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Primary productivity and anthropogenic disturbance as determinants of Upland Goose *Chloephaga picta* distribution in southern Patagonia

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A species distribution may be determined by its responses to patterns of human disturbance as well as by its habitat preferences. Here we investigate the distribution of the Upland Goose *Chloephaga picta*, which has been historically persecuted by farmers and ranchers in Patagonia because it feeds on crops and pastures and is assumed to compete with sheep for forage. We assess whether its current breeding distribution is shaped by persecution by ranchers or whether it can be better explained by differences in habitat primary productivity and preference for wetlands, or by other anthropogenic disturbances not associated with ranching. We built species distribution models to examine the relative effect of environmental and anthropogenic predictors on the regional distribution of Upland Goose. We performed vehicle surveys in the province of Santa Cruz, Argentina, in two years, surveying 8000 km of roads and recording 6492 Geese. Generalized additive models were used to model the presence/absence of Geese in 1-km cells. The models suggested that Upland Goose distribution is not currently affected by rancher control, as the species is more abundant in areas with high sheep stocking levels, but it is positively influenced by primary productivity and negatively influenced by urban areas. Anthropogenic disturbance caused by urban areas and oil extraction camps had a greater impact in limiting the species distribution than sheep ranching.

Keywords: human disturbance, large-scale habitat models, primary productivity, semi-arid steppe, species distribution models, wildlife–livestock conflicts.

Anthropogenic impacts are a major factor in determining bird distributions and population trends (Newton 2004, Coombes *et al.* 2008, Møller 2008). Disturbance can take many forms, for example direct impacts such as habitat alteration, hunting or persecution (Brawn *et al.* 2001, Thiollay 2006), and others of a more indirect nature, such as additive reactions to human recreational activities (Gill 2007, Kerbiriou *et al.* 2009). The current geographical ranges of many bird species may reflect not only their habitat preferences but also human disturbance (Caughley & Gunn 1996). In areas long inhabited by humans, the original bird communities may have been trimmed, and thereby reduced to a subset of relatively tolerant species (Blumstein 2006, Devictor *et al.* 2007). However, the early effects of human disturbance on sensitive birds could be best detected in protected or remote, recently or scarcely populated areas (Trainor 2007, Lees & Peres 2008).

There is empirical evidence that many birds avoid human disturbance and that their population sizes can be negatively affected, but little is known on the real magnitude of human disturbance at the scale of a species distribution. To estimate the effects of human disturbance it is necessary to model the expected distribution of the species based on habitat preference, quality and availability, and then estimate the effect of human

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disturbance on the distribution. This can be facilitated by species distribution models, which allow us to build statistical explanations of the regional distribution of species, considering independently or simultaneously environmental predictors. In this way we can take advantage of natural experiments created by the specific histories of human disturbance in different regions.

Geese are highly sensitive to human disturbance, even when this does not involve persecution or habitat transformation. For example, escape flights as a response to tourist presence may significantly increase the rate of nest predation (Madsen *et al.* 2009), and disturbance from traffic decreases feeding time in suitable pasturelands and results in habitat loss (Gill *et al.* 1996). Southern Patagonia is one of the most remote and least populated areas in the world. Relatively low-impact land uses, such as extensive livestocking, have been the dominant human activity in the region after colonization by Europeans 200 years ago. Natural habitats in the area (semi-desert, shrub-steppe and grass-steppe) appear to be only moderately transformed by human use. In this scenario geese in southern Patagonia seem to be suitable for the study of the early effects of human disturbance on the regional distribution of a species.

The Upland Goose *Chloephaga picta* is one of the five endemic sheldgoose species of South America (Martin 1984), and is the only one with a broad distribution. It is an herbivorous species and a potential competitor with livestock. Conflict with humans has so far been resolved with persecution in other areas dominated by cereal production (Summers & Grieve 1982, Martin 1984, Blanco *et al.* 2003, Blanco & De la Balze 2006, Petracci *et al.* 2009). Since 1931 it has been considered an agricultural pest in Argentina (Pergolani de Costa 1955). Although very few data exist on Upland Goose ecology, distribution and conservation status, hunting of the Upland Goose has been encouraged across its entire range, and has been allowed without restrictions on numbers, sex or age of birds killed (Martin *et al.* 1986, Blanco *et al.* 2002, Blanco & De la Balze 2006, Petracci *et al.* 2009).

As little is known on the breeding distribution of the Upland Goose, one of our aims was to produce a distribution map of the species for the province of Santa Cruz using species distribution models. This technique produces useful maps of a species distribution (e.g. Jeganathan *et al.* 2004 for the Jerdon's Courser *Rhinoptilus bitorquatus*, Gottschalk *et al.* 2007 for the Caucasian Black Grouse *Tetrao mlokosiewiczi*), even in areas where published distribution maps seem reliable, e.g. Europe (Bustamante & Seoane 2004). At the same time, we wanted to test the hypothesis that the distribution of Upland Goose in the semi-arid steppes of southern Patagonia could reflect a conflict with ranchers. Between 1970 and 2005, sheep husbandry has declined across southern Patagonia due to a combination of natural catastrophes and low prices of wool and meat (Oliva *et al.* 1995, González & Rial 2004). As a result, sheep ranching has been abandoned on many estates and, under the hypothesis that Upland Goose numbers were controlled by ranchers, reduced persecution could have allowed bird populations to increase. This hypothesis predicts that the abundance of Upland Goose will be higher in areas with low levels of sheep stocking, as observed in another large grazer, the Guanaco *Lama guanicoe*, a presumed competitor with sheep (Pedrana *et al.* 2010).

We also tested whether two alternative hypotheses could better account for the spatial distribution of the Upland Goose. One, which we term the productivity hypothesis, is that Upland Goose distribution primarily reflects the availability of relatively mesic environments, and predicts a higher probability of finding Upland Geese in more productive environments, close to wetlands and streams. The second, which we term the anthropogenic disturbance hypothesis, assumes that illegal hunting and frequent disturbance will be greater around centres of human activity, making these places less suitable for the species, and predicts a lower probability of Upland Goose occurrence closer to places where human population is greater. In Santa Cruz, such places are urban centres and oil extraction camps, the latter reflecting the main and most recent industrial activity in the province.

METHODS

Study area

The study was conducted in Santa Cruz Province (46–53°S, 65–73°W), with an extent of 245 865 km^2 (6.5% of Argentina; González & Rial 2004). The area is characterized by hills and plains dissected by small streams and rivers flowing from the Andes. Vegetation is highly uniform, apparently untransformed by human activity, and dominated by a mixed steppe of grass and shrubs, rarely exceeding 0.5 m in height (Movía *et al.* 1987, Rial 2001). Associated with streams, river valleys and endorheic depressions are ponds, lagoons and temporary flooded wet meadows, locally called *mallines*, with hydrophytic vegetation communities. The *Nothophagus* forests that occur in the Andean slopes were excluded from the study area because this habitat is not used by Upland Goose. The climate is dry and cold with strong westerly winds. There are marked climatic gradients, with precipitation decreasing from west to east, and temperature from northeast to southwest (González & Rial 2004). Since its colonization by Europeans, sheep ranching has been the only economic activity across most of the study area, followed in more recent times by local oil and gas extraction. Agriculture is of marginal importance and tends to occur only around urban areas. Average human population density is 0.8 inhabitants/km^2, concentrated in 11 urban areas with more than 2000 inhabitants (96.0% of the total population in Santa Cruz) and, to a lesser extent, in small villages and near oil extraction camps (1.4%). Human population density in the countryside is < 2 inhabitants/100 km^2 (INDEC 2001).

Study species

Upland Goose populations occur in southern Argentina and Chile. The continental subspecies C. *picta picta* seems to be migratory, whereas a sedentary subspecies C. *picta leucoptera* occurs in the Falkland Islands (Summers & Grieve 1982). From September to March, Upland Geese migrate to southern Patagonia (Argentina and Chile) where they breed and rear their chicks (nesting peaks in November), mainly in mesic habitats (ponds, bogs and wet meadows), while from April to August they winter in northern Patagonia (Rio Negro province) and southern Buenos Aires province, Argentina (Blanco & De la Balze 2006).

The Upland goose is herbivorous and feeds on natural pastures or cereal crops (Summers & Grieve 1982, Martin *et al.* 1986, Summers & McAdam 1993). It is a presumed competitor with sheep, yet the magnitude of damage to crops or pastures caused by grazing geese has been studied only in the Falkland Islands (Summers & McAdam 1993), where it has been suggested that livestocking benefits geese by controlling shrub regeneration and maintaining a high proportion of green pastures, whereas sheep benefit by eating goose faeces that have similar digestibility and nitrogen content to high-quality grass.

During the migratory season, and especially during winter, Upland Geese are killed in large numbers due to unregulated sport hunting and persecution by farmers (Blanco & De la Balze 2006, Petracci *et al.* 2009, 2010). Only as recently as 2008 the species was listed as vulnerable by the Argentine government and hunting was forbidden (Petracci *et al.* 2009, 2010).

Field surveys and sampling unit selection

We used road surveys from a vehicle to record the distribution of Upland Goose at the same time as other large species because of the open nature of the steppe environment, the low density of most target species and the large size of the region (which made other survey methods inefficient) (Travaini *et al.* 2007). Road surveys were conducted during two consecutive breeding seasons (November 2004 to February 2005, and December 2005 to January 2006). We first established which survey tracks (road segments) would be surveyed each year using stratified random sampling. We divided the study area into 12 regions, based on the combination of two environmental variables: mean Normalized Difference Vegetation Index (NDVI, as an index of green vegetation vigour and photosynthetic activity) and mean slope. We used NDVI because primary productivity could be an important driver of the distribution of fauna, and mean slope because terrain irregularity could affect detection during surveys and topography influences the presence of temporary wetlands. Further details about data sources and procedures are given by Travaini *et al.* (2007).

Using vector data of road coverage, we randomly selected road segments that summed to 4500 km of transects during the first year. To ensure that 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 ensured an unbiased distribution of survey effort between the two years, and almost 90% of public roads in the region were finally surveyed. Approximately 10%

of these roads are paved and on most roads traffic density is fewer than five vehicles per day. We checked that our survey method had sampled all vegetation communities in the area. Using the more detailed map available for the area (León *et al*. 1998) our survey covered all nine floristic regions in Santa Cruz and sampled a mean 3.4% of the surface of each region (range 2–5%).

Surveys were performed by two observers from a vehicle driven at a maximum speed of 40 km/h. When Geese were sighted we recorded flock size, sex composition and presence of goslings. Sightings were collected in a personal digital assistant (PDA) using the free software Cybertracker (http://www.cybertracker.co.za). The PDA was synchronized with a GPS unit (Garmin GPS MAP 76CS), which was used to record the precise location of the census track and sightings of Upland Goose flocks, as well as date, time and car speed. As official statistics on sheep distribution and numbers were not available we also recorded sheep sightings and modelled sheep occurrence as a function of environmental predictors (Pedrana 2010, see Supporting Information, Appendix S1, Fig. S1).

Environmental predictors

We selected nine potential predictors that summarized the most relevant environmental gradients and landscape features needed to test our three hypotheses on the factors influencing the regional distribution of Upland Goose. The set of predictors relevant to each hypothesis and their expected effects on Upland Geese distribution are summarized in Table 1.

We used the mean NDVI as a proxy of primary productivity. NDVI is the normalized ratio between the near-infrared and red surface

Table 1. Environmental predictor candidates for Upland Goose distribution models in relation to three different hypotheses.

Hypothesis	Predictor	Expected relationship with Upland Goose distribution	Predictor description
Rancher control	Sheep occurrence	Negative	Sheep stocking density estimated from a model of probability of contact with sheep (see Appendix S1 and Fig. S1)
Primary productivity	Mean_NDVI	Positive	Mean NDVI calculated using the VGT-S10 product, 10-day maximum composite values from the VEGETATION sensor on board of Spot-4 satellite (http://www.spot-vegetation.com) from April 1999 to March 2005
	Growth_period	Positive	Length of the vegetation growth period defined as the mean number of 10-day periods with NDVI values > 85
	Season_MAX	Occurrence in the breeding area at the month of maximum productivity	Month at which the NDVI reaches its annual maximum value
	CV_NDVI	Negative (for high Mean_NDVI)	Coefficient of variation of NDVI
	Distance_stream	Negative	Distance (km) to the nearest stream or river. Data obtained as a hydrographic vector coverage from the Instituto Geográfico Nacional de la República Argentina, http://www.sig.gov.ar
	Distance_wet meadow	Negative	Distance (km) to the nearest pond/bog/wet meadow obtained as a vector coverage from Mazzoni and Vázquez (2004)
Anthropogenic disturbance	Distance_urban	Positive	Distance (km) to the nearest urban area with ≥ 2000 inhabitants. Data obtained as a vector coverage of points from the Instituto Geográfico Nacional de la República Argentina, http://www.sig.gov.ar
	Distance_oil	Positive	Distance (km) to the nearest oil camp. Data obtained as a vector coverage of points from the Instituto Geográfico Nacional de la República Argentina, http://www.sig.gov.ar

NDVI, Normalized Difference Vegetation Index.

reflectance and its cumulative value is considered an adequate proxy of net primary productivity at regional and global scales (Gilabert *et al.* 1995, Ricotta *et al.* 1999). NDVI satellite images were acquired by the VEGETATION sensor on board SPOT-4 satellites (http://www.spot-vegetation.com), and data were provided as 10-day maximum value composites at 1-km spatial resolution. We calculated the mean NDVI, its coefficient of variation as a measure of variability in net primary productivity, the month at which the NDVI reached its annual maximum, and an estimate of the length of the vegetation growth season, using six consecutive years of satellite data (April 1999 to March 2005; Table 1). 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, to the nearest river or stream, and to the nearest wet meadow or *mallín* (taken from Mazzoni & Vázquez 2004) were calculated in a GIS. The probability of contact with sheep in a cell, a proxy of sheep stoking density, was taken from a predictive map built with data recorded during our surveys (supporting Appendix S1, Fig. S1, Pedrana 2010).

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 on grid cells and factors influencing detectability

Presence/absence modelling requires us to define a spatial unit in which presence or absence of the species is recorded. In this case we used the 1-km grid cells defined by the NDVI satellite data. We considered that a 300-m buffer on both sides of the track line defined the area that was effectively covered for Upland Goose by the observer (Blanco *et al.* 2003, J. Pedrana, J. Bustamante, A. Rodriguez and A. Travaini pers. obs.). We overlaid the surveyed tracks with a 300-m buffer on both sides on top of the 1-km grid, and selected all grid cells that partially or totally overlapped with the 300-m buffer. Upland Goose sightings (n = 683) were represented on selected cells. Grid cells with one or more Upland Goose sightings were considered presences and the remaining cells were considered absences.

The probability of detecting at least one goose in a 1-km cell is affected by the proportion of the cell that is covered by the survey. We calculated the variable AC300 as the fraction of the 1-km cell surface included in the 300-m buffer on both sides of the census transect. This variable was included as a fixed term in the models using a spline with three degrees of freedom to correct for its effect on the detection probability of Upland Geese (Travaini *et al.* 2007). This solution was preferred to using an offset in the model as this allows us to model a non-linear relationship with AC300. This, in practice, is equivalent to empirically fitting a detection curve. Although the survey protocol was standardized, there are unavoidable survey factors that affect fauna detectability that are rarely considered in species distribution modelling. For example, we tried to survey at a constant speed of 40 km/h, but speed recorded by the GPS indicated that within a cell mean vehicle speed was variable depending on road condition, weather and number of contacts with fauna. The longer it takes to go through a cell the higher the probability of a contact. For this reason we assessed whether vehicle speed (Speed), time of day (Time_day) or day of year (Date, starting 1 September) had any influence on Upland Goose detectability. Time of day could have an influence due to changes in goose activity and because of the influence of light levels on detectability. Date could have an effect if not all geese had arrived at the beginning or had started migration before the end of our surveys. Predictive models were refitted correcting for survey factors that had a significant influence, showing that models were robust to the most important survey biases.

Model fitting

We fitted generalized additive models (Hastie & Tibshirani 1990) using as response variable the presence/absence of Upland Goose in a 1-km cell with binomial errors and a logit link. As the number of cells with presence (n = 413) was low compared with the number of cells with absence (n = 13 299), we decided to use a resampling scheme to obtain a balanced sample (McPherson *et al.* 2004, Liu *et al.* 2005), randomly selecting 413 out of the 13 299 cells with absence. We reserved a random sample of 20% of cells with presence and 20% of cells with absence for model cross-validation and used the remaining 80% for model fitting. This procedure was repeated 100 times. In each repetition the cells with presence were the same (but a new cross-validation sample with replacement was obtained) while cells with absence were sampled without replacement. Predictors for the models were selected from the initial set by a backward–forward stepwise procedure starting from a full model that included all potential predictors relevant to a particular hypothesis. We used the step.gam routine in S-PLUS 2000 (Mathsoft 1999) to fit the models. Predictors were initially included in the models as smoothing splines with three degrees of freedom. The Akaike Information Criterion (AIC) was used to retain a term (Sakamoto *et al.* 1986). From the 100 models built with the resampling procedure for each hypothesis, we selected those that ranked as the best model ≥ 10 times. We then repeated this resampling procedure with each of the selected models, in which the predictors were fixed, but the degrees of freedom of the splines were allowed progressively to be reduced from three to one. Again we retained the models that were selected ≥ 10 times. Finally, we used the unique matrix with the complete dataset in which original prevalence was maintained (Jiménez-Valverde & Lobo 2006) to compare the alternative models within each hypothesis that were as good as the best model in terms of AIC (Burnham & Anderson 2002). We considered as competing models those for which the differences between AIC and the AIC of the best candidate model (the one with the smallest AIC) was $\Delta_i \leq 4$ (Burnham & Anderson 2002). For those models we also calculated the AIC weight w_i (the relative model likelihood), which assesses how much the model is supported by the data, relative to the set of competing models.

The same procedure was used to build a final model starting with all relevant variables retained in the best models for each hypothesis. The final model tested simultaneously the relative predictive power of all environmental factors. All the models for each hypothesis and the final model were refitted correcting for any significant effect of survey factors.

Model validation

Each time a dataset was generated, 80% of the data was used to build a model and the remaining 20% was reserved to validate it. The area-under-the-curve (AUC) of the receiver operating characteristic 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 (when model discrimination is not better than random) to 1 (perfect discriminatory ability, Pearce & 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 mean predictive ability of the final model was tested with a Mann–Whitney *U*-test (Crawley 2002).

Distribution of Upland Goose in Santa Cruz

We used the final model corrected with survey factors to build a predictive map of current Upland Goose distribution in Santa Cruz province, Argentina. 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 to make predictions on the new data matrix, and then exported the predicted values at the scale of the response from S-Plus back to IDRISI to produce a probability map. The estimated probability of contact with Upland Geese was categorized into three classes to ease interpretation of the distribution.

RESULTS

Along 8000 km of road transect we recorded 683 sightings with Upland Geese (6492 individuals in total). All contacts were groups of two or more birds.

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 Upland Geese in a 1-km cell showed a significantly non-linear increase with the proportion of the cell that was included in the 300-m buffer (Table 2, Fig. 1). Among survey-specific variables, the probability of detecting Upland Geese decreased with car speed and survey date, and had a maximum around midday (Model 1 in Table 2, Fig. 1a).

Table 2. Competing generalized additive models obtained by stepwise selection for each hypothesis on the variables influencing Upland Goose occurrence in the semi-arid steppes of Santa Cruz province, southern Patagonia. There is a model on the effect of survey-specific variables and a general model in which all hypotheses are considered simultaneously.

Code	Model	AIC	Δ_i	w_i
Survey-specific variables				
1	**AC300$_3$** + Speed + Date + *Time_day$_3$*	2713	0	0.88
2	**AC300$_3$** + Speed + Date	2717	4.01	0.12
Rancher control hypothesis				
3	**AC300$_3$** + **Livestock$_3$**	2753	0	0.88
4	**AC300$_3$** + **Livestock**	2757	3.99	0.12
Primary productivity hypothesis				
5	**AC300$_3$** + **Mean_NDVI$_3$** + Distance_wet meadow$_3$ + Distance_stream$_3$	2266	0	0.74
6	**AC300$_3$** + **Mean_NDVI$_2$** + Distance_wet meadow$_3$ + Distance_stream$_3$ + **CV_NDVI**	2269	3.00	0.16
7	**AC300$_3$** + **Mean_NDVI$_3$** + Distance_wet meadow$_3$ + Distance_stream$_3$ + **CV_NDVI**	2270	4.00	0.10
Anthropogenic disturbance hypothesis				
8	**AC300$_3$** + Distance_urban$_3$ + *Distance_oil$_3$*	2722	0	0.67
9	**AC300$_3$** + Distance_urban$_2$ + *Distance_oil$_3$*	2724	2.28	0.33
General models				
10	**AC300$_3$** + **Mean_NDVI** + **Distance_urban** + Distance_wet meadow$_3$ + Distance_stream$_3$ + **CV_NDVI**	2233	0	0.55
11	**AC300$_3$** + **Mean_NDVI$_2$** + **Distance_urban** + Distance_wet meadow$_3$ + Distance_stream$_3$ + **CV_NDVI**	2234	1.01	0.45

For each model, the Akaike Information Criterion (AIC), the difference between AIC of the current model and the most-parsimonious model (Δ_i), and the Akaike weights (w_i) are given. Predictors with a positive effect are marked in bold, and those with a clear maximum in italics. Numerical subscripts denote the degrees of freedom of the smoothing spline.

Contrary to the prediction of the rancher control hypothesis, we found a positive relationship between Upland Goose presence and the probability of sheep presence (Model 3 in Table 2, Fig. 1b).

The most-parsimonious model of Upland Goose presence among those testing the productivity hypothesis contained three variables: Mean_NDVI, Distance_wet meadow and Distance_stream (Model 5 in Table 2). As predicted by this hypothesis, the probability of Upland Goose presence increased with mean NDVI, whereas it decreased with distance to the nearest wet meadow and stream (Table 2, Fig. 1c).

The variables Distance_oil and Distance_urban were retained in the best model among those testing the anthropogenic disturbance hypothesis (Model 8 in Table 2). However, contrary to the prediction of this hypothesis, the probability of Upland Goose presence did not vary with the distance to the nearest city within the first 100 km, and decreased beyond this distance (Fig. 1d). The probability of Upland Goose occurrence increased slightly with distance to the nearest oil camp. This effect was observed within 100 km of oil camps, and was reversed beyond this distance, producing a bell-shaped relationship (Models 8 and 9 in Table 2, Fig. 1d). This initially suggests some large-scale spatial pattern in Upland Goose distribution that correlates with distance to urban areas and distance to oil camp, but gives limited support to the anthropogenic disturbance hypothesis.

When predictors for all hypotheses were considered simultaneously in a model of Upland Goose presence, the final model included Mean_NDVI, Distance_urban, Distance_wet meadow, Distance_stream and CV_NDVI (Models 10 and 11, Table 2). In this case, the two competing models supported both the primary productivity and the anthropogenic disturbance hypothesis, as Upland Goose presence increased with mean NDVI and with distance to urban area and declined with distance to wet meadow and distance to stream (Table 2).

All models of Upland Goose presence were significantly improved by the consideration of survey-specific variables but the environmental predictors included did not change (Table 3). The final general model included Mean_NDVI, Distance_urban, Distance_wet meadow, Distance_stream and CV_NDVI, and two survey correction factors, vehicle speed and date (Model 20 in Table 3, Fig. 2). This final model also supported both the

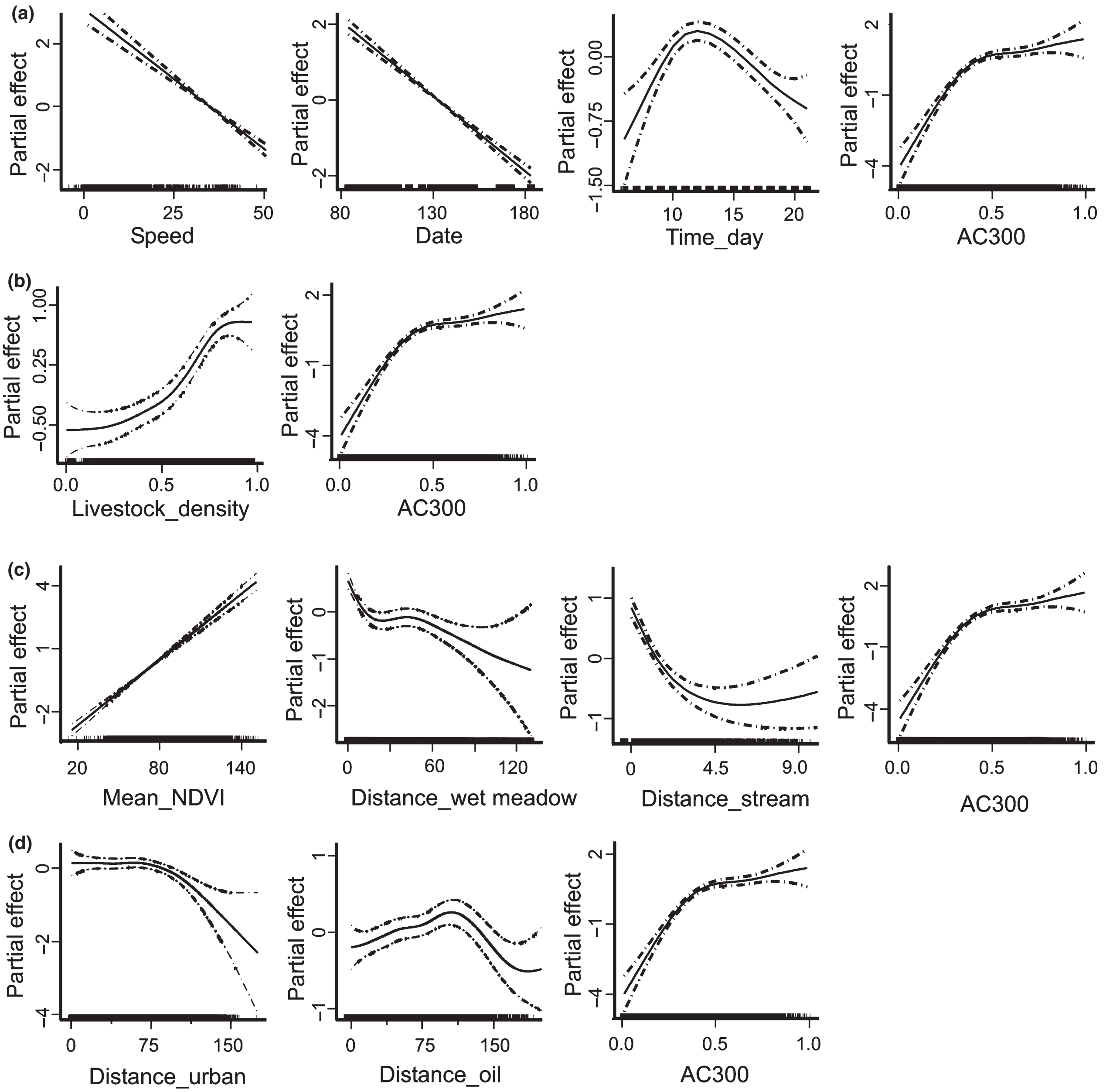

Figure 1. Partial effects of the predictors included in the most-parsimonious model for each alternative hypothesis about the variables influencing Upland Goose presence: (a) survey-specific variables (Model 1 in Table 2), (b) rancher control hypothesis (Model 3 in Table 2), (c) primary productivity hypothesis (Model 5 in Table 2) and (d) anthropogenic disturbance hypothesis (Model 8 in Table 2). Dashed lines represent 95% confidence intervals for the mean effect.

primary productivity and the anthropogenic disturbance hypotheses.

Model validation

We built 100 habitat models significantly different from null models according to AIC and exhibiting fair discrimination ability (AUC ≥ 0.8) for every set of predictors. The predictive models for Upland Goose fitted the data very well, with mean AUC ranging from 0.89 ± 0.02 to 0.94 ± 0.01 (Table 4), which suggests that they were robust and could have been considered potentially useful to predict the distribution of this species (Elith 2000, Harrell 2001).

Table 3. Competing generalized additive models obtained by stepwise selection for each hypothesis on the variables influencing Upland Goose occurrence in the semi-arid steppes of Santa Cruz province, southern Patagonia, including the correction for survey-specific variables. General models are those in which all hypotheses are considered simultaneously.

	Model	AIC	Δ_i	w_i
Rancher control hypothesis				
12	**AC300$_3$** + **Livestock$_3$** + Speed + Date + *Time_day$_3$*	2658	0	0.88
13	**AC300$_3$** + **Livestock** + Speed + Date + *Time_day$_3$*	2662	3.99	0.12
Primary productivity hypothesis				
14	**AC300$_3$** + **Mean_NDVI$_3$** + Distance_wet meadow$_3$ + Distance_stream$_3$ + Speed + Date + *Time_day$_3$*	2165	0	0.77
15	**AC300$_3$** + **Mean_NDVI$_2$** + Distance_wet meadow$_3$ + Distance_stream$_3$ + Speed + Date + *Time_day$_3$*	2169	3.71	0.12
16	**AC300$_3$** + **Mean_NDVI$_2$** + Distance_wet meadow$_3$ + Distance_stream$_3$ + **CV_NDVI** + Speed + Date + *Time_day$_3$*	2169	4.00	0.10
Anthropogenic disturbance hypothesis				
17	**AC300$_3$** + Distance_urban$_3$ + *Distance_oil$_3$* + Speed + Date + *Time_day$_3$*	2662	0	0.48
18	**AC300$_3$** + Distance_urban$_2$ + *Distance_oil$_3$* + Speed + Date + *Time_day$_3$*	2662	0.13	0.45
19	**AC300$_3$** + Distance_urban + *Distance_oil$_3$* + Speed + Date + *Time_day$_3$*	2666	3.95	0.07
General models				
20	**AC300$_3$** + **Mean_NDVI** + **Distance_urban** + Distance_wet meadow$_3$ + Distance_stream$_3$ + **CV_NDVI** + Speed + Date	2122	0	0.58
21	**AC300$_3$** + **Mean_NDVI$_2$** + **Distance_urban** + Distance_wet meadow$_3$ + Distance_stream$_3$ + **CV_NDVI** + Speed + Date	2123	1.01	0.42

For each model the Akaike Information Criterion (AIC), the difference between AIC of the focal model and the AIC of the most-parsimonious model (Δ_i), and the Akaike weights (w_i) are given. Predictors with a positive effect are marked in bold, and those with a clear maximum in italics. Numerical subscripts refer to the degrees of freedom of the smoothing spline.

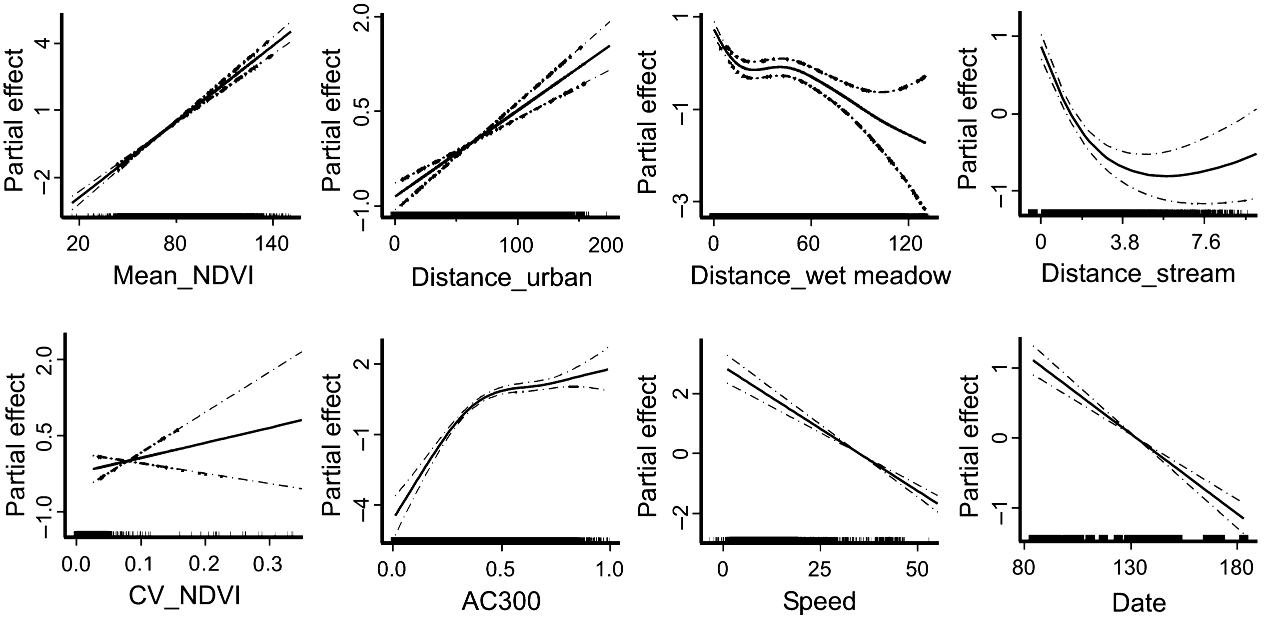

Figure 2. Partial effects of predictors included in the best general model of Upland Goose presence corrected for survey-specific variables (Model 20 in Table 3). Dashed lines represent 95% confidence intervals for the mean effect. The relationships with livestock density and distance to urban areas have the opposite sign to that predicted by the respective hypotheses (see text for details).

Among general models, Model 20 (Table 3) had the highest predictive ability, and this was significantly higher than the predictive ability of final models representing a single hypothesis, either the productivity hypothesis ($z = 5.22$, $P < 0.001$) or the anthropogenic disturbance hypothesis ($z = 11.59$, $P < 0.001$). This suggests that both primary productivity and anthropogenic disturbance

Table 4. Cross-validated predictive power of the most-parsimonious model representing each of the alternative hypotheses about the factors influencing Upland Goose distribution. Mean area-under-the-curve (AUC) values were computed for 100 replicate parameterizations of the models. All 100 replicates had AUC ≥ 0.7. Estimates were not made for the ranching control hypothesis because it was not supported by the data.

	AUC (± se)
Primary productivity hypothesis	0.92 ± 0.01
Anthropogenic disturbance hypothesis	0.89 ± 0.02
General model	0.94 ± 0.02

should be taken into account when modelling Upland Goose regional distribution.

Predictive cartography of Upland Goose distribution

We generated a predictive map of Upland Goose distribution taking into account all the effects contained in the best general model (Model 20 in Table 3), estimated for a complete cell, and assuming that road surveys were performed on 11 January at a speed of 35 km/h. To facilitate interpretation, the relative probability of occurrence was simplified into three classes (Fig. 3).

This map shows that, although Upland Geese have been sighted everywhere in Santa Cruz, the species is not uniformly distributed. The probability of Upland Goose presence increases toward the south of Santa Cruz province, although there are small areas of high probability of occurrence, associated with watercourses and wetlands, scattered across the centre and north of the region.

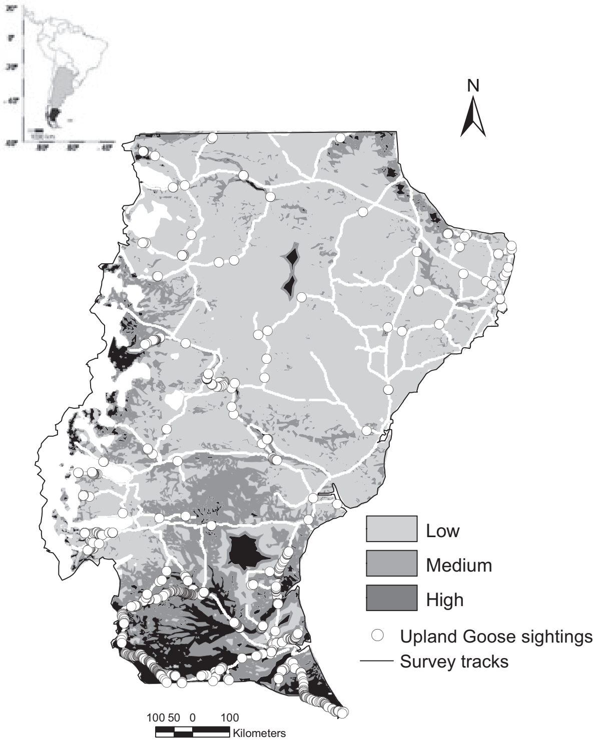

Figure 3. Upland Goose distribution in Santa Cruz province, Argentina. Values represent the probability of Upland Goose contact in a 1-km cell predicted by Model 20 (Table 3) and are categorized into three classes (low: < 0.33, medium: 0.33–0.66, high: > 0.66). Areas in white correspond to regions without predictions: sea, lakes, forested areas, or outside the model's environmental space. Survey track locations are indicated by lines and Upland Goose sightings are indicated by circles.

DISCUSSION

Species distribution models of the Upland Goose in Patagonia suggest that: (1) primary productivity is the main driver of the Upland Goose distribution in the arid steppes of Santa Cruz; (2) mesic habitats such as streams, rivers and wet meadows are preferred habitats, and allow Upland Geese to occupy otherwise unproductive steppes; (3) competition with sheep and direct persecution by ranchers has no noticeable effect on Upland Geese distribution; and (4) urban areas and probably also oil camps may have a negative impact on Upland Goose distribution, or at least they appear to be more disturbed in these areas. There are two other technical conclusions that should not be disregarded: (5) models based on a single set of predictors (such as the anthropogenic disturbance hypothesis) can easily lead to erroneous conclusions and (6) survey-specific corrections (e.g. speed, date, time) are usually needed for robust species distribution modelling.

The hypothesis that the distribution of Upland Goose in Santa Cruz was mainly driven by persecution by sheep ranchers was not supported by our results, as Upland Geese were more abundant in the areas with higher sheep stocking densities.

There was clear support for one of the alternative hypotheses that indicates that the regional distribution of the Upland Goose is mainly driven by primary productivity in the Patagonian steppe. The species is more abundant in the more productive sites, as estimated by the mean NDVI, which are also the sites currently keeping higher sheep stock densities. Although the Upland Goose is probably one of the *Chloephaga* species that is less dependent upon wetlands, being present in dry pastures and arable land for most of the year (del Hoyo *et al.* 1992), our models show that its abundance increases close to wet meadows and streams or rivers. Although these habitats have high NDVI values, the Upland Goose distribution is probably also influenced by small wet meadows and temporary streams that have little impact on the 1-km mean NDVI. The association of Upland Goose with wetlands and streams reported in other studies (Summers & Grieve 1982, Martin *et al.* 1986) may reflect the distribution of relatively productive sites rather than a strict dependence upon water. Productive mesic habitats such as *mallines* and streams seem to be of special value for this species in the semi-arid habitats of the Patagonian steppe because they provide more abundant forage and perhaps also a higher quality substrate to build their nests (Martin *et al.* 1986, Summers & McAdam 1993).

Although the local effects of disturbance by hunting (Madsen 1995, Tamisier *et al.* 2003), recreational activities (Mallord *et al.* 2007, Cardoni *et al.* 2008), roads (Fahrig & Rytwinski 2009) and other human activities are well established, the anthropogenic disturbance hypothesis alone was not able to explain the regional distribution of the Upland Goose. The model built for the anthropogenic disturbance hypothesis, considering the spatial distribution of urban areas and oil camps in Santa Cruz, may reflect other spatial gradients in the region. For example, urban areas are not randomly distributed in the region and tend to be associated with river valleys where water and the more productive habitats preferred by Upland Goose are present. However, anthropogenic disturbance had a clear negative effect when the Upland Goose distribution was corrected for productivity and habitat preference, showing a negative relationship between Upland Goose presence and proximity to urban areas. This makes clear the importance of considering all potential predictors simultaneously in species distribution modelling (Burton 2007). Sometimes, the effect of particular factors on the distribution of a species can be masked by others with stronger effects. The relationship with oil camps was similar to that of urban areas but weaker and did not enter the final models. As all our surveys were from roads, we cannot reject the possibility that the Upland Goose avoids proximity to roads in areas where they are more frequently disturbed, for example close to urban areas and oil camps. If this was the case, urban areas or oil camps would have a minor influence on regional Upland Goose distribution.

Our study shows that even when effort is made to standardize the survey protocol there are unavoidable survey factors influencing the results. We show that these factors can be controlled statistically and care should be taken to check that conclusions are robust and do not change when correction factors are included in the models.

Contrary to expectation, our models show that sheep ranching had no negative effect on Upland Goose distribution. The distribution map generated by the final model indicates that areas with a high probability of Upland Goose occurrence are concentrated in the southern sector of Santa Cruz province, an area with above average rainfall where productive pastures abound (González and Rial 2004) that are mainly devoted to extensive sheep ranching with high stocking densities. Indeed, Martin *et al.* (1986) reported that Upland Goose prefers to share space with livestock, which keep the grass short and create open spaces for grasses to grow. This suggests that direct competition between sheep and Upland Geese (both feed on the same grasses; Summers & Grieve 1982) and direct persecution by ranchers may be compensated for by the higher habitat quality and productivity of these areas. Other geese species have also been found to benefit from mammalian grazers that keep grass short, favour sprouting, promote plant diversity and supply nitrogen (Vickery *et al.* 1994, Prop *et al.* 1998, van der Wal *et al.* 2000). Human population density in the countryside in Santa Cruz is very low (two individuals per 100 km^2), and the possibility of efficient geese control by ranchers is unlikely. But this cannot be generalized to all large herbivores in the area as direct or indirect competition with sheep may influence the distribution of other large grazers such as Guanacos (Pedrana *et al.* 2010).

The repercussions of bird behavioural avoidance of humans at the population level often remain unknown. Our results illustrate the early effects of human disturbance on birds in remote regions with very low human density. They support the results of other studies in which surrogates of human disturbance were negatively correlated with bird occupancy in sparsely populated areas (Osborne *et al.* 2001, Le Cuziat *et al.* 2005, Urquiza-Haas *et al.* 2009). Our analysis also provides the first approximation to the factors influencing the breeding distribution of the Upland Goose in Santa Cruz province, Argentina. Our species distribution model generates a map that can be a useful tool for governmental agencies to establish conservation management priorities for the species. This map constitutes a significant improvement to previous published knowledge on the distribution of the species (del Hoyo *et al.* 1992, De la Peña & Rumboll 1998, Narosky & Yzurieta 2003) that assumes a uniform breeding distribution across Patagonia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Distribution of sheep stocking levels in Santa Cruz (Argentina).

Appendix S1. Model of current sheep stocking levels in Santa Cruz (Argentina) using contact with sheep in road surveys.