhea. We selected variables based on available information on habitat requirements of this species and on data provided by members of our research group, who have more than 10 years of field-work experience on rheas.

Two main sets of habitat variables were identified: one related to land-cover types (i.e., vegetation and water availability) and the other to human presence. Vegetation has been identified as an important factor influencing the selection of nesting and foraging habitats by rheas as well as their vigilance behavior (Codenotti et al., 1995; Martella et al., 1995, 1996; Reboreda and Fernández, 1997; Codenotti and Álvarez, 2000; Bazzano et al., 2002; Fernández and Reboreda, 2002; Bellis et al., 2004a,b; Herrera et al., 2004). To our knowledge, there are no studies about the use of water by rheas in the wild, but we assumed that they drink water either from natural or artificial water sources (e.g., cattle drinkers) (Martella and Navarro, pers. comm.). Moreover, on the edges of natural water bodies there are riparian communities dominated by dicot

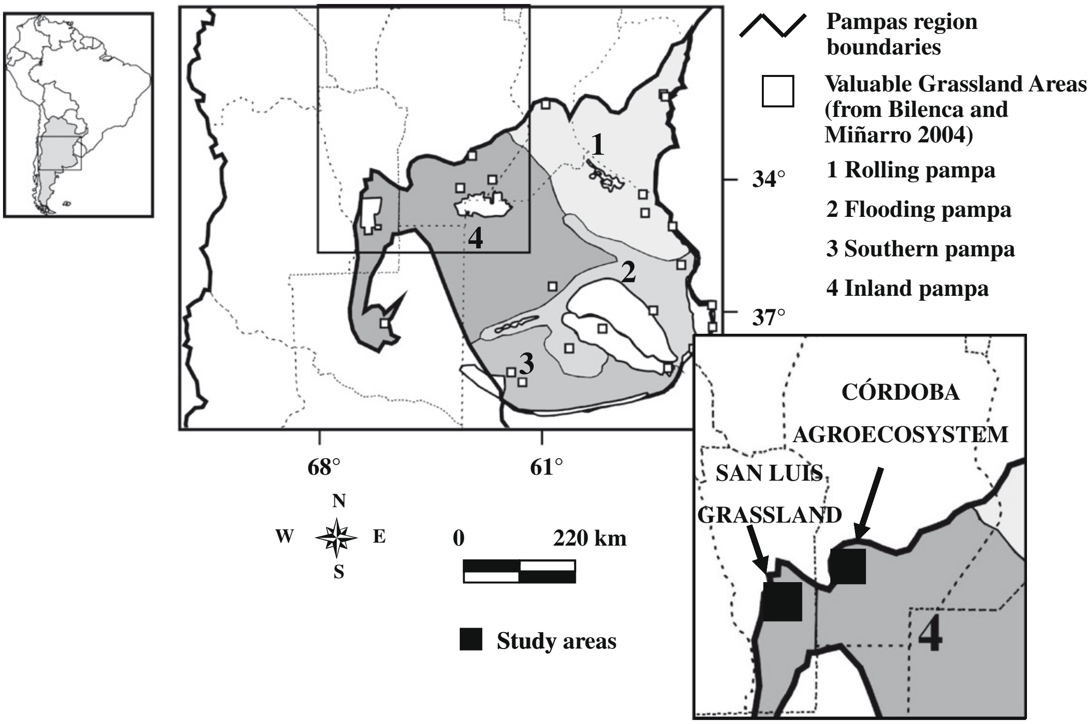

Fig. 1. Location of the two study areas in the Inland pampa within the Argentine pampas region.

species (Herrera et al., 2004); because short-lived wild forbs are the preferred food item of rheas (Martella et al., 1996) natural water bodies and the surrounding habitats may be suitable drinking and feeding sites for this bird species.

Therefore, the first set of variables included six land-cover types: (a) bare ground, represented by dunes, harvested and ploughed plots, and bare ground trampled by cattle; (b) forests, comprising tree patches dominated by *G. decorticans*, *P. caldenia*, and *P. alpataco*; (c) pastures, consisting in plots cultivated only with *M. sativa* or with a combination of *M. sativa*, *Festuca* sp. and *Avena* sp.; (d) grasslands, represented by native grasses, such as *E. muticus*, *B. springfieldii*, *C. retusa*, *S. plumigerum*, *E. lugens*, *S. subinclusus*, *A. spegazzini*, *P. ligularis*, and *P. lanuginosa*, as well as exotic ones, such as *E. curvula*, and *D. eriantha*; (e) croplands, which were plots cultivated with *G. max*, *Z. mays*, *A. hypogea*, and *Heliantus annuus*; and (f) natural water bodies, such as ponds, streams, and rivers.

To build the land-cover maps, we used Landsat 5 TM images (date 16 December 2004; Path/Row 230/084 for the grassland area and Path/Row 229/083 and 229/084 for the agro-ecosystem area). The resolution of the six Landsat bands corresponding to visible and reflected infrared (IR) is 30 × 30 m and 120 × 120 m for the thermal band. Although the grassland area image was cloud-free, there were some clouds in the middle-eastern part of the agro-ecosystem image. These images were georeferenced to the Lat/Long projection (Datum WGS 84) using 50 ground control points obtained in the field with Global Positioning System (GPS), at sites easily identifiable in the image, and were scattered over the scene (ENVI 4.0, 2003). As we did not need the entire Landsat scene for future analysis, we used only a spatial subset comprising the areas over which Greater rheas were surveyed. Between October and December 2004, two field ground surveys were made to recognize and measure areas that represented the different land-cover types. These areas were digitized as polygons in the satellite images and a supervised image classification was performed using the Maximum Likelihood algorithm (Eastman, 2001; ENVI 4.0, 2003). For a suitable statistical characterization, more than 70 pixels were digitized for each land-cover type (Eastman, 2001). The land use/land cover information gathered from the field covered 225.5 km^2 of the grassland area and 175 km^2 of the agro-ecosystem, representing 4.6% and 4.4% of each study site, respectively. The largest land-cover type in the grassland area was pasture, followed by grassland, whereas in the agro-ecosystem area the most extensive type was cropland, followed by grassland (Appendix A). The overall classification accuracy, obtained by a contingency matrix (ENVI 4.0, 2003), was 96% for the grassland area and 89% for the agro-ecosystem, which indicates a high percentage of correct pixel classification. The six data layers built for each study area were five maps of vegetation, representing the proportion of: bare ground, forests, pastures, grasslands and croplands, and a map representing the distance to water. They were in the form of digital raster maps with the same resolution as the satellite images.

Because human presence here is related to an increased risk of predation (Martella et al., 1996; Bellis et al., 2004a), the second set of habitat variables was represented by main, secondary, and unclassified roads; towns and cities; and ranch houses. These variables were developed using topographic maps (1:25,000, Instituto Geográfico Militar), which were scanned, imported, and georeferenced using the resample procedure (Eastman, 2001). They were also in the form of digital raster maps represented by three data layers: distance to roads (m), distance to towns and cities (m), and distance to ranch houses (m).

The six-wire fences (even with some twisted barbed wire strands) typically used to separate paddocks in this region do not provide an effective barrier to rhea movement. Moreover, the ability of individuals to cross fences is a common behavior frequently seen in the field (Martella et al., 1996; Bellis et al., 2004b). Consequently, wire fences were not included as a variable that could influence rhea presence.

2.3. Greater rhea presence–absence data

Presence data on Greater rheas were obtained from aerial surveys conducted in each area in December 2004, during the Greater rhea post-reproductive season (Giordano et al., 2008). The sampling areas covered 113 km^2 in the grassland area and 95 km^2 in the agro-ecosystem, representing approximately 2.3% of each study area. As aerial surveys may not accurately document Greater rhea true absence data, 200 random points were generated per study area to represent non-occurrence locations (often called pseudo-absences). Then, a subset of these absence points was selected, so that the total number of random absences matched Greater rhea presence points: 26 points for the grassland area and 10 points for the agro-ecosystem. To select these absence points, we used the following criteria: a square area equal to the species home range (11 km^2 for the grassland area and 3 km^2 for the agro-ecosystem, Bellis et al., 2004a) was delineated around each presence–absence point. The surrounding pixels around a presence point were assumed to support suitable habitat. So, we first removed those absence points whose areas overlapped the areas delineated around each presence point. Then, as neighboring absence localities could cause clustering and could lead to data redundancy, those absence points whose areas overlapped were also removed. Because absences still outnumbered the presences, the remaining points were selected at random.

To measure habitat variables, the selected set of presence–absence points was overlaid on each of the nine map layers and a sample square area around each point was defined. It represented 20% of the estimated home range for the Greater rhea: 2.2 km^2 in the grassland area and 0.6 km^2 in the agro-ecosystem. This value was chosen because it is considered the minimum area that satisfactorily meets the habitat requirements of an individual (Glenz et al., 2001; Posillico et al., 2004). The average value of all pixels within each sample area represented the habitat data obtained for statistical analysis.

2.4. Data analyses

A logistic regression analysis, which examined the relationship between the occurrence of Greater rheas and the characteristics of their habitat, was conducted to estimate a habitat suitability function (HSF) for each study area (INFOSTAT 7p, 2007). The group of land-cover variables was considered separately from that of human presence, following recommendations for small sample sizes (Balbotín, 2005). Because aerial surveys for Greater rhea data gathering is costly and time consuming, we split the initial set of presence-pseudo-absence points into two random sub-samples: one for estimating the HSF and the other for validation purposes. A univariate analysis was performed to measure the association of each independent variable with the response variable, according to the results of the Wald test. Before performing the multivariate analysis, we tested the presence of multicollinearity using the Spearman's rank coefficient, and a $|r_s| > 0.6$ was considered a suitable criterion for discarding variables (INFOSTAT 7p, 2007). Then, a forward stepwise process was applied with a significance level of $p = 0.1$ for adding variables. To assess the fit of the models we used Chi-square goodness of fit test, classification tables and McFadden's-R^2. Variable retention was based on statistical and biological considerations (Section 3.1 of Results). We also used Receiver Operating Characteristic (ROC) curves (Stata/SE 10.0, 2007) for evaluating the accuracy and discriminating power of the statistical models. In this analysis, the power of the model's predicted values to discriminate between positive and negative cases was quantified by the Area under the ROC curve (AUC) measure, also known as concordance index, which varies from 0.5 (discriminating power not better than chance) to 1(perfect discriminating power) (Liu et al., 2005; Nogués-Bravo and Aguirre, 2006).

Following Akçakaya (2005), the habitat map layers and the HSF were incorporated into the Spatial Data subprogram of the RAMAS GIS software to obtain a map of habitat suitability indices (HSI) for each area. These maps were then used to define habitat patches by identifying areas of high suitability, where Greater rheas might survive and reproduce. The Spatial Data subprogram employs a patch-recognition algorithm to define the spatial structure of the habitat patches, with the incorporation of two parameters: threshold habitat suitability (THS) and neighborhood distance (ND). THS for patches is the minimum habitat suitability (HS) value needed for reproduction of the species modeled (Akçakaya, 2005). In this work, we assumed that the locations where Greater rhea males were seen with chicks were habitats where the species can reproduce. Therefore, THS of 0.86 and of 0.90 for the grassland area and the agro-ecosystem, respectively, were the minimum HS values where Greater rhea males were observed with chicks during the aerial survey. Only those pixels that had habitat values equal to or greater than these THS were considered in the patch-recognition process. ND represents the spatial scale at which the population can be assumed to be panmictic and can be estimated from the foraging distance of an individual (Akçakaya, 2005). Here, we estimated ND as the average maximum distance traversed by a Greater rhea within its home range. Then, ND values of 141 pixels (~4.3 km) for the grassland area and of 55 pixels (~1.7 km) for the agro-ecosystem were estimated using data from Bellis et al. (2004a). Habitat suitability values were then calculated for each 0.0009 km^2 pixel in each study area. Finally, the structure of suitable habitat patches was defined and the center-to-center and edge-to-edge distances among suitable patches were calculated.

3. Results

3.1. Univariate and multivariate analysis

Table 1 shows the results of the univariate analysis only for the variables that were significant in the Wald test ($p < 0.1$). The coefficient signs indicate that in the grassland area, the probability of detecting rheas increase with increasing proportion of pastures and proportion of grasslands and decreasing proportion of croplands, as well as with decreasing distance to natural water bodies. On the other hand, the higher the proportion of bare ground in the agro-ecosystem, the lower the probability of observing rheas.

The following habitat variables: proportion of forests from the grassland area and proportion of grasslands, proportion of croplands, and distance to water from the agro-ecosystem area, were discarded because their Spearman's coefficient was higher than |0.6|, indicating that they were correlated with other variables.

The forward stepwise logistic regression indicated that the occurrence of Greater rhea in the grassland area was best predicted by the model that first incorporated the proportion of pastures and then the proportion of grasses (Table 2). The probability of rheas' presence was positively associated with these two variables. On the other hand, Greater rhea occurrence in the agro-ecosystem was negatively related to the proportion of bare ground. All significant variables were included in the models. Although the proportion of pastures in the agro-ecosystem area was not significant (Table 2), we added this variable to the agro-ecosystem model because it is biologically important for the species studied. As a result, the predictive power of the model was improved

Table 1
Variables that resulted significant (p value < 0.1) in the univariate analysis.

Variable	Coefficient	S.E.	Wald test	p value
Grassland				
Pastures	7.23	3.19	5.13	0.024
Grasslands	4.49	2.46	3.32	0.068
Cropland	−10.60	4.78	4.91	0.027
Distance to water bodies	0.02	0.01	7.08	0.008
Agro-ecosystem				
Bare ground	−30.52	17.87	2.92	0.088

Table 2
Parameters and fit for the models describing Greater rhea presence–absence in two areas of central Argentina.

	Variables	Coefficient	S.E.	*p*
Grassland	Constant	−3.04	1.15	0.00
	% Of pasture	7.57	3.34	0.02
	% Of grassland	4.53	2.27	0.04
Model (χ^2) = 17.09, d.f. = 2, p = 0.00				
Agro-ecosystem	Constant	1.84	1.76	0.29
	% Of bare ground	−43.81	27.75	0.10
	% Of pasture	18.30	14.52	0.20*
Model (χ^2) = 6.95, d.f. = 2, p = 0.03				

* This variable was incorporated because it improved the predictive power of the model, although it rendered non-significant.

(McFadden's-R^2 = 0.33 without the variable pasture; McFadden's-R^2 = 0.50 with the addition of the variable). According to the model Chi-square statistic overall models for both areas were statistically significant (Table 2). Both models correctly predicted 88.46% and 80.00% of the presences for the grassland area and the agro-ecosystem, respectively (Cut value 0.50). A model concordance of 89% in the grassland area and of 96% in the agro-ecosystem area indicated a high predictive power.

3.2. Habitat suitability maps

Fig. 2 shows the habitat suitability maps obtained from the estimated HSF for each study area. Fifty-one percent of the grassland

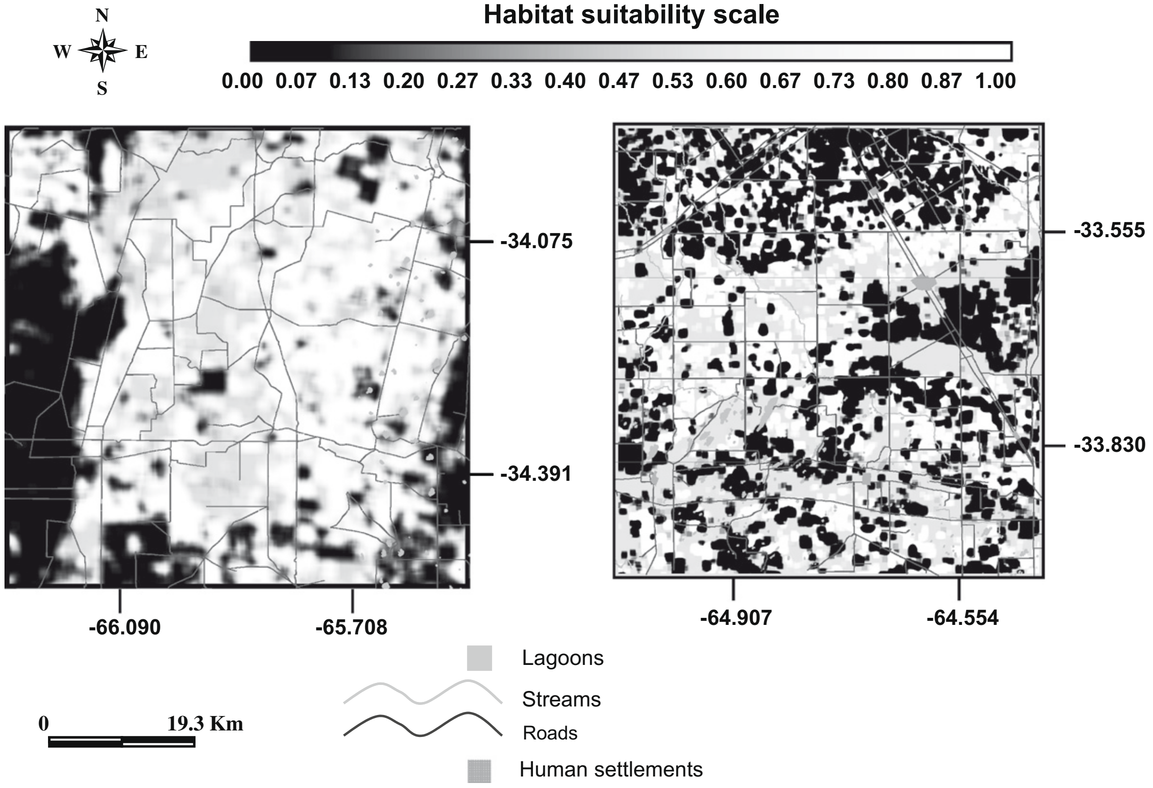

Fig. 2. Maps of habitat suitability indices (HSI) for the grassland area (left image) and the agro-ecosystem (right image). HS values range from black (0 = unsuitable habitat) to white (1 = most suitable habitat).

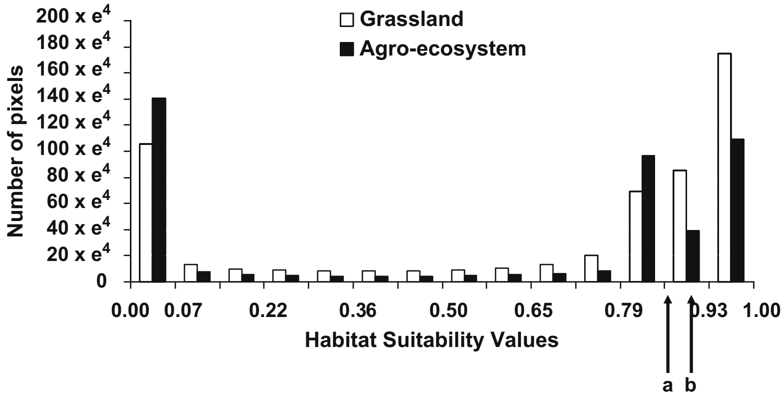

Fig. 3. Frequency distribution (number of pixels) of habitat suitability values for Greater rheas in the grassland and the agro-ecosystem. Arrows indicate the threshold habitat suitability for: (a) the grassland area and (b) the agro-ecosystem.

area had habitat values equal to or greater than THS (⩾0.86), whereas only 28% of the agro-ecosystem area was suitable for Greater rheas (THS ⩾ 0.90) (Fig. 3). Of the 26 rheas detected in the grassland, 61.5% occurred in locations with THS ⩾ 0.86, and the remaining ones were present in habitats of qualities ranging from low to intermediate (HS = 0.05–0.84). On the other hand, in the agro-ecosystem, of the 10 Greater rheas observed, 7 showed HS values ⩾0.90 and only three were in locations below THS. However, the latter observations had all HS values very close to THS (HS = 0.85–0.87). HSF re-estimated with half of the data set successfully predicted the model observations because a large proportion of rhea locations (i.e., 62.0% in the grassland area and 80.0% in

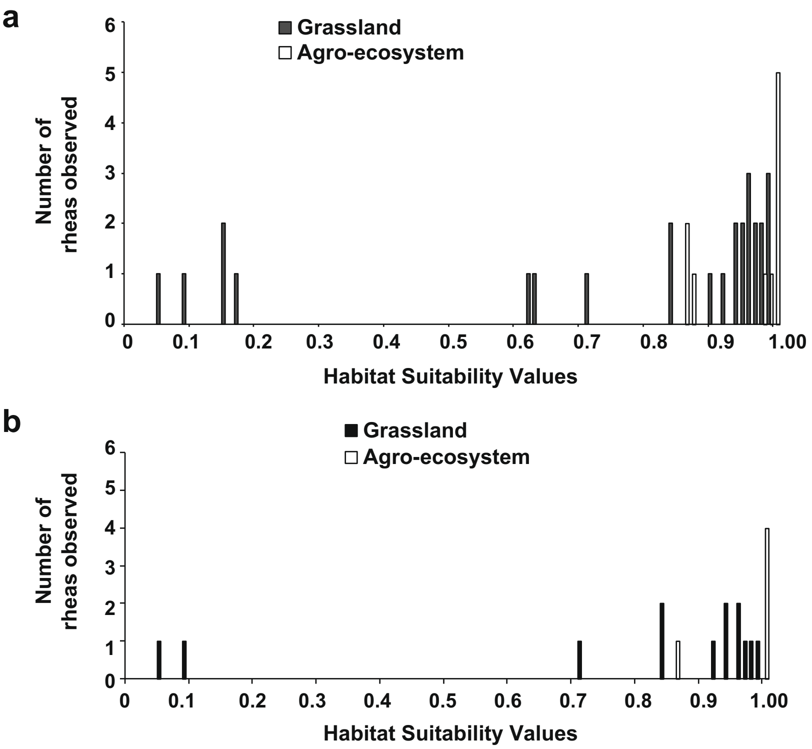

Fig. 4. Frequency distribution of habitat suitability values of Greater rhea presence points in the two study areas, indicating: (a) estimated HSF based in the half data set and (b) validation of the HSF (i.e., the predicted HS values based on the remaining half of the data set).

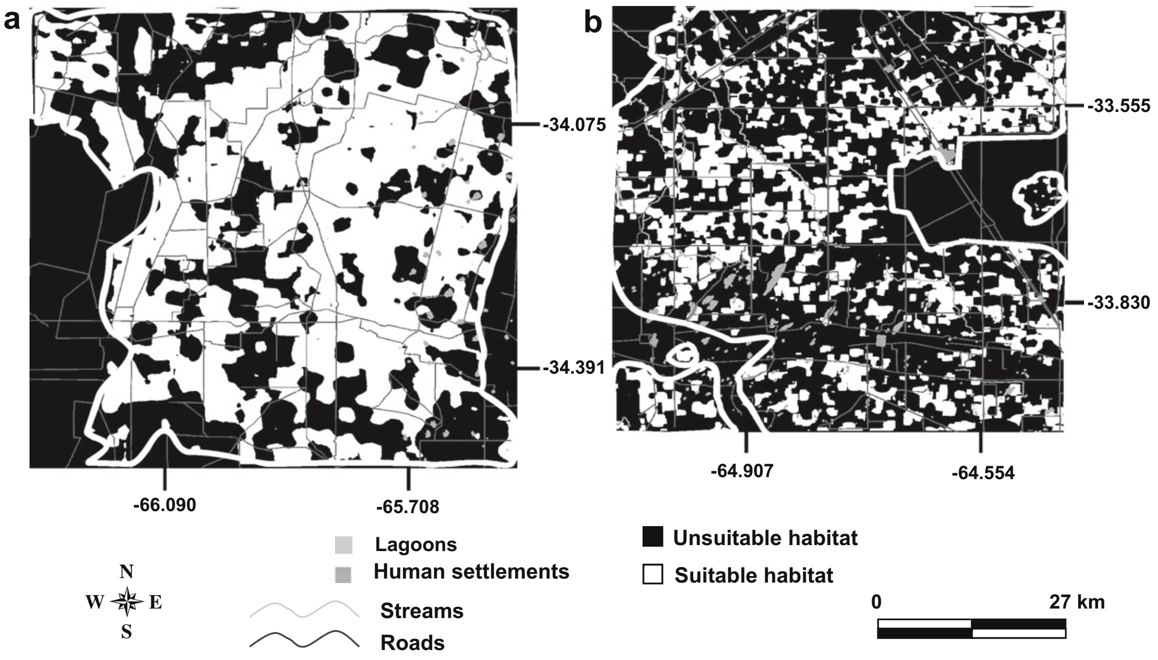

Fig. 5. Maps showing the patches of suitable habitat for the Greater rhea in (a) the grassland area and in (b) the agro-ecosystem in central Argentina. The thin white lines show the borders of each patch.

Table 3
Patch structure of suitable habitat for Greater rheas in each study area.

	Patch number	Average habitat suitability	Geographic coordinates (Lat/Long)*	Patch size (km^2)
Grassland	**1**	0.94	34°12′36.0″S; 65°49′48.0″W	2507
Agro-ecosystem	**1**	0.95	33°39′36.0″S; 64°27′0.0″W	6
	2	0.97	33°53′24.0″S; 64°58′12.0″W	3
	3	0.98	33°57′0.0″S; 65°0.0′0.0″W	45
	4	0.98	33°40′12.0″S; 64°49′12.0″W	1075

* Geographic coordinates measured at the center of the patch.

the agro-ecosystem) were in pixels with predicted habitat values equal to or greater than THS (Fig. 4).

3.3. Patch structure

Based on the habitat suitability map and the patch-recognition parameters, we found one suitable habitat patch in the grassland area and four in the agro-ecosystem (Fig. 5). In the former, the single large patch comprised about 51% of the total study area, whereas the largest patch in the agro-ecosystem, which represented 95% of all suitable patches, was much smaller, as it occupied only 27% of the total area (Table 3).

The single patch identified in the grassland area occupied almost the entire central portion of the study area. On the other hand, the biggest patch in the agro-ecosystem covered a large proportion of the northern, central and south-eastern part of the study area, whereas the remaining three small patches were located in the surrounding areas: two of them were to the south-west and the other one was to the middle-east. In the agro-ecosystem, center-to-center distances between patches varied from 7 to 59 km, whereas edge-to-edge distances ranged between 1.8 and 49 km (Table 4).

4. Discussion

4.1. Habitat relationships and suitability

Identifying the habitat variables that influence species occurrence is imperative to predict the spatial distribution of suitable habitat for threatened species (Walter et al., 2005). According to models of habitat use (Herrera et al., 2004) and habitat suitability developed for Greater rhea (Bellis et al., 2008), we found that vegetation variables have a great influence on the occurrence of this species in a given habitat.

In the grassland area, where cattle grazing predominates and the proportion of pastures (36%) and semi-natural grasslands (32%) is greater than that of annual crops (7%) (Appendix A), the probability of Greater rhea presence increases because individuals can largely meet their basic nutritional, survival and reproductive requirements (Martella et al., 1995, 1996; Fernández and Reboreda, 2002; Bellis et al., 2004b, 2008). On the other hand, in the agro-ecosystem, where crops prevail over grazing, Greater rhea occurrence might be affected by the high rates of disturbance associated with annual cropping (i.e., soil rotation and harvesting), which may induce individuals to be clustered in certain sites where the rate of disturbance is low. This situation is of great concern, mainly because not all suitable patches predicted are populated by greater rheas to date, and also because the area of agro-ecosystem that is devoted to annual crops is currently increasing (Viglizzo et al., 2005).

In the grassland area, rhea density is significantly higher than in the agro-ecosystem (Giordano et al., 2008). Therefore, if habitat selection by rheas follows an ideal free-distribution (Fretwell and Lucas, 1970), the possibility of individuals selecting high-quality habitats within the grassland area might be low. This may explain why rheas occur not only in places high suitability but also in sites within all the HSI range below the THS estimated in this paper (HSI = 0.00–0.86). On the other hand, in the agro-ecosystem, rheas observed outside the patches (30%) were located in a very narrow HSI range (0.86–0.87) that was close to THS. Therefore, if the better habitat quality observed in the agro-ecosystem patches leads to a higher reproductive rate than intermediate or low quality habitats, it could compensate the loss of individuals as a result of habitat conversion, exerting a rescue effect in the area. An alternative explanation to the phenomenon of rheas being grouped in high-quality patches in the agro-ecosystem could be that this area is acting as an ecological trap (Kristan, 2003; Shochat et al., 2005): Greater rheas select sites in response to the habitat characteristics they detect at a given time. This selection would make them highly vulnerable to the rapid changes in land use that are taking place, particularly in this area (annual crop increase of 3.78%, INDEC, 2004), and they would suddenly find themselves in currently unsuitable sites that were suitable a short period before. Another explanation could be that rheas were clumped in the agro-ecosystem because the matrix, where the suitable patches are embedded, is of an extremely low quality compared to that of the grassland area.

Although here we found that suitable habitat is 35% greater in the grassland area compared to that reported by Bellis et al. (2008), both works arrive at the same conclusion: the critical need to preserve the remaining natural habitat of rheas. The main differences between the work of Bellis et al. (2008) and the present study are that in the former the authors worked with vegetation texture as explanatory variables and rhea group size as the dependent variable. Additionally, our work might have overestimated habitat quality at certain locations because of the lack of true absence data and the low number of observations. Therefore, if absence data become available by future studies, the habitat suitability function obtained here may be narrowed, excluding some of the areas currently included in the suitable patches, and a percentage closer to that found by Bellis et al. (2008) may be obtained.

Table 4
Center-to-center and edge-to-edge distances between patches in the agro-ecosystem.

	Patch 1	Patch 2	Patch 3
Center-to-center distances (km)			
Patch 2	54	–	–
Patch 3	59	7	–
Patch 4	26	32	38
Edge-to-edge distances (km)			
Patch 2	49	–	–
Patch 3	48	1.8	–
Patch 4	3.7	4.5	3.7

4.2. Patch structure

Our study provides useful knowledge about the spatial pattern of patches of suitable habitat for Greater rhea in central Argentina.

It shows that the conversion of grasslands into croplands threatens rhea populations in the wild, as it occurs in the agro-ecosystem area, which is composed of four isolated suitable habitat patches. On the contrary, the grassland area would act as a large and continuous patch of suitable habitat, probably because land-use conversion in this area is still less extensive than in the agro-ecosystem.

The subdivided patch structure observed in the agro-ecosystem suggests that within this area rhea populations might represent a metapopulation, where local populations may persist because of dispersal of individuals. According to the center-to-center distances, rheas are expected to disperse only between patches 2 and 3, because they are separated by a shorter distance than the maximum traversed by rheas in that area (7.8 km; Bellis et al., 2004a). As Greater rheas were observed only in patch 4, dispersal does not seem to occur at all. On the other hand, if edge-to-edge distances are considered, rhea dispersal between patches would be higher than in the center-to-center distance situation, because rheas could move between patches 1 and 4, 2 and 3, 2 and 4, and 3 and 4. In this case, patch number 4 would act as a source of dispersal of individuals to the rest of the patches. As dispersal has important implications in a metapopulation structure, these results stress the need for further research to identify the type of dispersal that this ratite may have in this area. This particular aspect may be of importance for conservation, because the current progressive advance of croplands might increase the isolation of local rhea populations, intensifying the threat to the species persistence in this agro-ecosystem.

4.3. Conservation recommendations

The limited information regarding how the prevalent land use determines the spatial arrangement of suitable habitat for the Greater rhea is one of the weak aspects of current conservation plans. The novelty of our research is that the suitable patch maps we have developed, which are the first of their type in Latin America, allow the identification of high-priority areas where the species may survive and reproduce. However, despite the relevance of these maps for predicting rhea occurrence, we recommend prioritizing a continuous monitoring program in the agro-ecosystem area to forecast possible changes in the structure of patches and, consequently, in the status and performance of rheas, because their mere presence in this highly changing habitat does not guarantee its long-term persistence.

Preserving suitable habitats for rheas will be critical for the persistence of wild populations of this species. Nevertheless, as most land in the study region is privately-owned, this conservation approach may generate some conflicts with landowners who perceive a possible decrease in their monetary income. Therefore, as crop expansion continues, management schemes in agricultural areas should be focused on reconciling the interests of producers and conservationists to preserve some habitats with features similar to those of the grassland area.

The methodology we employed in the present study is an additional contribution to conservation schemes. It may be extrapolated, although cautiously, to predict spatial distribution and habitat quality of rheas in other areas within their distributional range, as well as to other species with similar habitat requirements.

4.4. Final remarks

Although the present work is focused on a single species within a single region, the Greater rhea is a highly conspicuous species and an icon of the pampas grasslands. It also can be considered an umbrella species, because the conservation of its optimum habitat will contribute to the protection of several native species and neartic migrants (which use the pampas grasslands as wintering grounds; Vickery et al., 1999; Di Giacomo and Krapovickas, 2005). Therefore, the issue we intend to stress through the current study is the relevance of the working protocol, which can be applied to identify grassland areas suitable for other species and/or other regions of the world.

Table A.1
Area and proportion of each land cover category for the grassland area and the agro-ecosystem.

Land cover type	Grassland		Agro-ecosystem	
	Area (Km^2)	Percentage	Area (Km^2)	Percentage
Unclassified	12.295	0.25	264.368	6.60
Grasslands	1568.838	31.74	1138.305	28.41
Forest	910.042	18.41	193.834	4.84
Pastures	1778.212	35.98	407.585	10.17
Croplands	348.994	7.06	1394.198	34.80
Bare ground	309.195	6.25	591.466	14.76
Water bodies	14.980	0.30	16.448	0.41

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Appendix A

See Table A.1.

Appendix B. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.10.022.

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