MODELING HABITAT SUITABILITY FOR GREATER RHEAS BASED ON SATELLITE IMAGE TEXTURE

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Abstract. Many wild species are affected by human activities occurring at broad spatial scales. For instance, in South America, habitat loss threatens Greater Rhea (*Rhea americana*) populations, making it important to model and map their habitat to better target conservation efforts. Spatially explicit habitat modeling is a powerful approach to understand and predict species occurrence and abundance. One problem with this approach is that commonly used land cover classifications do not capture the variability within a given land cover class that might constitute important habitat attribute information. Texture measures derived from remote sensing images quantify the variability in habitat features among and within habitat types; hence they are potentially a powerful tool to assess species–habitat relationships. Our goal was to explore the utility of texture measures for habitat modeling and to develop a habitat suitability map for Greater Rheas at the home range level in grasslands of Argentina. Greater Rhea group size obtained from aerial surveys was regressed against distance to roads, houses, and water, and land cover class abundance (dicotyledons, crops, grassland, forest, and bare soil), normalized difference vegetation index (NDVI), and selected first- and second-order texture measures derived from Landsat Thematic Mapper (TM) imagery. Among univariate models, Rhea group size was most strongly positively correlated with texture variables derived from near infrared reflectance measurement (TM band 4). The best multiple regression models explained 78% of the variability in Greater Rhea group size. Our results suggest that texture variables captured habitat heterogeneity that the conventional land cover classification did not detect. We used Greater Rhea group size as an indicator of habitat suitability; we categorized model output into different habitat quality classes. Only 16% of the study area represented high-quality habitat for Greater Rhea (group size ≥15). Our results stress the potential of image texture to capture within-habitat variability in habitat assessments, and the necessity to preserve the remaining natural habitat for Greater Rheas.

Key words: Argentina; grassland; Greater Rhea; habitat suitability; remote sensing; Rhea americana; texture.

INTRODUCTION

Conservation of wildlife habitat has become an increasing imperative as rates of habitat destruction continue to rise (e.g., Nagendra 2001). Considering the challenges for wild species, there is a clear need to better understand spatial distribution of wildlife populations and species–habitat relationships. Conservation is most effective when efforts can be focused on habitat most suitable for a species of concern, but the challenge is to identify high-quality habitat across large areas.

Identifying high-quality habitat for a given species can be difficult both because of logistical constraints, and

because of limited knowledge of habitat requirements. Complete surveys alone are rarely feasible when mapping high-quality habitat for a large area because field investigations are expensive (Osborne et al. 2001, Gibson at al. 2004), and field data may quickly become outdated as habitat changes. However ground surveys can be combined with remotely sensed data to build predictive models, which in turn can be applied to broad areas of similar habitat. Spatially explicit habitat modeling, i.e., the use of statistical models to predict the locations of suitable habitat, can also be used to test ecological hypotheses regarding the response of individuals to land cover, topography, and land use (Guisan and Zimmermann 2000, Ottaviani et al. 2004). Because of their importance for both science and management, habitat models incorporating remotely sensed data have been used to predict occurrence and abundance patterns for many species (Elith et al. 2006), including wolves (Mladenoff et al. 1995), bustards (Osborne et al. 2001),

butterflies (Luoto et al. 2002), bears (Posillico et al. 2004), and eagles (Balbontín 2005).

In many habitat modeling studies, species presence–absence or abundance patterns are related to habitat measures derived from remotely sensed imagery (Turner et al. 2003). Commonly, a land cover classification is generated and used to predict species distribution based on land cover class abundance and landscape indices (Gottschalk et al. 2005). The application of landscape indices to satellite image classification has substantially contributed to the conservation of endangered species, by broadening the scales of consideration to those relevant to species of interest (McAlpine and Eyre 2002). However the problem is that land cover classifications are rarely based on the real habitat requirements of specific wildlife species, and classifications commonly aggregate habitat types, which causes errors in habitat models (Hepinstall and Sader 1997, Luoto et al. 2004). Another limitation of land cover classifications is that they ignore habitat variability within a given land cover class, an attribute which may strongly influence habitat selection and use by wildlife species. For example, the spatial arrangement of foliage height diversity may determine the number of breeding species in a local area (MacArthur and MacArthur 1961).

One approach that overcomes limitations of land cover classifications for habitat modeling is to incorporate image-based measures of habitat heterogeneity into habitat models (St-Louis et al. 2006). Image-based measures do not depend on a land cover classification, but are rather derived directly from the satellite image (Haralick et al. 1973). Image texture measures are a group of indices that can quantify the variability of vegetation as a continuous variable. As such, texture is advantageous compared to vegetation classification because many statistical algorithms perform better with continuous variables. Thus, texture measurements may have great potential in terms of identifying spatial habitat heterogeneity but to date only few studies have used texture to assess wildlife–habitat relationships. Where it was used, texture successfully predicted the occurrence of forest bird species (Hepinstall and Sader 1997), avian species richness in a semiarid ecosystem (St-Louis et al. 2006), and the abundance of Horned Larks (*Eremophila alpestris*), Brewer's Sparrows (*Spizella breweri*), and Sage Sparrows (*Amphispiza belli*) in Idaho (Knick and Rotenberry 2000). Texture also successfully differentiated territories of two morphs of a passerine species (Tuttle et al. 2006). However, we are not aware of any studies that used texture to predict habitat suitability for a species of conservation concern.

Our main goal was to evaluate the applicability of texture measures as a potential tool for modeling habitat suitability in conjunction with other ecological variables using Greater Rhea (*Rhea americana*) as our test species. We chose Greater Rhea because this species is threatened by habitat destruction and is experiencing severe population declines throughout its range, yet habitat suitability at broad scales remains poorly understood. Focused conservation efforts are needed to prevent extirpation or even extinction of Greater Rheas.

The Greater Rhea is a charismatic bird species endemic to South America that has been classified as a near-threatened species by the International Union for Conservation of Nature (IUCN 2007). Greater Rheas mainly inhabit grassland ecosystems, one of the most human-modified and least protected biomes in the world (Demaría et al. 2003). In Argentina, Greater Rheas have undergone substantial population declines largely due to habitat loss and poaching (Bucher and Nores 1988, Martella and Navarro 2006). However, Greater Rheas can survive in agricultural areas if there is a mix of fields containing alfalfa (*Medicago sativa*) and clover (*Melilotus sp*), plus grasslands containing some wild dicotyledons (e.g., *Plantago lanceolata*, *Conyza bonariensis*, *Cirsium vulgare*, *Phyla canescens*; Bellis et al. 2004a, Herrera et al. 2004). Unfortunately, grassland and alfalfa fields are increasingly converted to croplands (soybean *Glycine max*, sunflower *Heliantus annus*, corn *Zea mays*, wheat *Triticum aestivum*, etc.), which has adversely affected wild populations of Greater Rheas (Bellis 2004). These land use changes occur not only in Argentina but also throughout the range of Greater Rhea in the savannas and grasslands of South America.

Our study had two major objectives: (1) assessing the potential of satellite image texture measures for wildlife habitat models, and (2) identifying habitat attributes that affect presence and group size of Greater Rheas (*Rhea americana*) at the home range level in central Argentina and mapping habitat quality with image texture.

METHODS

Study area

Our research was conducted in the pampas grasslands of Argentina, located in the south-central part of San Luis province (Fig. 1). In Argentina, most of the pampas (94%) was transformed in agroecosystems (Bertonatti and Corcuera 2000, Díaz-Zorita et al. 2002); however, grasslands still persist in areas considered unsuitable for crops. The San Luis pampas belongs to the semiarid western extreme of the pampas grassland; it is characterized by sandy soils and rolling hills with both fixed and active dunes. Climax vegetation is composed of native grasses with islets of tree species, such as *Goeffroea decorticans*, *Prosopis caldenia*, and *Prosopis alpataco*. The dominant native grass species is *Sorghastrum pellitum*, mixed with *Elyomurus muticus*, *Bothriochloa springfieldii*, *Chloris retusa*, *Schizachyrium plumigerum*, *Eragrostis lugens*, *Sporobolus subinclusus*, *Aristida spegazzini*, *Poa ligularis*, and *Poa lanuginosa* (Anderson et al. 1970, Anderson 1973).

In the San Luis pampas, land transformation due to ranching is the most important process affecting the extent of this ecosystem; crop production is sporadic because of low annual rainfall (<500 mm; León et al.
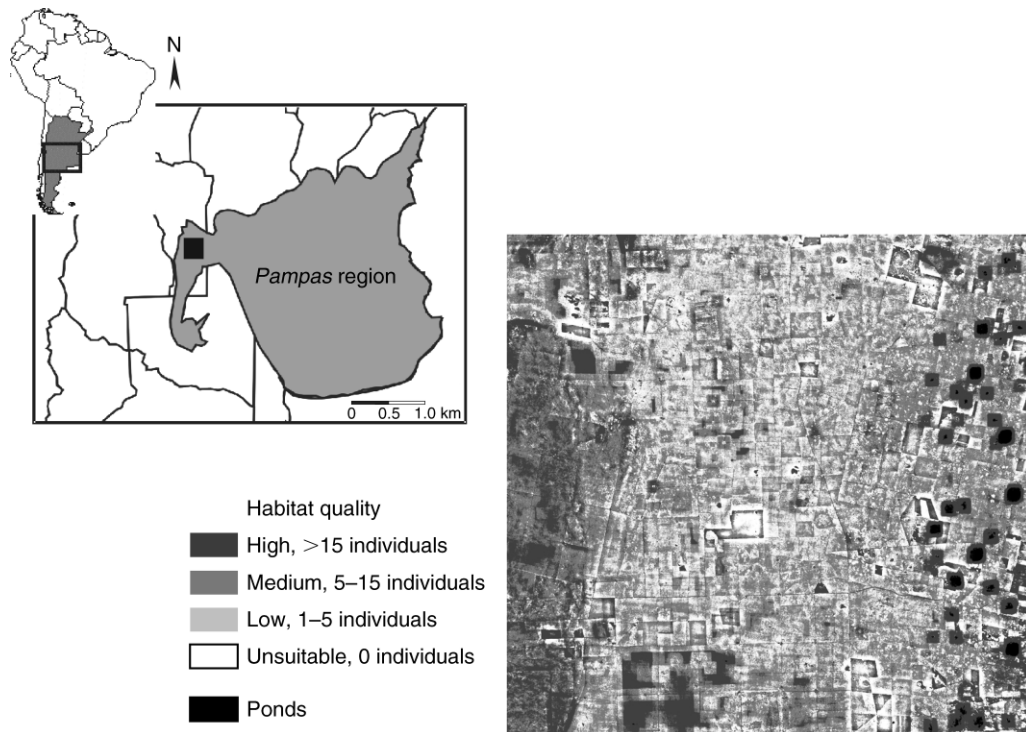
Fig. 1. Habitat suitability maps for Greater Rheas estimated from using group size as an indicator of habitat quality.

1984). The grasslands are not uniform, partly due to the conversion of native grasslands through introduction of exotic grass species including *Eragrostis curvula* and *Digitaria eriantha* to increase grassland forage quality for livestock (Demaría et al. 2003). Four years of study in the pampas comparing the San Luis grassland with an adjacent area totally transformed to an agroecosystem showed that agricultural expansion, especially the increase of lands devoted to crops, reduced Greater Rhea abundance and disrupted the spatial distribution of the species (Bellis 2004, Giordano et al. 2008). Because San Luis pampas is the last great grassland Greater Rhea habitat in Argentina, we focused this study on an area of 4782 km^2 dominated by grassland (55%) with crops and alfalfa fields present in lower proportions (15% and 5%, respectively).

Field survey

Two aerial counts were conducted in the study area in 2004 following the approach developed by Caughley (1974), Caughley and Sinclair (1994), and Sutherland (1996). The first survey was conducted in May prior to the September through November breeding season (Bruning 1974, Reboreda and Fernández 1997), and the second survey was conducted in December, during the December to February post-reproductive season. Aerial counts were performed from a Cessna 182 airplane flying at an average speed of 120 km/h and an average altitude of 100 m. The flight direction was west to east across each site, to avoid glare. The sampling technique consisted of six strip transects 52 km in length spaced at regular intervals of 10.4 km. The coordinates of the flight path were generated in advance, and the pilot carefully followed the survey design using a global positioning system (GPS). The navigator determined the beginning and end of each survey line. In the scheme of flight controllable sources of bias, such as strip width, altitude and speed (Caughley 1974) were carefully monitored, and these variables were held constant.

Two observers seated side by side in the Cessna, which has high wings, collected the data. Each observer scanned a 170 m wide strip of ground delineated by streamers on the aircraft's wing struts. Observers recorded the number of Greater Rheas, at the moment they were perpendicular to the aircraft; even if they had been detected in advance; therefore, counting and position recording was almost simultaneous. Observers marked Greater Rhea locations with a Garmin 12XL GPS (GPS eTrex Legend; Garmin International, Olathe, Kansas, USA). The average positional error for the GPS locations during our survey was 9.2 m. Visibility within the strip transect that was surveyed was comparable for all habitat types.

Biological characteristics of the species

Greater Rhea (see Plate 1) is a non-territorial species that commonly lives in flocks in a loosely cohesive social system (Bruning 1974, Martella et al. 1995, Reboreda and Fernández 1997). The most important components of the Greater Rhea diet (90%) are native short-lived

PLATE 1. Adult Greater Rhea (*Rhea americana*) in an experimental field near Córdoba, Argentina. Photo credit: J. L. Navarro.

forbs (*Phyla canescens*, *Plantago lanceolata*, *Conyza bonariensis*, *Descurainina* sp., and *Cirsium vulgare*) and alfalfa (*Medicago sativa*); wild and cultivated gramineous species (*Eragrostis* sp., *Agropyron* sp., *Stipa* sp., *Cenchrus* sp., *Secale cereale*, and *Trichloris* sp.) are eaten in lower proportions. Greater Rheas also consume seeds (*Zea mays, Bromus* sp., and *Sorghum* sp.), fruits (*Cenchrus pauciflorus*, *Argemone subfusiformis*), invertebrates (pieces of teguments of several insects: Hemiptera, Orthoptera, and Coleptera), and small vertebrates (*Bufo* sp., *Teius* sp.; Yagueddú and Viviani Rossi 1985, Martella et al. 1996). Previous studies have shown that Greater Rheas prefer habitats where dicotyledonous species are available (Codenotti and Alvarez 2000, Bellis et al. 2004*a*, Herrera et al. 2004). In agroecosystems, alfalfa fields are the most commonly used habitat by Greater Rheas. In addition to meeting foraging requirements, the open habitat of alfalfa fields facilitates vigilance and escape from predators (Codenotti and Alvarez 2000, Bellis et al. 2004*a*). At present, despite legal protection of Greater Rheas by the national government of Argentina, humans are their main predator, persecuting and shooting individuals throughout their range (Martella and Navarro 2006). Behavioral studies of the species (Martella et al. 1995, Reboreda and Fernández 1997, Fernández et al. 2003) have shown that large group size benefits individual Greater Rheas by reducing the risk of predation and increasing the time available for feeding. Further, research showed that large groups occur in habitat with high food availability. The number of Greater Rheas at a location, i.e., group size, can thus be used as an index for habitat quality at that location. Group size was selected over abundance or density because they have different effects (Estevez et al. 2007). Whereas the density is determined by the number of individuals per unit of space, the group size, i.e., the number of individuals that form a group, is closely associated with behavioral features related to the cost–benefit balance of resource availability (Beauchamp 2001, Fernández et al. 2003). However, we note that group size is not a measure of absolute density, and that our estimates may have been affected by different detectability functions of Greater Rheas in different habitats. To solve these limitations in future studies, we recommend using survey methods adjusted for incomplete detection (Thompson 2002) as a rigorous approach in the estimation of response variable. In the case of gregarious species such as Greater Rheas, distance sampling would be the preferred technique because it allows consideration of the group size (ancillary data)

TABLE 1. Independent variables selected for the habitat suitability analysis of Greater Rheas in the pampas grasslands of Argentina.

Habitat requirements, variables	Description of the variable	Units
Food		
Land cover	grassland, crops, forest, bare soil, and dicotyledons	proportion
Water	distance to nearest water	km
NDVI	a proxy for vegetative cover and biomass	index value
Heterogeneity of NDVI	coefficient of variation (CV)	%
Nesting and refuge		
Land cover	grassland, crops, forest, bare soil, and dicotyledons	proportion
Vegetation structure		
Texture, first order (TM bands)	mean (3-4-5-7), variance (1 to 5)	index values
Texture, second order (TM bands)	mean (3-4-7), variance (4-5-7), homogeneity (7), correlation (1 to 7), and second moment (1 to 7)	index values
Additional		
Human impact	distance to nearest house, distance to nearest road	km

and the number of groups (clusters) per unit of space as a density measure (Buckland et al. 2001).

Habitat measures

Understanding factors affecting Greater Rhea foraging and survival allows selection of relevant habitat elements as model inputs from among those that might affect Greater Rhea distribution. The main ecological variables known to influence Greater Rhea habitat suitability in relation to food, water, and nesting requirements, as well as human disturbance are summarized in Table 1.

Water bodies, roads, and human settlements were digitized from a topographic map of the study area (1:250 000; Military Geographic Institute, Buenos Aires, Argentina). Besides their importance as a source of drinking water, plant communities dominated by dicot species are found on the edges of water bodies (Herrera et al. 2004), and are an important source of food. Roads and houses were selected as indices of human disturbance. The digitized information on water bodies, roads, and houses was transformed into a continuous variable of distance expressed in kilometers using ENVI GIS (ENVI 2004). Vegetation patches, normalized difference vegetation index (NDVI), and texture measures were calculated from a satellite image (December 2004 Landsat 5 TM image, path 230, row 084) using ENVI GIS (ENVI 2004). The spatial resolution chosen for our analysis was based on the home range of the species. In grassland, Greater Rhea home range averages 11 km^2 (Bellis et al. 2004b). We used a sampling area that approximates 20% of Greater Rhea home range, following the method of Laymon and Barrett (1986) and Posillico et al. (2004). Thus the spatial resolution applied to the analysis was a 1.5 × 1.5 km moving window, including 2500 pixels. The mean value of all pixels within the window was calculated for each variable.

Land cover of the study area was classified based on a 2004 Landsat 5 TM image (path 230, row 084) from the summer season (December). Using ground control points from topographic maps (1:250 000) the satellite image was georeferenced to a Universal Transverse Mercator projection (zone 20 S, datum WGS 84). We conducted a supervised maximum likelihood classification using training sites for which land cover was known from field reconnaissance. A post-classification accuracy assessment showed an overall accuracy (calculated by summing the number of pixels classified correctly and dividing by the total number of pixels used for the accuracy assessment) of 94.6% and a kappa coefficient = 0.76 (ENVI 2004). The proportion of each land cover class was summarized for each 1.5 × 1.5 km moving window.

We calculated the NDVI (normalized difference vegetation index; Paruelo et al. 1997, Oesterheld et al. 1998, Posse and Cingolani 2004) as an indication of vegetation abundance. NDVI was calculated using the following formula:

$$\frac{\text{near-infrared(TM4)} - \text{red(TM3)}}{\text{near-infrared(TM4)} + \text{red(TM3)}}.$$

NDVI values fall between −1 and +1; higher values show higher proportions of photosynthetically active green vegetation, and negative values indicate nonvegetated surfaces. Also, we calculated the coefficient of variation (CV, %) of the NDVI as a surrogate measure of vegetation heterogeneity.

Image texture is the visual effect produced by the spatial distribution of tonal variation in adjacent pixels (Baraldi and Parmiggiani 1995). Texture analysis characterizes the stochastic properties of the spatial distribution of gray levels in an image (Dong-Chen and Wang 1990). There are two types of texture measures: first-order (occurrence) and second-order (co-occurrence). First-order texture measures are based on the number of occurrences of each gray-level within a given processing window. Second-order texture measures use a gray-tone spatial dependence matrix (i.e., co-occurrence matrix) to calculate texture values. The co-occurrence

matrix contains the relative frequencies with which pixel values co-occur in a given neighborhood (Haralick et al. 1973, Dong-Chen and Wang 1990, Baraldi and Parmiggiani 1995, Tso and Mather 2001). Following the approach of St-Louis et al. (2006), we calculated four first-order texture measures (mean, variance, entropy, and skewness), and eight second-order texture measures (mean, variance, homogeneity, contrast, dissimilarity, entropy, second moment, and correlation) for each 1.5×1.5 km moving window. The 12 texture indices were calculated separately for each of the six Landsat TM bands with 30-m resolution. Texture analysis was conducted in ENVI (ENVI 2004).

Global positioning system locations of each Greater Rhea group were implemented into the GIS ENVI (ENVI 2004) and checked for accuracy against a GIS layer from the Military Geographic Institute of Argentina. The error detected was <30 m (i.e., 1 Landsat pixel), which we deemed acceptable given that the habitat analysis was performed at a resolution of 1.5×1.5 km.

Model building

The texture analysis resulted in 72 texture variables (12 texture measures for each of the six bands) and an additional 10 ecological variables. In order to avoid colinearity, a pairwise correlation matrix of all predictors was constructed. As many texture variables were highly correlated we chose a 0.95 threshold to reduce the total number of variables to a point where model selection procedure runs efficiently. The correlation analysis among the 82 independent variables showed high correlations ($r \geq 0.95$; $P < 0.001$) for 45 of the 3321 pairwise comparisons. For these pairs, we retained the variable with the highest r value among the two and eliminated the other variable from further analysis. In the end, a set of 38 independent variables (28 texture measures and 10 ecological variables) was retained for further analysis (Table 1). Scatterplots of the response variable and the covariates did not indicate a need for data transformation. We performed a leaps analysis using the software package R (R Development Core Team 2007). The leaps procedure utilizes a branch and bound strategy for predicting the best subsets of the explanatory variables in linear regression without the requirement of a link function. It scans systematically through all subsets at the same time, "leaping" over those nonoptimal subsets (Furnival and Wilson 1974, Miller 2002). Due to our small sample size (36 points), the regression subset was bounded by a maximum number of six explanatory variables. This restriction is within the upper edge recommended considering the size of data set and the number of observation per variable (about seven in our case; Neter et al. 1990). We examined the 25 best subsets including two to six predictors, for a total of 125 models. For each of these 125 models, adjusted R^2, the corrected form of Akaike Information Criteria (AIC$_c$), and ΔAIC$_c$ (i.e., AIC$_c$ −

min AIC$_c$) were calculated to determine the best models of Greater Rhea group size (Hurvich and Tsai 1989, Whittingham et al. 2006). AIC$_c$ is recommended for small sample sizes, specifically when the number of samples ($n = 36$) divided by the number of parameters ($k = 4$–8 for the different dimension models) is smaller than 40. ΔAIC$_c$ values allow a quick comparison and ranking of candidate models. As a rule of thumb, models having a ΔAIC$_c$ with values varying <2 from the best model have substantial support, models with values between three and seven have less support, and models with ΔAIC$_c$ >10 miss some important explanatory variables (Burnham and Anderson 2002). We used a ΔAIC$_c$ odd of four for determining the models that are equally strong at predicting Greater Rhea group size. This cutoff was chosen because smaller cutoffs yielded only slight differences in predictive power (e.g., difference in adjusted $R^2 < 0.01$).

In order to examine the role of spatial dependence in the final models, we assessed the pattern of spatial autocorrelation with semivariance analysis (Legendre et al. 2002). We used this analysis because it is robust, it allows identification of outliers in exploratory data analysis, and it is a good estimator to reduce the sensitiveness to outliers (Sun et al. 2003). These characteristics as well as the simplicity of its estimation make the semivariogram one of the techniques most widely available for use by landscape ecologists (Meisel and Turner 1998). We calculated a semivariogram of each selected model, plotting the semivariance of residuals against the distances between pairs of points and, in all cases, there was no evidence of spatial dependence.

The predictive power of models was evaluated by means of a leave-one-out cross validation procedure. This is an appropriate testing method when the data set is quite small and/or when each sample is likely to have unique information that is relevant to the model (Guisan and Zimmermann 2000, Miller 2002, Ottaviani et al. 2004). A model was developed using a single observation from the original sample as the validation data, and the remaining observations as the training data. Using the model estimated from the training data a prediction was made for that observation. This procedure was repeated for all 36 observations. The average error was computed and used to evaluate the model.

Finally, we constructed habitat suitability maps for Greater Rheas in our study area. The regression equation of the best selected model was mapped using ENVI GIS (ENVI 2004). The resulting map predicted different habitat qualities for the species at a scale of home range.

RESULTS

A total of 36 groups of Greater Rheas were recorded in the study area during the 2004 survey. In these groups, we detected 157 Greater Rheas, nine as solitary individuals and 27 groups that ranged from two to 20

TABLE 2. Frequency of times each variable was incorporated in the top 63 models for which the ΔAIC_c compared to the highest ranked model was <4.

Description, independent variables	Number of variables in the models				
	2	3	4	5	6
Second order texture					
Variance TM band1	0	0	1	0	0
Variance TM band2	0	0	1	0	6
Variance TM band3	0	0	0	0	3
Variance TM band4	0	1	18	2	12
Variance TM band5	0	1	3	0	1
Mean TM band3	0	0	0	7	25
Mean TM band4	0	0	1	2	10
Mean TM band5	0	0	0	0	0
Mean TM band7	0	0	0	0	1
Homogeneity TM band7	0	0	1	1	6
Correlation TM band3	0	0	1	0	0
Correlation TM band4	1	5	25	7	25
Correlation TM band5	0	0	2	0	0
Correlation TM band7	0	0	2	0	0
Second moment TM band1	0	0	1	1	2
Second moment TM band2	0	0	1	0	1
Second moment TM band3	0	1	3	1	3
Second moment TM band4	0	0	0	0	0
Second moment TM band5	0	0	1	0	0
Second moment TM band7	0	0	0	0	1
First order texture					
Variance TM band4	0	1	6	2	5
Variance TM band7	0	1	1	0	0
Variance TM band5	0	0	1	0	0
Mean TM band4	0	0	1	5	15
Mean TM band7	0	0	0	0	1
Ecological					
Grassland proportion	0	0	1	0	4
Crops proportion	0	0	2	0	4
Forest proportion	1	5	25	0	0
Alfalfa proportion	0	0	1	0	0
NDVI	0	0	0	7	25
CV_NDVI (%)	0	0	1	0	0
Number of models estimated	1	5	25	7	25
Maximum R^2_{adj}	0.61	0.7	0.72	0.77	0.8
Minimum R^2_{adj}	0.61	0.67	0.69	0.75	0.78

Note: The minimum and maximum adjusted R^2 values obtained for this group of models are shown in the last two rows.

individuals with an average group size of 4.36 ± 0.7 individuals (mean ± SE).

Habitat models

Of the total of 125 models estimated, 63 had a ΔAIC_c <4 (Table 2). The best models, which used five or six independent variables, explained up to 75% of the variability in Greater Rhea group size. None of them included variables related to human disturbance such as proximity to roads and houses.

Of this group of models, we selected the most parsimonious ones, which included five predictor variables (Table 3). In all cases, the use of spectral information including multiple texture measures and NDVI produced the best results. Texture measures derived from Landsat TM bands 3 and 4 exhibited the highest predictive power; the other bands captured substantially less or no variability. The association

between these variables and Greater Rhea group size was negative for texture measures derived from TM bands 1, 3, and 7 and the NDVI, and positive for texture based on TM band 4 (Table 3). The overall accuracy of cross-validation procedure of these seven best models ranged from 50% to 69% (Table 3).

The regression equation of the best model (model 1, Table 3) was used to map habitat suitability across the entire study area. The resulting habitat suitability map predicted the group size of Greater Rheas in each 1.5 × 1.5 km cell. Based on our assumption that Greater Rhea group size is an indicator of habitat suitability, model output was categorized into four habitat quality classes. Areas where group sizes of >15 individuals were defined as high quality, group size of five to 15 individuals was considered moderate quality, and one to five individuals was defined as low quality habitat. Areas with zero individuals were defined as unsuitable habitats (Fig. 1).

TABLE 3.   Most-parsimonious models selected for estimating habitat suitability of Greater Rheas.

Model	AIC_c	ΔAIC_c	R^2	Overall accuracy (%)
1) $y = 23 + (1.68 \times$ variance TM band4$) - (5.56 \times$ mean TM band3$) + (4.74 \times$ correlation TM band4$) + (1.92 \times$ mean TM band4[1st]$) - (186.32 \times$ NDVI$)$	163.98	0	0.805	69.4
2) $y = 33.45 - (5.75 \times$ mean TM band3$) + (4.61 \times$ correlation TM band4$) + (0.11 \times$ variance TM band4[1st]$) + (1.84 \times$ mean TM band4$) - (192.6 \times$ NDVI$)$	164.03	0.06	0.804	69.4
3) $y = 30.06 - (5.31 \times$ mean TM band3$) + (4.05 \times$ mean TM band4$) + (4.76 \times$ correlation TM band4$) + (0.12 \times$ variance TM band4[1st]$) - (180.63 \times$ NDVI$)$	165.49	1.51	0.797	58.3
4) $y = 70.67 - (6.45 \times$ mean TM band3$) - (40.92 \times$ homogeneity TM band7$) + (4.96 \times$ correlation TM band4$) + (2.03 \times$ mean TM band4[1st]$) - (218.05 \times$ NDVI$)$	166.76	2.78	0.789	69.4
5) $y = 54.01 - (6.91 \times$ mean TM band3$) + (4.59 \times$ correlation TM band4$) - (26.31 \times$ second moment TM band1$) + (2.11 \times$ mean TM band4[1st]$) - (232.35 \times$ NDVI$)$	166.93	2.95	0.788	50.0
6) $y = 33.14 - (5.84 \times$ mean TM band3$) + (5.08 \times$ correlation TM band4$) - (34.03 \times$ second moment TM band3$) + (1.96 \times$ mean TM band4[1st]$) - (199.32 \times$ NDVI$)$	167.16	3.18	0.787	63.9
7) $y = 17.58 + (1.77 \times$ variance TM band4$) - (4.94 \times$ mean TM band3$) + (4.15 \times$ mean TM band4$) + (4.85 \times$ correlation TM band4$) - (157.56 \times$ NDVI$)$	167.75	3.77	0.784	55.6

Notes: For these models ΔAIC_c compared to the highest ranked model was <4. The values of AIC_c, ΔAIC_c, R^2, and overall accuracy of leave-one-out cross-validation procedures are shown. The superscript "1st" indicates first-order texture variables.

DISCUSSION

Our models represent a successful first attempt to predict areas of different habitat quality for Greater Rheas in grasslands of central Argentina. According to our models, Greater Rhea group size was related to the spatial heterogeneity of habitat as measured by texture variables and NDVI. The selection of these variables is likely due to use of these resources by Greater Rheas to satisfy basic foraging requirements.

Image texture was a crucial element in the estimation of the habitat suitability map for Greater Rheas, and distinguished subtle variations within grasslands. Second-order texture measures, especially correlation, were most efficient at quantifying habitat attributes that influence Greater Rhea group size. Correlation is a measure of gray tone linear dependencies in the image (Baraldi and Parmiggiani 1995). Pixels near each other are more correlated than distant ones, suggesting that image elements are aggregated. Mean texture value was included frequently in the best models (Table 3); this measure represents the average distribution of gray level (Dong-Chen and Wang 1990), hence high values of mean indicate more bright areas (such as bare ground and grassland), and fewer dark areas (such as forests or shadows) in an image. Second-order variance was also included frequently in the best models; this measure captures the spatial pattern of gray level deviation (Baraldi and Parmiggiani 1995), and is a good indicator of spatial heterogeneity. Finally, two texture variables poorly represented in the models were angular second moment and homogeneity, which both characterize the textural uniformity of the image elements (Baraldi and Parmiggiani 1995, Guo et al. 2004).

Among the six TM bands, texture measures based on the near-infrared (NIR, TM4) band had the greatest explanatory power in relation to Greater Rhea group size. Because the NIR band is sensitive to vegetation and the amount of biomass, variations in the textural characteristics of this band likely capture difference in vegetation cover. In grasslands, sites with higher forb cover and higher forb species richness have higher reflectance in NIR (Guo et al. 2000, 2004).

Wild forbs and cultivated dicotyledons are a preferred food item for Greater Rheas (Yagueddú and Viviani Rossi 1985, Martella et al. 1996). Sites with dense grassland vegetation may also exhibit greater abundance of these plants. Thus, the discrimination power of image texture measures may be very useful for assessing vegetation heterogeneity, indicative of dicotyledons, within grassland.

The inverse relationship between NDVI and Greater Rhea group size is most likely related to the presence of bare soil in the area. Although our study area was dominated by grasslands, 14.4% (688 km^2) of the area consisted of nonvegetation patches, resulting from human activities. Dicotyledons are the most common species in the vegetation gaps after a disturbance in grassland (Bock and Bock 1992, Kinucan and Smeins 1992, Edward and Crawley 1999, Bullock et al. 2001, Hayes and Holl 2003) because herbaceous dicots dominate the initial stage of succession (Omacini et al. 1995). Consequently, the areas classified as bare soil patches were likely to contain an abundance of the feeding resources that Greater Rheas prefer. Additionally, the reflectance of exposed ground areas might affect the response of red wavelengths (TM3; Lawrence and Ripley 1998, Weis et al. 2004) interfering with the

reflectance of TM band 3, and thus changing the expected relationship between the red wavelengths and Greater Rhea group size.

The habitat preferences identified in our models are consistent with field studies of Greater Rhea use of landscapes. In both grassland and agricultural lands, individual Greater Rheas adjust their movements and home range size in response to food availability (Bellis et al. 2004b), and they forage preferably in habitat with a high proportion of dicots (Codenotti and Alvarez 2000, Bellis et al. 2004a, Herrera et al. 2004).

Human disturbance affects Greater Rheas negatively, and illegal hunting in particular is a major conservation concern (Bucher and Nores 1988, Bellis et al. 2004a, Martella and Navarro 2006). However, contrary to our expectations, the anthropogenic variables included in this study were not strong predictors of Greater Rhea distribution. It may be that the variables we used to quantify human impact do not adequately represent the threat Greater Rheas face from humans.

The prediction of high-quality habitat allows identification of the most critical areas for Greater Rhea conservation within this study area. The assignment of habitat into high, medium, low, and unsuitable quality classes was made under the premise that group size of Rheas is a good indicator of habitat quality. Individual Greater Rheas select habitats where the profitability of feeding is counterbalanced by the corresponding cost of predation (Codenotti and Alvarez 2000, Bellis et al. 2004a). Foraging in large groups benefits individuals by reducing predation risk through the dilution effect (Fernández et al. 2003). Additionally, as the opportunities for feeding are more frequent in large groups and when food occurs in clumps (Beauchamp 2001), we are able to assume that habitats with high food abundance or quality will support larger groups than areas without these characteristics.

The validation phase is important in assessing the predictive capability of any habitat model (Guisan and Zimmermann 2000, Luck 2002, Ottaviani et al. 2004). For Greater Rheas, model performance was moderately good (cross-validation accuracy of 50–69%). Low abundance of Greater Rhea groups and high natural variance in group size (which can reach 50 individuals; Reboreda and Fernández 1997) may have contributed to the limited predictive power of the model. Despite these limitations, the habitat model developed here is an important first step, and although it can be improved, it is a very good approach to understand the habitat requirements of Greater Rheas in grassland environment at landscape scale.

In future work it may be fruitful to consider an alternative to the bounded leaps procedure in the model fitting stage. For analysis of small data sets methods known to be robust to overfitting include Beiman Cutler classifications (BCC). This bootstrap aggregation method is particularly powerful when there are many explanatory variables (Lawrence et al. 2006).

CONSERVATION IMPLICATIONS

The majority of the study area was identified by the model as poor quality habitat where large groups of Greater Rhea, i.e., >15 individuals, are unlikely to occur. Argentine grassland, like most of South American grassland, has experienced strong modification due to human land use. In San Luis province, the conversion of natural to exotic grasslands and agroecosystems is widespread and perhaps irreversible (Demaría et al. 2003). Trends of expanding land use lend urgency to the need to preserve the remaining natural habitat for Greater Rhea and for other grassland species as well. Our results will contribute to such conservation efforts by clarifying important predictors of Greater Rhea habitat quality and through spatial explicit depiction of the distribution of high-quality habitat. The use of texture variables derived from satellite images is an important component in studies of habitat because it captures spatial heterogeneity within a given land cover class at both broad and fine scales simultaneously. Here, we recommend the use of texture analysis as a promising tool in the modeling of habitat suitability. We consider that managers can use predictive models such as those derived here to identify areas that will support high abundance of individuals and predict the consequences of land use on patterns of occurrence and abundance of wildlife species.

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SUPPLEMENT

Raw data used in statistical analysis of Greater Rhea habitat models (*Ecological Archives* A018-071-S1).