Analysis of the spatial variation in the abundance of lesser rheas using density surface models

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Abstract

Context. The study of the spatial variation in abundance of wild populations and the identification of factors explaining the observed patterns are key both to understand aspects of basic ecology and the effects of human activities. This is usually difficult to evaluate for low-density and widely distributed species, such as the lesser rhea (*Rhea pennata pennata*), an endemic bird from South America. Recent advances in spatial modelling such as the density surface models (DSM) combine distance-sampling procedures with modelling techniques to produce maps of spatial variation in abundance, and its relationship with predictive variables.

Aims. We aimed to analyse the spatial distribution and abundance of lesser rhea, and the variables that affect its abundance in Península Valdés (PV) Argentine Patagonia.

Methods. We conducted 338.4 km of ground surveys of lesser rheas in PV during the end of the Austral summer of 2015. Spatial models were constructed using DSM. Ecological and human-related variables were included in the models to account for variation in the abundance of animals at 4-km^2 spatial resolution.

Key results. We estimated an overall density of 0.44 birds km^{-2} (CV = 32%) for the prediction area of 3320 km^2. High values of normalised difference vegetation index, a correlate of plant productivity, were associated with increased numbers of lesser rheas. The location of ranch buildings, indicators of human presence, had a strong negative effect on lesser rheas, although their abundance increased at high sheep stocking rates.

Conclusions. As reported by previous studies in different sites, the abundance of lesser rheas in our study area was low. The use of DSM allowed a detailed examination of the spatial variation, as well as the variables involved and the uncertainty of the prediction.

Implications. The use of DSM techniques can be a useful tool for conservation planning and monitoring. Spatial, high-resolution data combined with knowledge on the factors affecting the number of animals are crucial to target specific conservation actions and monitor their results, and should allow government agencies to make better decisions concerning conservation-oriented management.

Additional keywords: anthropogenic impacts, habitat selection, modeling, spatial ecology, vertebrates, *Rhea pennata pennata*.

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Introduction

The changes imposed on ecosystems by environmental and human-related factors often lead to variation in the distribution and abundance of wild species in space and time (Pullin 2002). The conservation-oriented management of modified landscapes requires the study of the spatial variation in the abundance of organisms (Fischer and Lindenmayer 2006), and also awareness of factors that influence their distribution patterns. Across the extensive rangelands, where domestic livestock, human and wild species populations depend on the same resources, it is particularly important to understand the relationships among ecological factors, human activities and their influence on the native wildlife.

The lesser rhea (*Rhea pennata*) is a large, flightless bird endemic to South America. Its southernmost subspecies *R. p. pennata* is widely distributed throughout the arid and semiarid lands of the Argentine Patagonia and southern Chile (Del Hoyo *et al*. 1992). Across the Patagonian grasslands and shrublands, lesser rheas share the habitat with sheep. Extensive ranching is still widespread since the introduction of sheep in

the 1880s (Soriano and Movia 1986). Habitat loss, egg collection and poaching have been identified as the main threats to lesser rhea populations (Bellis *et al.* 1999; Funes *et al.* 2000; Barri *et al.* 2008; Pedrana *et al.* 2011).

Lesser rhea densities were reported as low, and the available studies on distribution and abundance provide either the number of sightings per kilometre travelled, or estimate average animal densities across thousands of squared kilometres (De Lucca 1996; Funes *et al.* 2000; Pedrana *et al.* 2011; Baldi *et al.* 2015). There are no studies assessing the spatial variation in the abundance of lesser rheas at a higher resolution. In this work, we use a density surface model (DSM) to analyse the spatial variation in lesser rhea numbers across Península Valdés (PV), Argentina (Fig. 1). DSM combines spatial modelling techniques with distance sampling to estimate the number of animals either for the whole study area or any subregion of the area (Hedley and Buckland 2004). Our objectives were to account for spatial variation in the number of animals within the study area, and to assess the factors affecting the abundance of lesser rheas using a DSM.

We hypothesised that (1) habitat quality, (2) disturbance by humans and (3) land management shape the spatial variation in the abundance of *R. p. pennata*. In terms of habitat quality, we expect that high primary productivity and the availability of water sources will result in an increased abundance of lesser rheas. Second, lesser rheas will avoid ranch buildings, indicators of human presence and likely disturbance. Finally, values of land-management variables such as an increasing sheep stocking rate, small paddock areas and proximity to fences will be related to a lower abundance of lesser rheas.

Materials and methods

Study area

The study was conducted at PV, located in the Argentine Patagonia (Fig. 1). PV is a provincial protected area and also a UNESCO World Heritage Site since 1999. Extensive sheep ranching for wool production occupies most of the area, and although tourism is highly relevant for the local economy, it is mainly focussed towards the coastal wildlife. Ranches are fenced into paddocks of up to 2500 ha each. Ponds are temporary and dependent on the rain; thus, the water for the sheep is obtained through windmills and driven to permanent water sources where animals arrive to drink. Annual precipitation averages 210 mm, with a high interannual variation (Barros and Rivero 1982), and increases towards coastal areas.

The vegetation is characteristic of the southern Monte Phytogeographic Province, but shares plant species with the northern Patagonian Province (León *et al.* 1998). The Monte Phytogeographic Province is characterised by a tall shrubland covering 40–60% of the soil surface, and dominates the central and northern parts of the area. Whereas foliage cover in the Patagonian Province varies from 35% to 65%, but may increase substantially in rainy periods when annual plants contribute a high proportion of the total cover (Beeskow *et al.* 1995). The most common shrub species in the study site are *Chuquiraga avellanedae* and *Hyalix argentea*, whereas the most abundant grasses are *Nassella tenuis* and *Sporobolus rigens*.

Field surveys

We conducted ground, line-transect surveys (Buckland *et al.* 1993; Laake *et al.* 1993) of lesser rheas during the end of the Austral summer in 2015, totalling 338.4 km surveyed along secondary dirt roads and tracks (average transect length: 6 km; Fig. 1). All surveys were conducted from an open pick-up vehicle, traveling at 25 km h^{-1}, with two observers standing in the back. As the site comprised wide, predominantly flat areas where shrubs above 1.20 m tall are rare and scattered (Bertiller *et al.* 1980), early detection of animals and prompt data collection prevented potential bias in distance measuring as a result of occasional run-away behaviour. For every group of
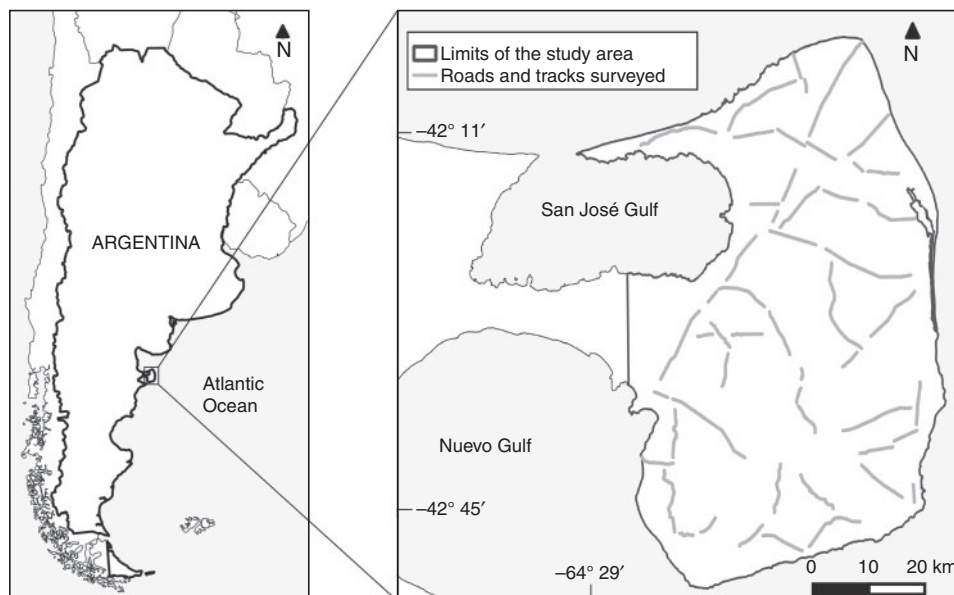

Fig. 1. Location of the Península Valdés and distribution of the survey transects.

lesser rheas detected, we stopped the vehicle, counted the number of animals by means of binoculars, recorded the distance from the transect line to the location where the group was standing at the time it was detected, using a laser rangefinder (Bushnell Yardage Pro 1000 Laser Range finder, Overland Park, Kansas, USA), and recorded our location and the angle relative to the group of animals by using a portable GPS (Garmin Oregon 550, Garmin, Olathe, KS, USA).

Predictor selection

To test our hypotheses, we identified eight variables as potential predictors of *R. p. pennata* abundance (Table 1). As a correlate of primary productivity, we calculated the mean normalised difference vegetation index (NDVI) for the spring–summer season of 2014–15 (from 21 September to 21 March). Mean NDVI was based on MODIS MOD13Q1 satellite images of 250-m spatial resolution available at https://lpdaac.usgs.gov (verified 15 March 2018). The current sheep stocking per paddock was obtained by consulting owners and workers of the ranches in March 2015. Data on the location of ranches, permanent water sources, wire fences delimiting the paddocks, and paddock's area were available at our institute but they were also checked and updated in the field, while working across PV between 2013 and 2015. Additionally, we included latitude and longitude as proxy variables to account for possible remaining variation. We obtained the values for each variable using the QGIS open source geographic information system (QGIS Development Team 2016) and packages reshape2, raster and ggplot2, (R Development Core Team 2015). The range of values of each variable across the study area was included as far as possible in the surveyed tracks. Multicollinearity in predictor variables could make it difficult to separate the effects on the response variable and to compare alternative models (Lennon 1999); thus, we evaluated the collinearity between pairs of covariates taking the values measured at each segment (see below). We considered two predictors not to be collinear when Pearson's correlation coefficients were <0.6.

Estimating the detection function

Using standard distance-sampling methodology, we fitted a detection function $g(y)$ to account for the probability of detecting lesser rheas. The detection model assumes that all groups (one or more lesser rheas) were detected at zero distance from the transect line, with detectability decreasing with an increasing distance from the line (Buckland *et al.* 2001). We evaluated the half-normal and hazard-rate functions as

candidate detection functions. Possible responsive movement by rheas during the survey was examined by plotting the detection functions and observed data grouped into different number of intervals. Possible effects of data truncation (in our case the removal of all observations beyond 584 m from the line, or 10% of the extreme sightings according to Thomas *et al.* 2010) were assessed using quantile–quantile plots (Q–Q plots) and the Cramer-von Mises test for both candidate functions. Then, we analysed the effect of the group size as a covariate, and chose the best model by using the Akaike information criterion (AIC, Burnham and Anderson 2002), the Q–Q plots and the Cramer-von Mises test. All analyses were performed using the 'Distance' package version 0.9.6 (Miller 2016*a*) for R.

Density surface model (DSM)

Following Miller *et al.* (2013) and DSM methodology, each transect line was divided into smaller segments of 1.8 km in length, totalling 192 segments. Subsequently, each observation was assigned to its corresponding segment according to its location. Given that there were no covariates other than distance in the detection function selected, the probability of detection ($\hat{p}$) was constant for all segments. We estimated the abundance ($\hat{n}$) in Segment j given $\hat{p}$, the number of observations in Segment j (R_j) and the number of animals (S_{rj}) of the Observation r_j, as follows:

$$\hat{n}_j = \sum_{r_j=1}^{R_j} \frac{S_{rj}}{\hat{p}}$$

Using generalised additive models (GAMs), we modelled n_j as the sum of smooth functions of uncorrelated predictor variables measured at Segment j. We used restricted maximum likelihood (REML) for smoothness selection (Reiss and Ogden 2009; Wood 2011). The concurvity of the smooth terms (Wood 2006) was estimated to assess the degree. We tested three response distributions, namely, Tweedie, negative binomial and quasi-Poisson. For each distribution, we built two 'base models'; one considered all the covariates as univariate smooths, and the other included, apart from the non-geographic, the geographic covariates (latitude, longitude) as a bivariate smooth. We performed the covariate selection in each base model by removing the non-significant covariates (with approximate P-values of >0.05; Marra and Wood 2011), and included an additional penalty for each smooth term, which allowed their degrees of freedom to decrease below 1 and, therefore, to remove the term from the model during fitting (Wood 2006, section

Table 1.   Variables proposed

Hypothesis	Variable	Description
Habitat quality	Mean NDVI	Mean normalised difference vegetation index
	Water dist.	Distance to the nearest, permanent water sources (m).Troughs for the sheep are either associated to windmills or tanks
Disturbance by humans	Ranch dist.	Distance to the nearest ranch building (m)
Land management	Sheep stock.	Sheep stocking rate (sheep km^{-2}) obtained per paddock
	Paddock size	Area of each paddock (m^2)
	Fence dist.	Distance to the nearest fence (m)
Proxy variables	Long.	Longitude projected into metres using universal transverse mercator zone 20
	Lat.	Latitude projected into metres using universal transverse mercator zone 20

4.1.6, 2011). Therefore, we obtained six models as final candidates (Table 2) and, subsequently, we selected the best-fitting model based on the inspection of residual plots (Figs S1–S6, Tables S1, S2, all available as Supplementary Material for this paper). Residual autocorrelation was checked by inspecting the correlogram, which showed the behaviour of the correlation between segments at a series of lags. Models were fitted using the 'dsm' package version 2.2.12 (Miller 2016*b*) for R.

Abundance and variance estimation

We overlaid a grid of 4-km^2 cells to our study area, obtaining a prediction area of 3320 km^2. On the basis of the cell covariate values, we predicted the number of animals for each cell resulting from the selected DSM, and, subsequently, obtained an overall estimate of abundance for PV. The uncertainty associated with the estimation was calculated by using the delta method (Ver Hoef 2012). Thus, we obtained the variance in the abundance of lesser rheas for each 4-km^2 cell.

Results

We recorded 37 observations of lesser rheas after surveying 338.4 km of ground transects, comprising a total of 110 individuals (0.11 observations km^{-1}). The detection function selected was the half-normal (data fit was not improved either

after data truncation or using group size as a covariate; Fig. 2). The average density estimated for the 3320-km^2 prediction area was 0.44 lesser rheas km^{-2} (CV = 32%) or 1452 individuals (Table 2); however, the abundance of animals was higher towards the eastern and south-western coast of PV (Fig. 3). Lower uncertainty of abundance estimates predicted was related to areas where lesser rheas were recorded (Fig. 4).

Pearson's correlation values were <0.6 for all combinations of pairs of potential predictors, so we assumed that there was not multicollinearity among them. The concurvity measures were very small, suggesting negligible concurvity (Wood 2006; Tables S3–S8, available as Supplementary Material for this paper). The deviance explained by the selected DSM was 53.3% (Table 2). Statistically significant variables included in the best-fitting model were mean NDVI ($P = 0.02$), distance to the nearest ranch building ($P = 0.003$), sheep stocking rate ($P = 0.004$) and geographic longitude ($P < 0.001$). The abundance of lesser rheas showed non-linear relationships with significant predictors (Fig. 5; Fig. S7, available as Supplementary Material for this paper). The number of birds decreased as NDVI increased from low to average values (0.2–0.25), and tended to increase as the mean NDVI grew above the average for the whole area (Fig. 5*a*). However, the confidence intervals of the curve tended to become too wide at the highest values, suggesting that the effect was associated to highest uncertainty, likely

Table 2.   Density surface models tested

The best-fitting model selected is shaded. Exp.Dev., percentage of explained deviance; Ab., total number of lesser rheas estimated for the study area; s.e., standard error; CV, coefficient of variation

Final model	Response distribution	Significant variables	Exp.Dev.	Ab.	s.e.	CV
A	Tweedie	s(mean ndvi)s(ranch dist.)s(sheep stock.)s(lon.)	53.3	1452	415	0.32
B	Tweedie[A]	s(mean ndvi)s(ranch dist.)s(sheep stock.)s(lat.+lon.)	55.1	–	–	–
C	Negative binomial	s(mean ndvi)s(ranch dist.)s(sheep stock.)s(lon.)s(lat.)	62	–	–	–
D	Negative binomial[A]	s(mean ndvi)s(ranch dist.)s(sheep stock.)s(lat.+lon.)	60.9	–	–	–
E	Quasi-Poisson	s(mean ndvi)s(ranch dist.)s(sheep stock.)s(lon.)	57.2	–	–	–
F	Quasi-Poisson[A]	s(ndvi mean)s(ranch dist.)s(sheep stock.)s(lon.+lat.)	55.1	–	–	–

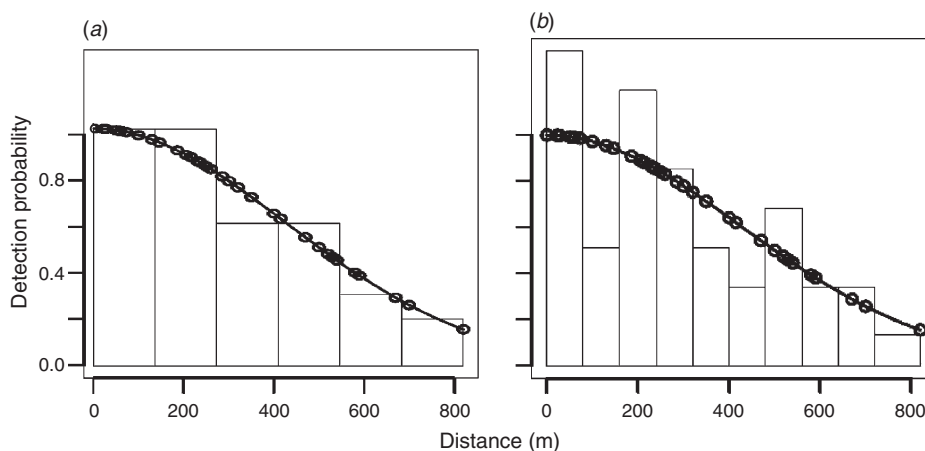[A]Using bivariate smooth for latitude and longitude.

Fig. 2. Distribution of perpendicular detection distances of lesser rheas sightings. Solid lines represent the half-normal detection function selected, whereas circles represent the sightings. (*a*) Observed data grouped into six different intervals; (*b*) observed data grouped into an increased (10) number of intervals.
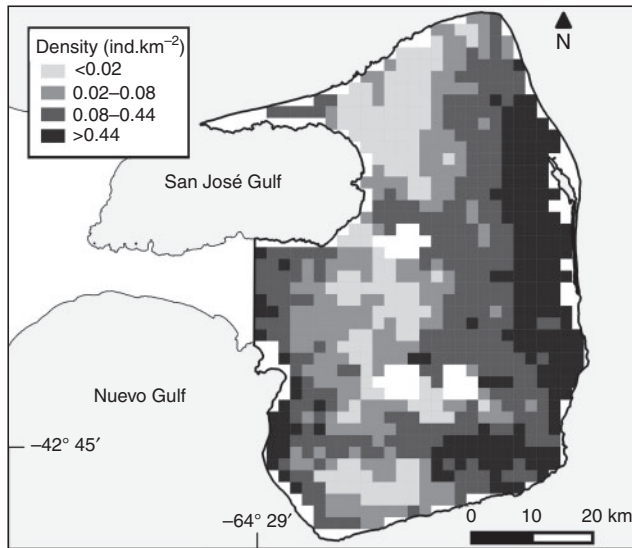
Fig. 3. Spatial variation in the abundance of lesser rhea. Abundance is expressed in terms of absolute density for each 4-km^2 cell, totaling a 3320-km^2 prediction area.
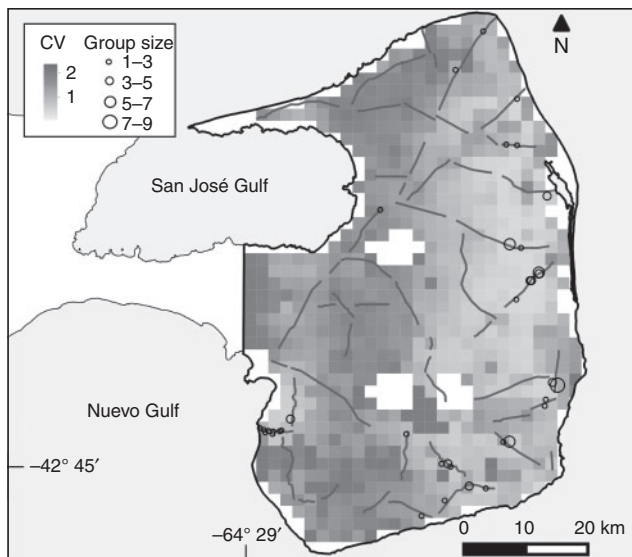

Fig. 4. Uncertainty associated with the predicted abundance of lesser rheas per cell, in terms of the coefficient of variation of the estimate. Circles represent observations of lesser rheas and lines the surveyed transects.

Fig. 5. Partial effects of the significant predictors on the abundance of lesser rheas according to the best fitting model. The grey shading represents 95% confidence intervals for the mean effect. The rug ticks at the bottom of the plot indicate the coverage of the range of values of each variable in the survey area. The number in parentheses in each 's' gives the effective degrees of freedom (a measure of flexibility) of each term.

Discussion

Our results provided the first assessment of the spatial variation in the abundance of *R. p. pennata* at a high resolution within a large area, using DSM techniques. The use of density surface models is recent, and has been applied to evaluate the spatial variation in the abundance of seabirds (Buckland *et al.* 2012; Winiarski *et al.* 2013, 2014), aquatic molluscs (Katsanevakis 2007; Katsanevakis and Thessalou-Legaki 2009) and marine and terrestrial mammals (Herr *et al.* 2009; Harihar *et al.* 2014; Schroeder *et al.* 2014). The combination of distance-sampling methods with spatial-modelling techniques allows us to estimate the abundance for either the whole study area or any subregion.

The overall density of lesser rheas estimated for the study area (0.44 birds km^{-2}, confidence interval: 95%CI 0.30–0.58) is higher than that obtained by Baldi *et al.* (2015; 0.28 birds km^{-2}, 95%CI: 0.23–0.33). However, comparisons should be careful as the previous study reported rhea density across different years (2006–15) and used conventional distance-sampling methodology. In terms of the average encounter rate obtained in the present study (0.11 groups of lesser rheas per kilometre travelled), our estimate falls within the range reported by other studies (Pedrana *et al.* 2011; Baldi *et al.* 2015) across different sites in the Argentine Patagonia (from 0.01 to 0.21 groups sighted per kilometre travelled), because the number of observations was very low after hundreds or thousands of kilometres surveyed. Both Pedrana *et al.* (2011) and Baldi *et al.* (2015) applied the same methodology, line-transect surveys by two observers standing in the back of a pick-up vehicle, across central and

being due to the low number of observations at NDVI values higher than 0.3 (Fig. 5*a*). Lesser rheas were more abundant as the distance from ranch buildings increased, although the effect was stronger beyond 2 km of distance, as the confidence interval was narrower, until ~6 km from the buildings (Fig. 5*b*). Abundance of lesser rheas tended to increase when stocking rates ranged from 30 to 50 sheep km^{-2}, otherwise it decreased (Fig. 5*c*). Longitude was related to the abundance of lesser rheas (Fig. 5*d*), because their numbers increased towards the coastal areas. We did not find spatial autocorrelation in the residuals (Fig. S8, available as Supplementary Material for this paper).
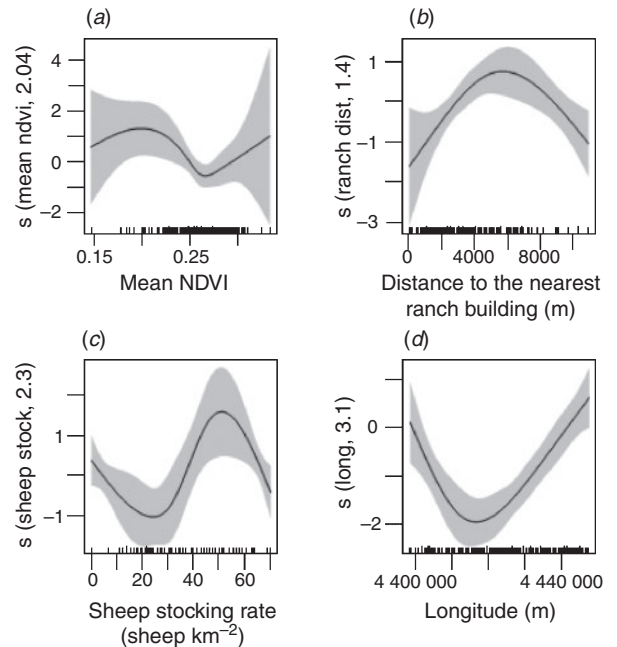
southern Patagonia. As stated above, the use of DSM allows for a detailed examination of the spatial variation in abundance, the variables accounting for that variation, and the uncertainty associated with the prediction of animal numbers per cell. As hypothesised, habitat quality, human presence and land management affected the abundance of lesser rheas in PV, although not all the associated predictors were significant. NDVI (a correlate of plant productivity), the location of ranch buildings, sheep stocking rate and the geographic longitude did all affect the abundance of birds. The responses of rhea abundance to the variation in the predictors were complex and non-linear. High NDVI values, being above the average for the whole PV, were associated with increased numbers of lesser rheas. Nevertheless, the assessment of the effects of covariates can be limited by extreme values and survey coverage, resulting in wider confidence intervals. The lowest NDVI values (<0.2, see Fig. 5*a*), were associated with dunes, which are uncommon across the area and, at the same time, difficult to access during the surveys, resulting in an increased uncertainty related to predictions at those cells. The location of ranch buildings, indicators of permanent human presence and possibly disturbance, had a strong effect on the abundance of lesser rheas. Although PV is a protected area, it is known that rural people kill lesser rheas for local consumption (Nabte 2010). A regional, distributional study on lesser rheas by Pedrana *et al.* (2011) conducted in Santa Cruz province found that birds were more likely to occur at high NDVI values. In the same large-scale survey, lesser rheas were less likely to be found close to populated places, such as towns or oil camps where human presence is permanent (Pedrana *et al.* 2011).

In terms of management, we found that the number of lesser rheas was positively associated with high, above-average sheep stocking rates (30–45 sheep km^{-2}, average 25 sheep km^{-2}; see Fig. 5*c*), whereas neither the size of the paddocks nor the distance to the nearest fence had significant effects. Previous studies have shown that sheep stocking rates in PV are higher across the grass-dominated steppes (Nabte *et al.* 2013). Although numbers of lesser rhea are low and we cannot rule out competitive interactions with the sheep, it is likely that the apparent coexistence between both species resulted from a low dietary overlap as reported by Bonino *et al.* (1986) and Somlo (1997). In addition, several studies have found that lesser rheas prefer open, grass-dominated habitats combining the availability of food and good visibility to detect predators (Bellis *et al.* 2004; Pedrana *et al.* 2011; Baldi *et al.* 2015). Thus, sheep stocking rates could work as a 'proxy' variable of the habitat type preferred by lesser rheas. However, the positive relationship between the abundance of lesser rhea and livestock density were not evident in other studies. For example, Rivas *et al.* (2015) found that high sheep and goat stocking rates could be associated to a greater presence of herders and, therefore, an increased risk of hunting, resulting in lower rhea abundance in northern Patagonia. Likewise, the significance of the geographic longitude in the abundance of lesser rheas could be reflecting the spatial variation in the precipitation regime. Average annual rainfall in PV decreases from the eastern coast towards the central areas, and increases again towards the west, reaching the coast of the Nuevo Gulf (Barros and Rivero 1982; Beeskow *et al.* 1987).

As reported by previous studies across different sites, we found that the abundance of *R. p. pennata* in our study area was low. The low abundance has implications on their functional role in the arid ecosystems, because lesser rheas were considered 'ecologically extinct' preys, consumed occasionally by the native carnivores (Novaro *et al.* 2000). Indirect evidence suggests that lesser rheas were abundant at the end of the 19th century, as the indigenous people traded tons of feathers to Buenos Aires, through the Welsh colonists settled in Patagonia (Gavirati 2003; Baldi *et al.* 2015). However, the alleged population decrease (BirdLife International 2016), the lack of data on population trends, a wide distributional range and global population size of *R. pennata* resulted in the species being classified as 'Least Concern' according to the IUCN Red List criteria. At the same time, recommended conservation actions to prevent poaching and egg collection (BirdLife International 2016) require reliable information on abundance and distribution of lesser rheas, as well as the factors shaping the observed patterns.

We believe that the use of DSM techniques to analyse the spatial patterns of abundance of lesser rheas can be a useful tool for conservation planning. Spatial, high-resolution data combined with the knowledge on the factors affecting the number of animals are crucial to target specific conservation actions and monitor their results, and should allow government agencies to make better decisions concerning conservation-oriented management. We expect that the current research on DSM, combined with the use of new technologies to allow for more effective surveys, will make a significant contribution to the knowledge of wild-species distribution, abundance and population trends.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

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