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# Conflict between the Greater Rhea and humans in agricultural landscapes: implications for conservation of the last large herbivore of the southern Pampas

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**Abstract.** South-eastern South America (SESA) hosts populations of a number of large herbivores, such as the Greater Rhea (*Rhea americana*). However, the natural grasslands of SESA have been subject to major transformation through agricultural development, primarily grazing, cropping and afforestation. Here, we assess the relative effects of environmental and anthropogenic predictors on the distribution of Greater Rheas in the southern Pampas at different spatial scales, and produce distributions maps of the species derived from habitat-suitability models. We undertook vehicle surveys in the southern Pampas over 2 years, surveying 4600 km of road each year, and recording a total of 146 sightings of 1353 individual Rheas. Generalised additive models were used to model the presence—absence of Greater Rheas in 250-m<sup>2</sup> cells. The habitat suitability models suggest that preferred habitats included areas of high elevation supporting waterbodies and landscapes of grazing fields and native habitats, whereas centres of human activity negative affect the distribution of the species.

Additional keywords: agroecosystems, Greater Rhea occurrence, habitat-suitability maps, landscape ecology.

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# Introduction

Declines in the diversity of grassland animals have largely been driven by the loss and fragmentation of natural habitats resulting from agricultural development (Collingham and Huntley 2000; Azpiroz et al. 2012). In grassland, grazing land and cropland the conservation of large native herbivores generally involves conflict because these herbivores are often assumed to compete with domestic grazers, such as cattle, for food or forage on croplands (Comparatore and Yagueddú 2007; Pedrana et al. 2014). They are also target species for legal and illegal hunting. As a result, most large herbivores of grassland ecosystems have been driven to extinction worldwide (Demaría et al. 2004; Li and Guo 2014). The natural grasslands of south-eastern South America (SESA) have been significantly transformed through the development of agricultural industries, particularly livestock grazing, arable agriculture and afforestation (Azpiroz et al. 2012). In SESA, ~45% of the original cover of natural grassland remains but even most of these remnants have been modified by livestock grazing (Bilenca and Miñarro 2004; Paruelo et al. 2004). The Río de la Plata grasslands are the largest complexes of temperate grasslands ecosystems in South America, comprising an area of approximately 750 000 km<sup>2</sup> (Soriano *et al.* 1991). These grasslands include the Pampas ecoregion of eastern-central Argentina (Bilenca and Miñarro 2004). Over the last 40 years, human landuse in the Pampas ecoregion has intensified, with an increase in the area under cultivation, mainly by Soybean crops (Grau *et al.* 2005; Aizen *et al.* 2009).

In the Pampas agroecosystems, human-induced habitat change and homogenisation, hunting and introduction of exotic species have negatively affected species diversity and populations of native birds (Bucher and Nores 1988; Codesido *et al.* 2011; Azpiroz *et al.* 2012). The Greater Rhea is a large, flightless native bird of grassland and grassland-like ecosystems of southern South America (Bruning 1974; Folch 1992) whose populations have declined and which persists mainly in agroecosystems of grassland and pastures of wild and cultivated dicotyledonous vegetation (Martella *et al.* 1996; Bellis *et al.* 2004*a*; Herrera *et al.* 2004). Local farmers have traditionally hunted or culled Rheas and often significantly reduced populations (Martella and Navarro 2006) because they believed the species damaged crops and competed with cattle for food. Only in 2008 was the Greater Rhea listed as Endangered by the Argentine government and

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hunting prohibited (López-Lanús *et al.* 2008). Globally, the Greater Rhea is classified as near-threatened (BirdLife International 2012), although Pampas populations are continuing to decline (Navarro and Martella 2011). Conservation efforts are thus needed to prevent extirpation or even local extinction of Greater Rheas from the Pampas grasslands.

Modelling habitat suitability and the distribution of species are increasingly important in conservation biology (Rodríguez et al. 2007). Many recent studies have used modelling to predict the presence or absence of species within geographical areas by examining species-habitat relationships at a large scale using combinations of geographic information systems (GIS) and statistical procedures (Hodder et al. 2014; Pütz et al. 2014). Multi-scale approaches are frequently used in the study of habitat preferences (Johnson 1980) because determination of ecological patterns depends on the spatial scale at which they are analysed (Wiens 1989). The use of species-distribution models allow researchers to build statistical explanations of the regional distribution of species, linking field observations to landscapescale explanatory predictors selected from a set of ecologically plausible candidate variables (Rodríguez et al. 2007). The resulting distribution models are used to construct habitat-suitability maps.

The human—Rhea conflict in agricultural landscapes and the near-threatened status of this species globally, and its endangered status in Argentina, make it necessary to study the role of environmental and anthropogenic drivers of the regional distribution of the species for a proper management of its population. Our study had three major objectives: (1) To assess the relative effects of environmental and anthropogenic predictors on the distribution of Greater Rheas in the southern Pampas ecoregion at different spatial scales; (2) to produce distributions maps of the species for the southern Pampas using habitat-suitability models; and (3) to detect priority areas for implementing management and conservation actions.

To achieve these objectives we tested several hypotheses. (1) The Environmental Hypothesis states that the distribution of Greater Rheas principally reflects the availability of suitable habitat near waterbodies, which provide a source of drinking water and food (Herrera et al. 2004). This hypothesis also predicts a higher probability of finding this species in flat and open zones where detection of predators and escape are easier (Bellis et al. 2004a). (2) The Human-disturbance Hypothesis is related to an increased risk of predation and illegal hunting near urban centres and paved roads (Martella et al. 1996). It presumes a lower probability of occurrence of Greater Rheas near urban areas and paved roads because human disturbance affects Rheas negatively (Bellis et al. 2004a). (3) The Landscape Composition and Configuration Hypothesis (hereafter Landscape hypothesis) postulates that the homogenisation of the southern Pampas region through the conversion of native grasslands to croplands and sown pastures for livestock (Bilenca and Miñarro 2004) affects the distribution of Greater Rheas. It predicts that the probability of occurrence of Rheas increases with the area of grassland (Giordano et al. 2010) or, in the agroecosystem, where pastures predominate relative to crops, Rhea occurrence might be affected by the high rates of disturbance associated with annual cropping activities (Giordano et al. 2010).

## Methods

Study area

The study was conducted in an area of 106 000 km² in the southern Buenos Aires province, which belongs to the Espinal and southern Pampas ecoregions of Argentina (36°27′–41°02′S, 63°23′–58°37′W). The southern, Espinal portion of the study area supports remnant xerophilic woodlands dominated by *Prosopis caldenia* within an agricultural matrix. The southern Pampas portion, covering the north of the study area, was dominated by grassland steppe of several species of *Stipa* and *Piptochaetium* (Soriano *et al.* 1991). However, this landscape has been intensively modified by anthropogenic activities. The study area is characterised by low to moderate topography, including the mountains of the Ventania System (Sierras de Ventania), lakes and marshes, and large areas of agriculture, including crops and livestock pastures.

## Study species

The breeding season of the Greater Rhea extends from August to January, and their mating system combines polygyny with sequential polyandry, in which only males incubate eggs and care for the chicks, with parental care extending until early winter (June–July) (Bruning 1974; Handford and Mares 1985). Greater Rheas use habitats selectively (Bellis *et al.* 2004*a*), for example, on a ranch devoted to production of organic livestock and crop in Córdoba Province, wild Rheas were observed using grazing pasture and grassland but were not recorded in crops during the reproductive, post-reproductive or non-reproductive periods (Bellis *et al.* 2004*a*).

## Field surveys

We undertook road-based surveys to determine the occurrence of Greater Rheas owing to the large size of the study area and open nature of the habitats (Travaini et al. 2007; Pedrana et al. 2011). Surveys were conducted from a vehicle driven at a maximum speed of 50 kmh<sup>-1</sup> during two non-breeding seasons (June–July of 2011 and 2012) and all tracks recorded using a GPS (Mio Digi-walker P550, http://www.mio.com, accessed 7 September 2015). We then randomly selected 110 survey tracks (segments of roads) comprising 4600 km of transects. In 2012, we surveyed the 110 survey tracks randomly selected from the surveys in 2011. Approximately 90% of the survey tracks were unsealed secondary roads with very low traffic density. Surveys were performed during daylight, between 0900 and 1600 hours. We did not conduct surveys in the late afternoon because light conditions were generally not good enough for detection of the species. When one individual or group of Rheas was sighted, we recorded the habitat type in which the sighting was located. We previously identified four main categories of habitat type: cropland, grazing land, native habitat and wetland. We recorded the position of the vehicle using a GPS, and measured the distance to the individual or the flock centre with a laser rangefinder (Bushnell 20-1916 Yardage Pro Sport 450 Laser Rangefinder, Overland Park, KS) and the angle of the animal relative to our bearing. We obtained our bearing relative to north from the inertial compass in the GPS unit. From these

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measurements, we were able to determine the actual positions of the Rheas. All data were collected using a digital form.

## Presence-absence analysis

We used presence-absence data collected through our surveys; thus, all tracks recorded with GPS units defined the route of our survey. We used the distance to Rheas that were sighted to estimate the area effectively covered. We used the software Distance 6.0 (http://distancesampling.org, accessed 3 September 2015) to fit a detection function to the distance data (Thomas et al. 2010). A 400-m buffer on both sides of all tracks was chosen to define the effective area surveyed, as 85% of all sightings were within this area. Presence-absence modelling requires defining units in which presence or absence is recorded. For this purpose, we overlaid all the surveyed tracks with 400-m buffers on top of a grid of 250 × 250-m cell size, given the spatial resolution of normalised difference vegetation index (NDVI) data (total number t of surveyed cells 34267). Then, the original 76 and 70 sightings register in 2011 and 2012 respectively was also overlaid. Grid cells with more than one sighting were considered a presence while all remaining cells were considered an absence (n = 31 121).

## Landscape variables

We characterised the study region using 21 potential predictors related to environmental, human and landscape characteristics (Table 1). A map of land-cover was constructed for the study area using the NDVI curves derived from a satellite MODIS (Moderate Resolution Imaging Spectroradiometer) sensor (composites from 16-day intervals, 250-m spatial resolution; National Aeronautics and Space Administration (NASA), Goddard Space Flight Center, available at http://modis-land.gsfc.nasa.gov/vi.html,

accessed 2 September 2015). We calculated the four parameters from the seasonal curves of NDVI using 24 scenes of satellite data (from June 2011 to July 2012): integrative NDVI corresponding to the sum of positive NDVI values over a year from June 2011 to June 2012 (NDVII): annual maximum values of the NDVI over a year (Max NDVI); annual minimum values of the NDVI over a year (Min NDVI); and interannual variability in productivity, calculated as (Max NDVI - Min NDVI)/NDVII. These parameters have been reported as a plausible way for describing vegetation characters relevant to wildlife (Pettorelli et al. 2005) and to capture important features of ecosystem functioning for temperate ecosystems (Paruelo et al. 2001; Alcaráz et al. 2006). We used the iterative self-organising data analysis (ISODATA) method to generate different categories or clusters (command ISODATA, IDRISI Taiga, Clark University, Worcester, MA; Eastman 2009). All outcome clusters were then assigned to the four different habitat categories: cropland, grazing land, native habitat and wetland. An error matrix was created to test the accuracy of cluster assignation and current habitat types based on 850 control points that were taken during the field survey. We obtained an overall accuracy of 78%, and the users' accuracy (error of commission) was 80% for cropland, 74% for grazing land, 70% for native habitat, and 80% for wetlands.

We also included two neighbourhood scales in our analysis, related to the average home-range of Greater Rheas, to encompass daily patterns of movement between feeding and resting areas and between habitat types. In grassland, the average homerange of Rheas is 11 km<sup>2</sup> (Bellis *et al.* 2004*b*) so we used circles of radius 1.8 km to encompass their range in this habitat; in agroecosystems, home-range is 3 km<sup>2</sup> (Bellis et al. 2004b), and we used circles of radius 1 km. We then extracted landscape variables from the constructed land-use map with Fragstats

Table 1. Description of the landscape variables used in the predictive distribution models developed for Greater Rheas in the southern Buenos Aires Province, Argentina

Hypothesis	Landscape variable	Variable description		
Environmental	Altitude Slope Distance.stream Distance.lake	Elevation above sea level (m) of the focal cell obtained from the SRTM  Terrain slope (%) in a 250-m pixel acquired from the SRTM  Straight-line distance (km) to the closest natural and artificial bodies of moving water  Straight-line distance (km) to the closest natural or artificial waterbody surrounded by land		
Human	Distance.urban Distance.road Land.use	Straight-line distance (km) to the nearest urban centre Straight-line distance (km) to the nearest sealed (pavement) road Habitat-type: cropland, grazing land, native habitat or wetland		
Landscape	Crop.area Grazing.area Native.area Wetland.area	Sum of the areas of all patches of each of the four habitat type (km²) (cropland, grazing land, native habit wetland) within a radius of either 1 or 1.8 km around a focal cell divided by 10 000 (to convert to ha)		
	Crop.edge Grazing.edge Native.edge Wetland.edge	Sum of the lengths of all edge segments in a habitat type, divided by the total habitat area (m <sup>2</sup> ) within a radius of 1 and 1.8 km around a focal cell and multiplied by 10 000 (to convert to ha)		
	PLADJ.crop	The number of like adjacencies involving the focal habitat type divided by the total number of cell adjacencies involving the focal habitat type, multiplied by 100 (to convert to a percentage) (i.e., the percentage of cell adjacencies involving the corresponding patch type that are like adjacencies). All background edge segments		
	PLADJ.grazing PLADJ.native PLADJ.wetlan	are included in the sum of all adjacencies involving the focal habitat type.		
	Patch.richness	Number of patches of habitat types within a radius of 1 and 1.8 km around a focal cell		

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(McGarigal et al. 2012). For each 1-km and 1.8-km radius circle, different landscape indices were calculated, based on the landcover map (Table 1).

Further, we calculated in a GIS (command DISTANCE, IDRISI Taiga, Clark University, Eastman, GA, 2009) distances from each  $250 \times 250$  m cell size to the nearest urban settlement, the nearest sealed (pavement) road, the nearest waterbody (e.g. lakes and flooded areas), and the nearest body of moving water (e.g. rivers and streams) (taken from the Instituto Geográfico Nacional, Argentina; available at http://www.ign.gob.ar, accessed 2 September, 2015; Table 1). We also acquired topographic data (altitude and slope) from the Shuttle Radar Topography Mission (SRTM; Jet Propulsion Laboratory, California Institute of Technology and NASA; available at http://www2.jpl.nasa.gov/srtm/ cbanddataproducts.html, accessed 2 September 2015; Table 1).

Multicollinearity of landscape predictors can make interpretation of alternative models difficult (Lennon 1999). We considered two predictors to be collinear when the Spearman rank correlation coefficient (Rs) was >0.6.

## Construction and validation of models

We used presence-absence data from our surveys to develop models and evaluate our hypotheses. We generated two datasets, one for constructing and another for evaluating the presenceabsence models (Guisan and Zimmermann 2000). The model construction dataset used the presence-absence data from 2011 and the model evaluation dataset used the presence—absence cells from 2012.

Models were constructed by fitting generalised additive models (GAM; Hastie and Tibshirani 1990) using a binomial error and a logistic link to determinate which landscape variables were most likely to affect the presence of Rheas. We used a resampling scheme (Pedrana et al. 2014), due to the relatively different number of presences (n = 76) and absences (n = 34121), randomly selecting 76 out of the 34 121 cells with absence. This procedure was repeated 100 times. In each repetition, the cells with presence were the same while cells with absence were sampled without replacement. Predictors for the models were selected from the initial set by a backward-forward stepwise procedure. The Akaike's Information Criterion (AIC) was used to retain a term. We considered as competing models those for which the differences between AIC and the AIC of the best candidate model (the one with the smallest AIC) was  $\Delta \leq 2$  (Burnham and Anderson 2002). Finally, the same procedure was used to build a general model starting with the complete set of potential predictors and simultaneously tested the relative predictive power of all of them.

Model evaluation was done by comparing predicted and observed values using a threshold-independent measure, in this case the curve (AUC) of the receiver operating characteristic (ROC) plot, which was computed for each of the 100 models (Murtaugh 1996). The AUC ranges from 0 (when model discrimination is not better than random) to 1 (perfect discriminatory ability). Predictive models are considered usable if AUC  $\geq$  0.7 (Harrell 2001).

# Habitat-suitability maps

We used the most parsimonious model for each hypothesis to build habitat-suitability maps for Greater Rhea in the southern Buenos Aires Province, Argentina. Predictions for the entire southern Buenos Aires Province were calculated using R version 3.2.2 (R Development Core Team 2014, available at https://www. r-project.org, accessed 2 September 2015) and illustrated on probability maps using IDRISI Taiga GIS software.

#### Results

Over the 2 years of the study, we surveyed 9200 km of road (the same 4600 km in each year) and made 146 sightings of Rheas (76 in 2011, 70 in 2012), comprising a total of 1353 individuals (666 in 2011, 687 in 2012). The number of sightings was 8% lower in 2012 than in 2011. We found a strong correlation between the predictors Distance.urban and Distance.road (Rs = 0.89). We selected Distance.urban as the best landscape variable predictors of these two.

## Fitting and evaluation of models

Among the GAM testing the Environmental hypothesis, the most parsimonious model of Greater Rhea presence incorporated three variables: Altitude, Distance.lake and Slope (Model 1 in Table 2). As predicted, the probability of Rhea occurrence decreased with increasing distance to the closest lake. Rhea occurrence was positively related to altitude and to mean slope (Fig. 1c), although this last trend was not observed at high mean slope values (Fig. 1a). Hence, our hypothesis was not clearly supported.

The variables Distance.urban and Land.use were retained in the best model among those testing the Human disturbance hypothesis (Models 3 and 4 in Table 2). As predicted, the probability of Rhea occurrence increased with increasing distance from the nearest urban centre and was greater on grazing land and in native habitats compared with other land-use types (Fig. 1b).

The best model among those being evaluated under the Landscape hypothesis constrained to a 1-km radius included Grazing.area and Native.area (Models 5 and 6 in Table 2). The probability of Greater Rhea occurrence increased with the total area of grazing land and native habitat within the 1-km circle (Fig. 1c). When constrained to a 1.8-km radius circle under the Landscape hypothesis, the most parsimonious model included Grazing.area, Native.area and Grazing.edge (Models 7 and 8 in Table 2). Rhea occurrence was positively associated with the total area of grazing land and native habitat and slightly negatively associated with the length of edges of grazing land (Fig. 1d).

When all potential predictors were considered simultaneously in a model of Rhea presence, the general model included Distance.lake, Grazing.area and Native.area (Models 9 and 10 in Table 2, Fig. 1e).

The mean AUC of the best models for each hypothesis and the general model ranged from  $0.74 \pm 0.02$  to  $0.80 \pm 0.02$  for the independent evaluation dataset (Table 2), indicating good discrimination ability and that it can be considered useful for predicting the distribution of the species.

## Habitat-suitability maps

The habitat-suitability map of Greater Rhea incorporating the best model under the Environmental hypothesis (Model 1 in Table 2), shows the probability of presence of Rheas is higher around lakes, which are generally dispersed across the study area (Fig. 2a). However, areas of high probability of occurrence are

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Table 2. GAM obtained by stepwise selection for each hypothesis of the variables influencing Greater Rhea occurrence

For each of the competing models, the Akaike Information Criterion (AIC) and the difference between AIC of the current model and the most-parsimonious model ( $\Delta$ AIC) are given. The most parsimonious model for each case is shown in bold and AUC values computed for 100 replicate parameterisations of the models are given. Numerical subscripts denote the degrees of freedom of the smoothing spline

Code	GAM Models	AIC	ΔΑΙС	AUC $\pm$ s.e.
Environme	ental hypothesis			
1	Altitude + Distance.lake + Slope <sub>3</sub>	166	0	$\boldsymbol{0.78 \pm 0.02}$
2	$Altitude_3 + Distance.lake_3 + Distance.stream_3$	168	2	
Human hy	pothesis			
3	Distance.urban <sub>3</sub> + Land.use	164	0	$\boldsymbol{0.75 \pm 0.01}$
4	Distance.urban <sub>3</sub>	166	2	
Landscape	hypothesis (1000-m radius)			
5	Grazing.area <sub>3</sub> + Native.area <sub>3</sub>	171	0	$\boldsymbol{0.74 \pm 0.01}$
6	$Grazing.area_3 + Native.area_3 + Patch.richness$	173	2	
Landscape	hypothesis (1800-m radius)			
7	Grazing.area <sub>3</sub> + Native.area <sub>3</sub> + Grazing.edge <sub>3</sub>	166	0	$\boldsymbol{0.76 \pm 0.01}$
8	Grazing.area <sub>3</sub> + Native.area <sub>3</sub>	167	1	
General m	odel			
9	Distance.lake <sub>3</sub> + Grazing.area <sub>3</sub> + Native.area <sub>3</sub>	159	0	$\boldsymbol{0.80 \pm 0.03}$
10	Distance.lake <sub>3</sub> + Grazing.area <sub>3</sub> + Altitude <sub>3</sub>	161	2	

concentrated in the centre of the region, associated with the mountains of the Ventania System, near the Atlantic coast, and in the Espinal region in the south of the study area (Fig. 2a). The habitat-suitability map of Rhea built under the Human disturbance hypothesis (Table 2) demonstrates that areas of low probability were located mainly around urban areas, which are scattered throughout the study area but with concentrations in the north and east of the Buenos Aires Province(Fig. 2b). The habitatsuitability map of Rhea under the best Landscape model constrained to a 1-km radius (Model 5 in Table 2), indicate areas of high probability of occurrence concentrated in the south-west of Buenos Aires Province (Fig. 2c) and areas of low probability of occurrence distributed across the north and centre of the Province, which coincide with the most developed areas (Fig. 2c). The habitat-suitability map of Rhea generated under the best Landscape model using constrained to 1.8-km radius (Model 7 in Table 2) shows a very similar pattern to that of the 1-km radius constraint, although the patterns are better defined (Fig. 2d).

Finally, the habitat-suitability map of presence of Greater Rhea built with the best general model (Model 9 in Table 2) is very similar to the habitat-suitability maps built under the Environmental and Landscape hypotheses (Fig. 2e).

## Discussion

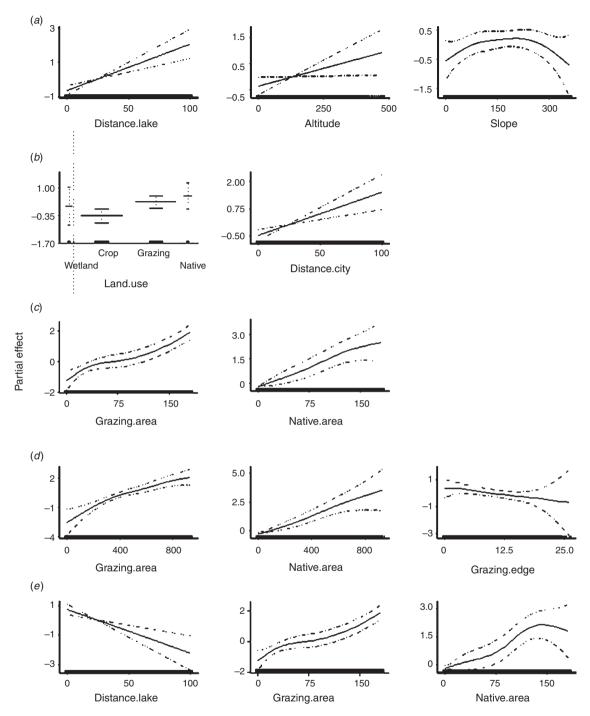
The habitat-suitability models of Greater Rhea presence suggest that: (1) the distribution of the species is strongly positively associated with areas of high elevation supporting waterbodies; (2) the distribution of the species is negatively associated with centres of human activity, which are also regions with greater road accessibility; and (3) the species prefers a heterogeneous landscape of grazing fields and native vegetation.

We found Greater Rheas preferentially selected areas near lakes and marshes, an association previously observed in the

Flooding Pampas of Buenos Aires Province (Herrera et al. 2004). As well as providing a source of drinking water, the quality of food for Rheas might also be better near waterbodies than away from them (Herrera et al. 2004). Habitats with a great proportion of dicots have been found to be optimal feeding sites for Rheas, and vegetation communities dominated by small dicot species are better established bordering waterbodies (Demaría 1993).

Human disturbance affects Rheas negatively and illegal hunting in particular is a major conservation concern (Bucher and Nores 1988; Bellis et al. 2004a; Martella and Navarro 2006; Pedrana et al. 2011). It is thus to be expected that occurrence of Rheas can be significantly explained by anthropogenic variables. However, the anthropogenic variables included in this study were not strong predictors of Rhea distribution, a result also found in earlier studies (Herrera et al. 2004; Bellis et al. 2008). It may be that the human variables we used to quantify human impact do not adequately represent the threat Rheas face or that human activities could have both positive and negative effects on Rheas. For example, hunting of Rheas is a negative effect but, conversely, some ranch owners may be protecting local populations of Rheas, resulting in increased local populations.

According to models of habitat use (Herrera et al. 2004) and habitat suitability developed for Rhea (Bellis et al. 2008; Giordano et al. 2010), we found that different land-uses have a great influence on the occurrence of this species. The probability of Rhea presence increases in grazing fields and semi-natural grasslands, at both spatial scales we adopted (1-km and 1.8-km radius circles), because individuals can largely meet their basic nutritional, survival and reproductive requirements within those areas (Fernández and Reboreda 2002; Bellis et al. 2004a, 2008; Giordano et al. 2010). A preference for grazing pastures reflects the food requirements of Rheas (Bellis et al. 2004a). Grazing pastures are mainly cultivated with Alfalfa (Medicato sativa), which is a preferred food item of Rheas (Martella et al. 1996). The



**Fig. 1.** Partial effects of the predictors included in the most-parsimonious model for each hypothesis of Greater Rhea presence: (a) Environmental hypothesis (Model 1 in Table 2); (b) Human hypothesis (Model 3 in Table 2); (c) Landscape hypothesis constrained to 1-km radius (Model 5 in Table 2); (d) Landscape hypothesis constrained to 1.8-km radius (Model 7 in Table 2); and (e) General model (Model 9 in Table 2). Landscape variables are defined in Table 1. Dashed lines represent 95% confidence intervals for the mean effect.

preference for pasture might also indicate a positive association with livestock, which keep vegetation short and create open spaces for grasses and other vegetation to grow.

Conversely, the lower probability of occurrence of Rheas in cropland might be a result of the high rates of environmental

disturbance associated with annual cropping (i.e. soil rotation and harvesting), which may cause Rheas to cluster in certain sites where the levels of such disturbance are low (Giordano *et al.* 2010). Further, as suggested by Bellis *et al.* (2004*a*), the decreased occurrence or absence of Rheas in cropland may also be

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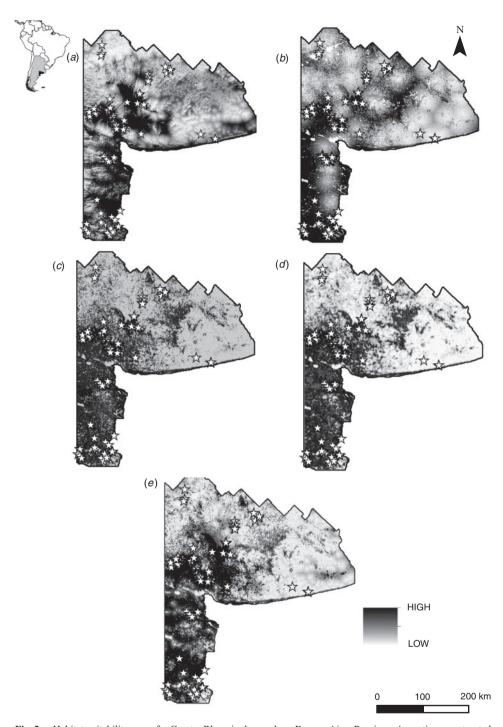


Fig. 2. Habitat-suitability maps for Greater Rheas in the southern Buenos Aires Province, Argentina, constructed from the most parsimonious model for: (a) Environmental hypothesis, (b) Human hypothesis, (c) Landscape hypothesis constrained to 1-km radius; (d) Landscape hypothesis constrained to 1.8-km radius; and (e) General model. For summary of models, see Table 2. Sightings of Greater Rheas are indicated by stars.

explained, at least in part, by the low digestibility of seeds (for Rheas) and the decreases in visibility and thus detection and escape from predators in tall crops, such as Sunflowers and Maize. Besides providing abundant food resources, grazing pastures are open with few obstacles to visibility, facilitating vigilance and escape. Previous studies of Greater Rheas have shown that

feeding and vigilance are incompatible behaviours (Lombardi 1994; Martella et al. 1995; Reboreda and Fernández 1997). Similar patterns of habitat use by this species were observed in agroecosystems in central Argentina (Bellis et al. 2004a), and in agricultural areas of southern Brazil (Codenotti and Alvarez 2000).

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The final habitat-suitability maps for Greater Rheas show that the most suitable areas are concentrated in the centre of the Buenos Aires Province, corresponding with (1) the hills and ranges of the Sierras de Ventania, (2) the south-west of the Province, and (3) near the Atlantic coast, which are all lessdeveloped regions where pastures and remnant native grasslands persist owing to the edaphic and rainfall constraints that are not favourable for the development of crops. We found a positive association between increasing altitude and increased probability of the presence of Rheas. Although it is not clear that Rheas respond to elevation per se, it is likely that elevation correlates with certain landscape components or soil-quality features (more productive environments typically occur in lowlands) which may have implications for habitat selection by the species (Giordano et al. 2010). Even though south-western Buenos Aires Province includes large areas of native habitats; this landscape is changing rapidly though the introduction of artificial irrigation (J. Pedrana,

When predictors were considered simultaneously in the general model only the distance to the nearest lake and the total area of grazing land and native habitat were retained. Nonetheless, the pattern remains consistent, given that the general model indicates that the occurrence of Greater Rhea is more likely where there are large areas of grazing land and native habitats near lakes and marshes. It is also worth noticing that the partial Landscape hypothesis using circles of 1.8-km radius gives additional information about the composition of the landscape configuration (e.g. small to medium-sized grazing fields) which is not obvious in the general model. This highlights the importance of building partial habitat-suitability maps of species, since it might help researchers to provide hierarchically structured recommendations based on the individual effects of drivers.

## Management implications

In Buenos Aires Province, the conversion of natural grasslands to pastureland and cropland is widespread (Baldi and Paruelo 2008). Trends of expanding anthropogenic land-use show the need to preserve the remaining natural habitat for Rhea and for other species that use grassland. Unfortunately, native grasslands and grazing pastures are increasingly being converted to croplands associated with new technologies and climate change, which has adversely affected the diversity of native birds in Pampas grasslands (Azpiroz *et al.* 2012) and specifically wild populations of Greater Rhea (Bellis *et al.* 2004*a*). Therefore, agricultural policies need to be developed to encourage conservation of native grasslands and pasture production over crops, both for the preservation of Greater Rheas and for other grassland bird species (Azpiroz *et al.* 2012).

Preserving suitable habitats for Greater Rheas will be critical for the persistence of wild populations of this species. Nevertheless, as most of the territory in the study region is privately owned, this conservation approach may generate some conflicts with landowners who perceive Rheas as detrimental for agricultural production. Therefore, as expansion of cropping continues, management schemes in agricultural areas should focus on reconciling the interests of agricultural producers and conservationists to preserve some habitats with features similar to those of natural grasslands (Giordano *et al.* 2010; Bernad 2012). Greater Rheas

select sites in response to the habitat characteristics they detect at any given time. This habitat selection would make them highly vulnerable to the rapid changes in land-use that are taking place, particularly in the Buenos Aires Province (INDEC 2002). Over the last 25–30 years, Buenos Aires Province has witnessed extreme agriculturisation growth, as crops increased by more than 30% between 1988 (25%) and 2008 (33%; INDEC 2002; Baldi and Paruelo 2008). Different kinds of benefits may derive from conserving species, including social (cultural, aesthetic, tourism), ecological and economical benefits. For example, Greater Rheas can be sustainably exploited by using their meat, eggs and leather. Numerous articles have studied the nutritional value of Rhea meat and the excellent qualities of Rhea leather (Garriz et al. 2009; Radogna et al. 2010).

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