Environmental factors influencing the distribution of the Lesser Rhea (*Rhea pennata pennata*) in southern Patagonia

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Abstract. The Lesser Rhea (*Rhea pennata pennata*) has suffered a marked decline in numbers over recent decades, probably mainly as a result of livestock production and overhunting. Our aim was to investigate the factors that determine the distribution of Lesser Rheas in southern Patagonia and to generate a predictive regional distribution map. We surveyed 8000 km of roads and sighted 795 Lesser Rhea individuals or flocks. We also estimated environmental predictors from remotely sensed data and analysed the occurrence of Lesser Rheas in relation to these predictors. The predictors we examined were associated with four hypotheses explaining the distribution of Lesser Rheas: the persecution by ranchers, primary productivity, topography, and anthropogenic disturbance hypotheses. We built models for each hypothesis. Our results suggest that the distribution of Lesser Rheas is not negatively affected by persecution by ranchers, as the species is more abundant in areas with high stocking levels of sheep, but is positively influenced by primary productivity and negatively by the proximity of human habitation. The resulting distribution map can be used as a management tool for government agencies and highlights the conservation priorities for managing this declining and emblematic species.

Additional keywords: Argentina, large-scale habitat models, ratite ecology, species distribution maps.

Introduction

The Lesser Rhea (*Rhea pennata*) is a large, flightless, cursorial ratite endemic to South America. It has three subspecies: *R. p. garleppi* from southern Peru through south-western Bolivia to north-eastern Argentina; *R. p. tarapacensis* in northern Chile; and *R. p. pennata* endemic to the shrub-steppes and semi-deserts of Patagonia (Folch 1992). The Lesser Rhea is currently categorised as near threatened globally (IUCN, Gland, Switzerland; http://www.iucnredlist.org/apps/redlist/details/141087/0, accessed 19 October 2011). In Argentina all subspecies were hunted without restrictions until 1975 and as a result they have suffered marked and progressive decline and subspecies *garleppi* is in danger of extinction (Folch 1992). Furthermore, some populations of subspecies *pennata* are at risk of local and regional extirpation (Bellis *et al*. 2006) and the subspecies has been considered functionally extinct as prey for native carnivores in north-western Patagonia (Novaro *et al*. 2000).

A diverse range of factors are responsible for the decline and fragmentation of Lesser Rhea populations, most of them related to

human activities (Martella and Navarro, 2006). Suggested reasons for the decline of Lesser Rheas are: loss of suitable habitat owing to livestock production (Bellis *et al*. 2006; Martella and Navarro 2006; Barri *et al*. 2009*a*), legal and illegal hunting above sustainable levels (Novaro *et al*. 2000; Bellis *et al*. 2004; Barri *et al*. 2008), and the development of oil industry (Golluscio *et al*. 1998; Funes *et al*. 2000).

The distribution and abundance of the Lesser Rhea has mainly been studied using ecological (Navarro *et al*. 1999; Funes *et al*. 2000; Bellis *et al*. 2006; Barri *et al*. 2008) and social surveys (Martella and Navarro 2006). Navarro *et al*. (1999) reported that the density of Lesser Rheas populations increases towards southern Patagonia. Therefore, it is thought that Santa Cruz, the southernmost province of Argentine Patagonia, could currently hold the largest wild populations. The potential distribution of the Lesser Rhea in Argentine Patagonia, as estimated from field surveys, covers 670 000 km^2 (Navarro *et al*. 1999). Nevertheless, large areas within this region have suffered a progressive degradation as a result of maintaining sheep numbers above

sustainable stocking rates (Golluscio *et al.* 1998; Abraham *et al.* 2005).

Research on the factors affecting Lesser Rhea conservation in Patagonia has been over fairly small scales (Bellis *et al.* 2006; Barri *et al.* 2008, 2009*a*, 2009*b*). However, large-scale studies are necessary to detect patterns of distribution (Scott *et al.* 2002; Rodríguez *et al.* 2007) and to link them with regional processes involved in the decline of the Lesser Rhea. It has been shown that models of species distribution can produce maps that improve knowledge of the distribution of species (Bustamante and Seoane 2004; Gottschalk *et al.* 2007) and are helpful for predicting where a given species could occur (Suárez-Seoane *et al.* 2002; Seoane *et al.* 2003).

The aim of this study was to investigate the factors that determine the distribution of Lesser Rheas in southern Argentine Patagonia, and to generate a predictive distribution map at the regional scale. We also tested four hypotheses regarding the factors that influence the distribution of Lesser Rheas:

- The persecution-by-ranchers hypothesis states that Lesser Rhea distribution in the Patagonian steppes reflects a direct conflict with ranchers and indirect effect of competition with sheep. Between 1970 and 2005, sheep husbandry has declined across this region owing to a combination of natural catastrophes and low prices for wool and meat (González and Rial 2004). As a result, sheep ranching was abandoned in many regions and, under this hypothesis, reduced persecution and competition could have allowed populations of Lesser Rheas to increase. This hypothesis predicts that the probability of finding Lesser Rheas is greater in areas with low stocking levels of sheep.
- The primary productivity hypothesis states that the distribution of Lesser Rheas is determined by the availability of more mesic environments within a semi-arid landscape. This hypothesis predicts a higher probability of finding Lesser Rheas in more productive environments, and close to wetlands, as these habitats offer abundant and better quality forage.
- The topography hypothesis states that the ruggedness of the terrain affects the distribution of Lesser Rheas, with the prediction that there is a higher probability of finding Lesser Rheas in flat open areas, where detection of predators and a subsequent quick escape are facilitated.
- The anthropogenic disturbance hypothesis postulates that unregulated hunting and frequent disturbance is greater around centres of human activity, and predicts a lower probability of the occurrence of Lesser Rheas closer to places of high human density.

Materials and methods

Study area

The province of Santa Cruz (46–53°S, 65–73°W) has an area of 245 865 km^2 (González and Rial 2004). The topography consists of hills and plains with vegetation dominated by a mixed steppe of grass and shrubs rarely >0.5 m in height. The *Nothophagus* forests that occur on the Andean slopes of the province were excluded from the study area. The climate is dry and cold, with strong predominantly westerly winds, and a marked gradient in precipitation – decreasing from west to east – and temperature –

decreasing from north-east to south-west (González and Rial 2004). Since its colonisation by Europeans, sheep ranching has been the only economic activity across the study area until the 1980s, when oil extraction has increased markedly. Average human population density is 0.8 inhabitants km^{-2}, concentrated in 11 urban areas with more than 2000 inhabitants. In the countryside, human density is <2 inhabitants per 100 km^2 (INDEC; http://www.indec.gov.ar/webcenso/provincias_2/provincias.asp, accessed 19 October 2011).

Field surveys and selection of sampling units

Road surveys were conducted during two consecutive spring–summers (November 2004–February 2005, and December 2005–January 2006). We first established which road segments would be surveyed by performing a stratified random sampling. We divided the study area into 12 regions, based on a combination of two environmental variables: mean NDVI (Normalised Difference Vegetation Index) and mean slope. We used mean NDVI because we hypothesised that primary productivity could be an important driver of Lesser Rhea distribution, and mean slope because terrain irregularity could affect the detection of birds during surveys (Travaini *et al.* 2007).

Using a vector coverage of roads, we randomly selected road segments that totalled 4500 km of transects during the first year. To ensure all strata were properly sampled, 1500 km were equally distributed among survey strata (125 km on each stratum) and 3000 km were distributed proportionally to the area of each stratum. During the second year, we randomly selected 3500 km of road segments not surveyed in the previous year. The stratification guarantees an unbiased distribution of survey effort considering that 90% of public roads were surveyed. Approximately 10% of these roads are paved and traffic density is <5 vehicles per day.

Surveys were done by two observers from a vehicle driven at a maximum speed of 40 km h^{-1}. When Lesser Rheas were sighted we measured the distance to the animal or to the centre of the flock with a laser range finder (Leica LRF 1200 Rangemaster, Leica, Solms, Germany) and the angle of the animal relative to our bearing. Our bearing was determined relative to north from the inertial compass in a global positioning system (GPS) unit (Garmin GPS MAP 76CS, Garmin, Olathe, KS, USA). Sightings were collected in a personal digital assistant (PDA; Tungsten T3, Palm Inc., Sunnyvale, CA, USA) using the free Cybertracker software (http://www.cybertracker.org/, accessed 19 October 2011). The PDA was synchronised with the GPS unit, which was used to record the precise location of the census track and the sightings, as well as date, time and vehicle speed.

Environmental predictors

We selected ten potential environmental predictors that summarised the most relevant environmental gradients and landscape features needed to test our hypotheses (Table 1).

We derived vegetation productivity variables from the Vegetation sensor of the Spot 4 satellite (http://www.spot-vegetation.com, accessed 19 October 2011), which monitors terrestrial vegetation cover at 1-km spatial resolution. We used NDVI images to estimate primary productivity (mean NDVI and its coefficient of variation), the month at which the NDVI reaches its

Table 1.   Hypotheses about the factors influencing the distribution of Lesser Rheas and variables used as predictors in models testing the hypotheses

Hypothesis	Variables
Persecution-by-ranchers hypothesis	**Sheep_density.** Sheep stocking level estimated from a model of sheep distribution (Appendix S1 in Pedrana *et al.* 2011)
Productivity hypothesis	**Mean_NDVI.** Mean Normalised Difference Vegetation Index calculated using the VGT-S10 product, which is a 10-day maximum composite value from the VEGETATION sensor of the Spot satellite (http://www.spot-vegetation.com) from April 1999 to March 2005
	Growth_period. Length of the vegetation growth period defined as the mean number of 10-day periods with NDVI values > 85
	CV_NDVI. Coefficient of variation of NDVI
	Season_MAX. Month at which the NDVI reaches its annual maximum value
	Distance_wet meadow. Distance (km) to the nearest pond-bog-wet meadow obtained as a vector coverage from Mazzoni and Vázquez (2004)
Topography hypothesis	**Altitude.** Mean altitude in metres above sea level in a 1-km pixel acquired from the Shuttle Radar Topography Mission (SRTM; http://www2.jpl.nasa.gov/srtm)
	Slope. Mean slope in degrees in a 1-km pixel acquired from the SRTM
Anthropogenic disturbance hypothesis	**Distance_urban.** Distance (km) to the nearest urban area with ≥2000 inhabitants. Data obtained from the Instituto Geográfico Nacional de la República Argentina (http://sig.gov.ar/, accessed 19 October 2011)
	Distance_oil. Distance (km) to the nearest oil camp. Data obtained from the Instituto Geográfico Nacional de la República Argentina (http://sig.gov.ar/)

annual maximum, and seasonality in vegetation growth using 7 consecutive years of data (April 1999–March 2005). We acquired topographic data (mean slope and altitude) from the Shuttle Radar Topography Mission (SRTM; http://www2.jpl.nasa.gov/srtm, accessed 19 October 2011). Distances from each 1-km cell to the nearest city (i.e. urban settlement with an estimated population size >2000 inhabitants), to the nearest oil camp, and to the nearest wet meadow (taken from Mazzoni and Vázquez 2004) were calculated in a geographical information system (GIS, IDRISI Kilimanjaro, Clark Labs, Worcester, MS, USA). The probability of contact with sheep in a cell, as a proxy of sheep stocking density, was taken from a predictive map built with data recorded during field surveys (appendix S1 in Pedrana *et al.* 2011).

Multicollinearity of environmental predictors can make interpretation of alternative models difficult (Lennon 1999). We considered two predictors to be collinear when the Spearman rank correlation coefficient (R_s) was >0.7. Among strongly correlated predictors, we retained those with the clearest ecological meaning for the species (Austin 2007).

Presence–absence data and factors influencing detectability

Tracks recorded with the GPS defined the route of our survey. We used the distance to Lesser Rheas that were sighted to estimate the area effectively covered. We used the software DISTANCE 5.0 (Thomas *et al.* 2010) to fit a detection function to the distance data (Buckland *et al.* 2001). A 300-m buffer on both sides of the track was chosen to define the effective area surveyed as 75% of all sightings of Lesser Rheas were within this area.

Presence–absence modelling requires defining units in which presence or absence is recorded. We used a 1-km grid defined by the spatial resolution of NDVI data. We overlaid the surveyed tracks with 300-m buffers on this 1-km grid and selected all cells that partially or totally overlapped with buffers. Lesser Rhea sightings (*n* = 795) were overlaid on selected cells. Grid-cells with ≥1 Lesser Rhea sightings were considered presences and the remaining cells were considered absences.

The probability of detecting an individual or flock in a 1-km cell was affected by the proportion of the cell that was effectively surveyed. We calculated the variable 'Area_surveyed' as the fraction of the cell surface included in the 300-m buffer on both sides of the survey transect and this variable was included as a fixed term in the models to correct for its effect on detection probability (Travaini *et al.* 2007; Pedrana *et al.* 2010). Although the survey protocol was standardised there are unavoidable survey variables that affect detectability of fauna that are rarely considered in species distribution modelling. For example, we tried to survey at a constant speed of 40 km h^{-1}, but speed recorded by the GPS indicated that, within a cell, mean speed varied with road condition, weather and number of contacts with fauna. For this reason we analysed if vehicle speed (Speed), time of day (Time_day), or calendar date (Date) had any influence on detectability of individuals. Time of day could affect our results through the influence of light levels on detectability, and Date could increase detectability of Lesser Rheas towards the end of the reproductive season when birds increase their tendency to congregate.

Model fitting

We fitted generalised additive models (GAM; Hastie and Tibshirani 1990) using as a response variable the presence or absence of Lesser Rheas in a 1-km cell using binomial errors and a logit link. As the number of cells with presence (*n* = 482) was low compared to the number of cells with observed absence (*n* = 13 230), we used a re-sampling scheme to obtain a balanced sample (Liu *et al.* 2005), randomly choosing 482 out of the 13 230 cells with absence. We reserved a random sample of 20% of cells with presence and absence for model cross-validation and used the remaining 80% for model fitting. This procedure was repeated 100 times. Predictors for the models were selected from the initial set by a backward-forward stepwise procedure (step.gam routine in S-PLUS 2000; MathSoft 1999), starting from a full model that included all potential predictors relevant to a particular hypoth-

esis. Predictors were initially included in the models as smoothing splines with 3 d.f. The Akaike's Information Criterion (AIC) was used to retain a term (Sakamoto *et al.* 1986). From the 100 models built with the re-sampling procedure for each hypothesis, we selected those that ranked as the best model ≥10 times. Then we repeated this re-sampling procedure with each of the selected models, in which the predictors were fixed, but progressive simplification of the degrees of freedom of the splines was allowed. Again we retained the models that were selected ≥10 times. Finally, we used a single matrix with the complete dataset where original prevalence was maintained (Jiménez-Valverde and Lobo 2006) to compare alternative models within each hypothesis that were as good as the best model in terms of AIC (Burnham and Anderson 2002). We considered as competing models those for which the differences between AIC and the AIC (Δi) of the best candidate model was ≤4.

The same procedure was used to build a general model starting with all relevant variables retained in the best models for each hypothesis.

Model validation

The area under the curve (AUC) of the receiver operating characteristic (ROC) plot was computed for each of the 100 models with each set of validation data to estimate its predictive power through cross-validation (Murtaugh 1996). The AUC ranges from 0 (model discrimination is not better than random) to 1 (perfect discriminatory ability; Pearce and Ferrier 2000). Predictive models are considered usable if AUC ≥0.7 (Harrell 2001). The difference between the mean predictive ability of the model selected for each hypothesis and the general model was tested with a Wilcoxon–Mann–Whitney test (Crawley 2002).

Distribution of Lesser Rhea in Santa Cruz

We used the best model to build a predictive map of the current distribution of Lesser Rheas in Santa Cruz Province. To produce this map we used the option in IDRISI Kilimanjaro (Eastman 2003) to export predictors as a data matrix to S-PLUS, applied the predict.gam procedure (MathSoft 1999) to make predictions based on the new data matrix, and then exported the predicted probability values from S-PLUS back to IDRISI. The estimated probability of Lesser Rhea occurrence was simplified into three probability classes to ease interpretation of the distribution.

Results

On 8000 km of road transect we made 795 sightings of Lesser Rhea individuals or flocks, comprising a total of 3462 individuals.

We found a high correlation between the predictors Growth_period and Mean_NDVI ($R_s = 0.87$), Growth_period and Season_MAX ($R_s = 0.89$), and Mean_NDVI and Season_MAX ($R_s = 0.93$). We chose Mean_NDVI as the best ecological representative of these three predictors.

As expected, the probability of sighting a Lesser Rhea showed a significantly non-linear decline with the proportion of the cell that was included in the 300-m buffer (model 1 in Table 2, Fig. 1). Among the survey-specific variables, we found that the probability of detecting a Lesser Rhea was also affected by time of day, survey date and vehicle speed (model 1 in Table 2).

Testing hypotheses

Contrary to the prediction of the persecution-by-ranchers hypothesis, the most parsimonious model showed that the probability of occurrence of Lesser Rheas varied little with low

Table 2.   Competing GAM models obtained by stepwise selection for each hypothesis of the factors influencing occurrence of Lesser Rheas in the semi-arid steppes of Santa Cruz Province, Southern Patagonia

For each model Akaike's Information Criterion (AIC) and the difference of AIC between the current model and the best model (Δi) are given. Subscripts refer to the degrees of freedom of the smoothing spline and no subscripts refer to linear terms (d.f. = 1)

| Model code	Models	AIC	Δi
	Survey-specific variables		
1	$Area\_surveyed_3 + Date_3 + Speed_3 + Time\_day_3$	3882.05	0
2	$Area\_surveyed_3 + Date_3 + Speed_3 + Time\_day_2$	3883.07	1.02
	Persecution-by-ranchers hypothesis		
3	$Area\_surveyed_3 + Sheep\_density_3$	3887.06	0
4	$Area\_surveyed_3 + Sheep\_density_2$	3890.64	3.58
	Productivity hypothesis		
5	$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_wet\ meadow$	3872.02	0
6	$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_wet\ meadow_3$	3873.28	1.26
7	$Area\_surveyed_3 + Mean\_NDVI_3$	3875.12	3.10
	Topography hypothesis		
8	$Area\_surveyed_3 + Slope + Altitude_3$	3940.29	0
9	$Area\_surveyed_3 + Altitude_3$	3941.41	1.49
	Anthropogenic disturbance hypothesis		
10	$Area\_surveyed_3 + Distance\_urban + Distance\_oil_3$	3837.03	0.00
11	$Area\_surveyed_3 + Distance\_urban_3 + Distance\_oil_3$	3839.16	2.13
	General models		
12	$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_urban + Distance\_wet\ meadow_3 + Distance\_oil_3 + Altitude$	3703.04	0
13	$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_urban_3 + Distance\_wet\ meadow_3 + Distance\_oil_3$	3705.23	2.19
	General models combined with survey-specific variables		
14	$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_urban + Distance\_wet\ meadow_3 + Distance\_oil_3 + Speed_3 + Date_3 + Time\_day_3$	3318.43	0
15	$Area\_surveyed_2 + Mean\_NDVI_3 + Distance\_urban + Distance\_wet\ meadow + Speed_3 + Date_3 + Time\_day_3$	3321.56	3.13
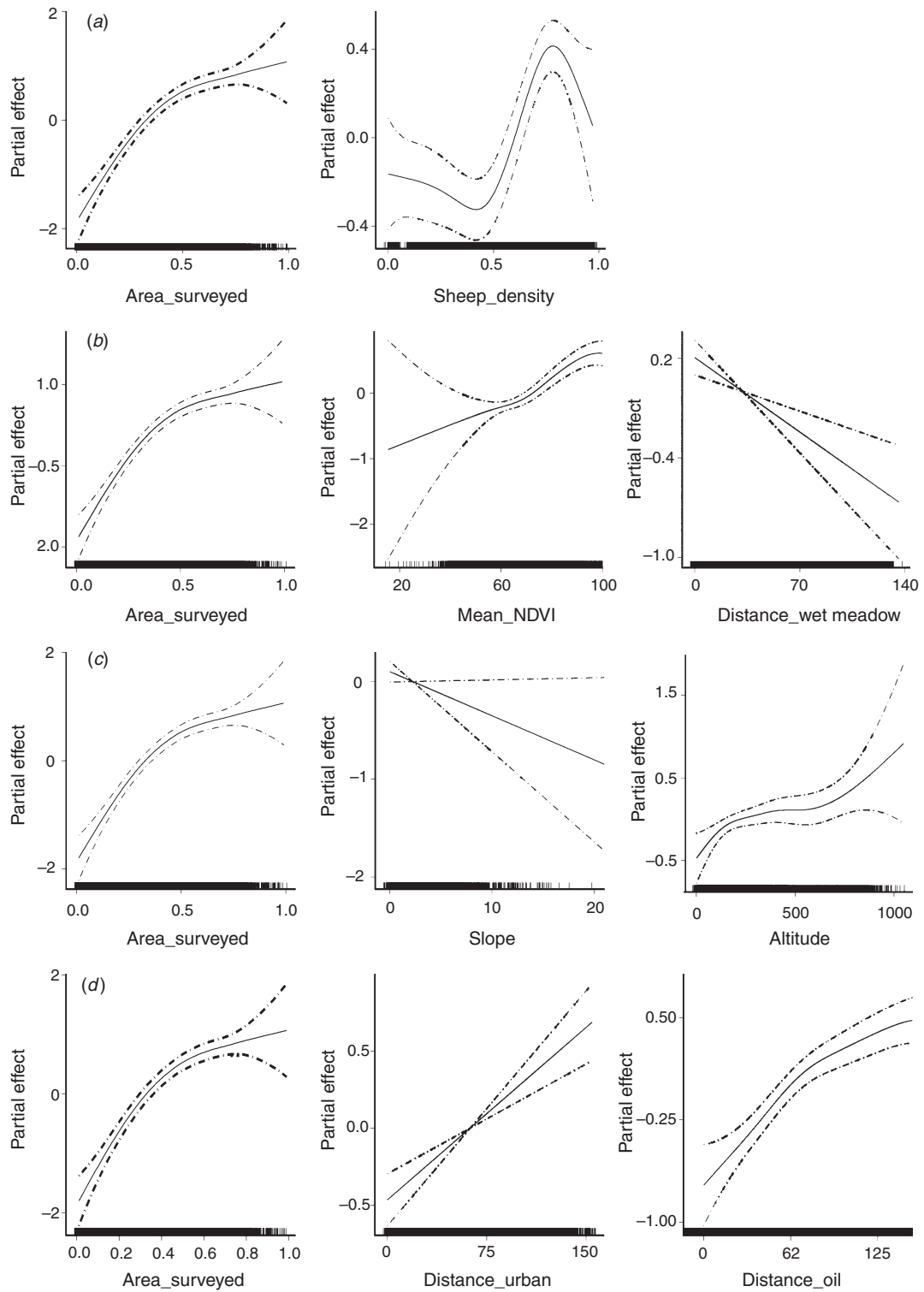
Fig. 1. Partial effects of predictors included in the most parsimonious models for each alternative hypothesis of the factors that influence the occurrence of Lesser Rheas: (*a*) persecution-by-ranchers hypothesis (model 3 in Table 2); (*b*) productivity hypothesis (model 5 in Table 2); (*c*) topography hypothesis (model 8 in Table 2); and (*d*) anthropogenic disturbance hypothesis (model 10 in Table 2). Dashed lines represent 95% confidence intervals for the mean prediction.

to moderate values of sheep abundance (probability of sheep presence <0.5, assuming that this probability is positively correlated with abundance; Pedrana *et al*. 2011) but increased with moderate to high values of sheep abundance (model 3 in Table 2, Fig. 1*a* probability of sheep presence ≥0.5).

The most parsimonious model of Lesser Rhea occurrence among the models being evaluated under the productivity hypothesis included Mean_NDVI and Distance_wet meadow (model 5 in Table 2). The probability of Lesser Rhea occurrence increased non-linearly with the mean NDVI and decreased linearly with the distance to the nearest wet meadow (Fig. 1*b*).

The best model among the models being evaluated under the topography hypothesis included slope and altitude (model 8 in Table 2). Lesser Rhea occurrence was negatively related to mean slope and positively related to altitude (Fig. 1*c*).

Two variables were retained in the best model under the anthropogenic disturbance hypothesis: Distance_urban and Distance_oil (model 10 in Table 2), indicating that Lesser Rhea occurrence strongly increased with distance to the nearest city and distance to an oil camp (Fig. 1*d*).

When all predictors were considered in a model of Lesser Rhea presence, the general model included: Mean_NDVI, Distance_urban, Distance_wet meadow and Distance_oil, and three survey-specific variables (time of day, census date, and vehicle speed; model 14 in Table 2, Fig. 2). The fit of model 14, which included survey-specific variables, was superior to the fit of model 12 that did not include them (Table 2). All models of Lesser Rhea presence were improved with the inclusion of survey-specific variables. These variables, however, did not alter the identity, sign, or the relative strength of the predictor effects (see Appendix) except the effect of altitude on Lesser Rhea occurrence was no longer significant (model 8 in Table 2). The probability of

detecting Lesser Rheas fluctuated seasonally, decreased with car speed, and reached a peak in the hours around midday (Fig. 2).

Model validation

The predictive models for Lesser Rhea distribution fitted the data well, with a mean validation AUC (±s.e.) better than a null model for every set of predictors: productivity model (0.72 ± 0.03), topography model (0.70 ± 0.02), anthropogenic disturbance model (0.73 ± 0.03), and general model (0.86 ± 0.02). The strong fit suggests that the models were robust and could be considered useful for predicting the distribution of the species (Harrell 2001). Among the general models, model 14 (Table 2) had the highest predictive ability, significantly higher than the predictive ability of final models representing a single hypothesis, either the productivity ($Z = 9.41$, $P < 0.001$), topography ($Z = 11.94$, $P < 0.001$) or anthropogenic disturbance hypotheses ($Z = 7.07$, $P < 0.001$).

Predictive mapping of the distribution of Lesser Rheas

The predictions of model 14 (Table 2) were translated to a GIS assuming that whole 1-km cells were effectively surveyed at 30 km h^{-1}, at the most favourable date in the middle of spring–summer (i.e. 20 January) and at the most favourable time (i.e. 1200 hours) (Fig. 3). This map shows that, although Lesser Rheas have been sighted almost everywhere in Santa Cruz Province, the species is not uniformly distributed (Fig. 3). The probability of occurrence of Lesser Rheas increased from north to south in Santa Cruz Province, although there are small areas of high probability of occurrence, close to the Andean slopes in the west and near wetlands scattered across the centre of the region.
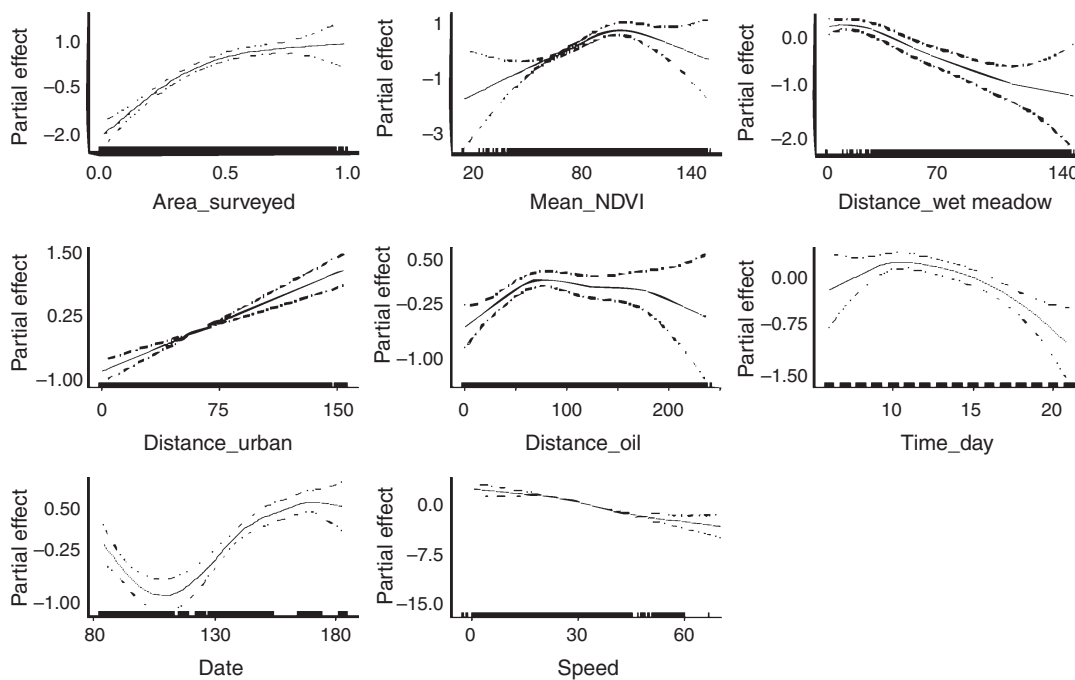

Fig. 2. Partial effects of predictors included in the best general model of Lesser Rhea presence corrected for survey-specific variables (model 14 in Table 2). Dashed lines represent 95% confidence intervals for the mean effect.
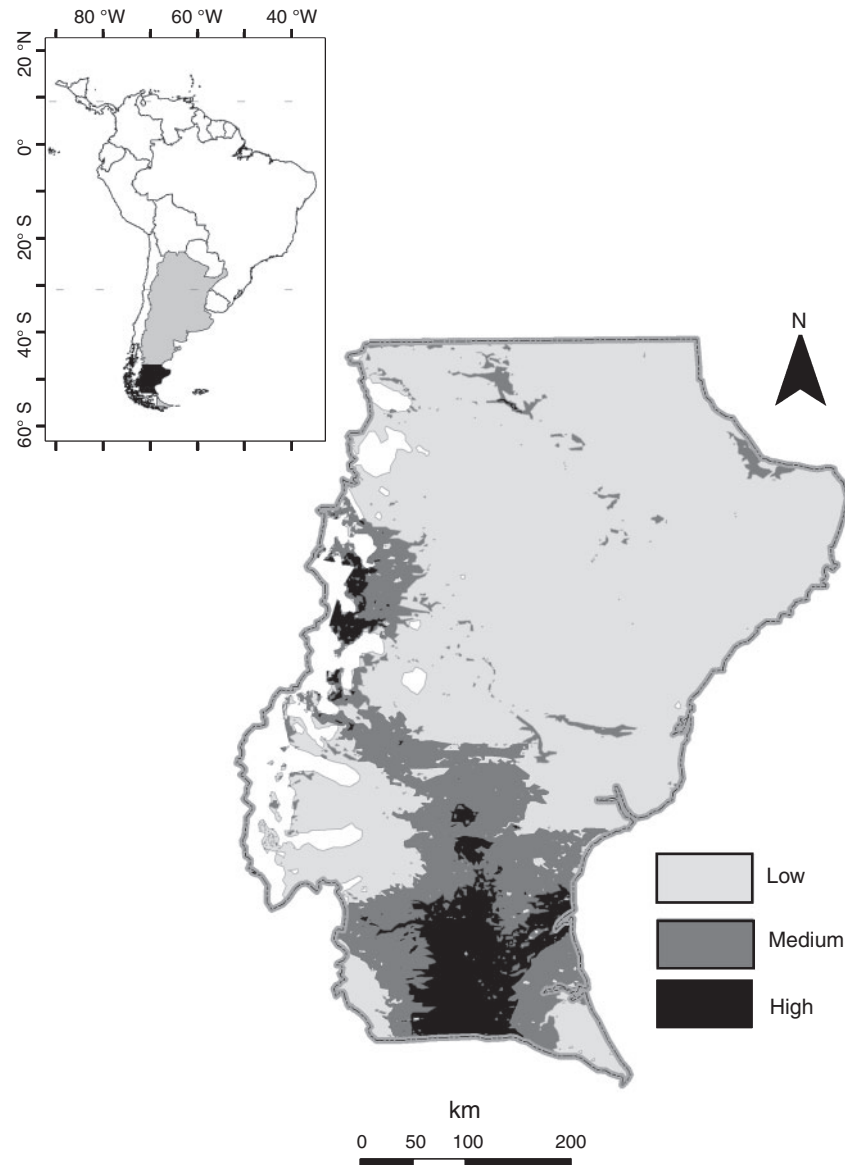
Fig. 3. The distribution of the Lesser Rhea in Santa Cruz Province, Argentina. Values represent the probability of recording a Lesser Rhea in a 1-km cell as predicted by Model 14 (Table 2). Probabilities are categorised in three classes (low, <0.33; medium, 0.33–0.66; high, >0.66). White represents areas of the region omitted from predictions: sea, lakes, forested areas or beyond the model's environmental space.

Discussion

The continuing decline of Lesser Rhea may cause local or regional extirpations unless conservation measures are undertaken (Bellis *et al.* 2006).

Our results highlight the main factors influencing the current distribution of Lesser Rheas and allow us to draw conclusions about the causes of this decline. In agreement with the productivity hypothesis, the occurrence of Lesser Rheas was positively associated with mean primary productivity and distance to the nearest wet meadow, in a regional context dominated by dry steppe habitat. Preference for wetlands has been observed in other populations of Lesser Rheas, presumably because wetlands

provide the best quality forage for adults and their chicks (Bellis *et al.* 2006; Barri *et al.* 2008, 2009*a*).

The occurrence of Lesser Rheas strongly increased with distance from the nearest city or oil camp. In accordance with the anthropogenic disturbance hypothesis, areas with low probability of Lesser Rhea occurrence were especially common in northern Santa Cruz, where oil exploitation currently concentrates (González and Rial 2004). Oil extraction is preceded by the development of a large number of roads in otherwise inaccessible areas. This activity not only affects wildlife by increasing traffic casualties and habitat degradation, but also by increasing access for poachers (Novaro *et al.* 2000; Bellis *et al.* 2004; Martella and

Navarro 2006). Funes *et al.* (2000) suggested that one of the major causes of the decline of the Lesser Rhea in north-western Patagonia was the opening of new roads associated with the expansion of the oil industry. The fact that Lesser Rheas stayed away from cities indicate that these birds might actively avoid areas where they are intensively hunted or disturbed by people (Funes *et al.* 2000; Novaro *et al.* 2000; Bellis *et al.* 2004). Navarro *et al.* (1999) also reported that the density of Lesser Rhea populations was negatively correlated with human density.

Our results suggest that the probability of Lesser Rhea occurrence is greater at higher elevations and in flat open areas, as predicted by the topography hypothesis. But, this association is not as strong as the one with primary productivity, and was not included in the final model. Because Rheas have a 'watch and run' anti-predator strategy (Bruning 1974), open flat areas favour vigilance and quick escape. However, given that the mesic, productive pasturelands that this species seems to prefer typically occur in flat terrain, and that the effect of topographical predictors became weaker in the general models, the good fit of the topographical models could be confounded with the distribution of high-quality forage, at least in part.

Contrary to our expectations, the persecution-by-ranchers models show that sheep ranching did not have a negative effect on the distribution of Lesser Rheas. The distribution map indicates that areas with high probability of Lesser Rhea occurrence are concentrated in the southern sector of Santa Cruz Province, which is an area with above average rainfall where productive pastures abound (González and Rial 2004). These productive pastures are mainly devoted to extensive sheep ranching with high stocking rates. Traditionally, some species such as Guanaco (*Lama guanicoe*) and Upland Goose (*Chloephaga picta*), have been considered pests by ranchers on the basis of assumed competition with sheep (Baldi *et al.* 2004; Blanco and De la Balze 2006) and, as a consequence, they were actively persecuted. Predictive habitat models for the Guanaco indicate that its distribution is restricted to areas of low productivity with low sheep stocking levels (Travaini *et al.* 2007; Pedrana *et al.* 2010). In contrast, the Lesser Rhea might not have suffered the same persecution, because there is little competition for food resources between Lesser Rheas and other herbivore species, such as Upland Geese, Guanaco and sheep (Bellis *et al.* 2004). In addition, it seems that agricultural activities and sheep ranching did not influence Lesser Rhea occurrence (Bellis *et al.* 2004). Moreover, Barri *et al.* (2009b) found out that sheep stocking at moderate levels (0.25–1 sheep ha^{-1}) did not affect species reproductive success (Barri *et al.* 2008, 2009b).

Our study also shows that even when care is taken to standardise the survey protocol there are unavoidable survey factors that influence the results. Here we show that these factors can be controlled statistically and researchers should check that their conclusions are robust and do not change when correction factors are included in the models.

Species distribution models of the Lesser Rhea in Patagonia suggest that: (1) primary productivity is the main driver of the distribution of the species in the arid steppes of Santa Cruz; (2) mesic habitats like wet meadows are selected habitats, and allow Lesser Rheas to occupy otherwise unproductive steppes; (3) urban areas and oil camps may have a negative effect on the distribution of Lesser Rheas or, at least, that Lesser Rheas appear

to be more disturbed near these areas; and (4) current levels of competition with sheep and of direct persecution by ranchers have no noticeable effect on the distribution of Lesser Rheas.

Finally, we believe that our statistical distribution model generates a map of the distribution of Lesser Rheas that can be a useful tool for governmental agencies to establish conservation management priorities for the species, and for identifying regions where local-scale ecological studies of this species should be conducted.

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Appendix.   Competing GAM models obtained by stepwise selection for each hypothesis of the factors that influence the occurrence of Lesser Rheas in the semi-arid steppes of Santa Cruz Province, including corrections for survey-specific variables

For each model Akaike's Information Criterion (AIC) and the difference of AIC between the current model and the best model (Δi) are given. Subscripts refer to the degrees of freedom of the smoothing spline and no subscripts refer to linear terms (d.f. = 1)

Models	AIC	Δi
Persecution-by-ranchers hypothesis		
$Area\_surveyed_3 + Sheep\_density_3 + Date_3 + Speed_3 + Time\_day_3$	1033.90	0.00
Productivity hypothesis		
$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_wet\ meadow_3 + Date_3 + Speed_3 + Time\_day_2$	984.09	0.00
$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_wet\ meadow_3 + Date_3 + Speed_3 + Time\_day_2$	985.50	1.41
$Area\_surveyed_3 + Mean\_NDVI_3 + Date_3 + Speed_3 + Time\_day_3$	986.25	2.15
Topography hypothesis		
$Area\_surveyed_3 + Slope + Date_3 + Speed_3$	1028.49	0.00
$Area\_surveyed_3 + Altitude_3 + Date_3 + Speed_3$	1031.33	2.84
$Area\_surveyed_3 + Altitude + Date_3 + Speed_3$	1032.36	3.88
Anthropogenic disturbance hypothesis		
$Area\_surveyed_3 + Distance\_urban + Distance\_oil_3 + Time\_day_2 + Date_3 + Speed_3$	1012.76	0.00
$Area\_surveyed_3 + Distance\_urban_3 + Distance\_oil_3 + Time\_day_2 + Date_3 + Speed_3$	1014.19	1.43