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BIODIVERSITY RESEARCH

Where do Swainson's hawks winter? Satellite images used to identify potential habitat

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ABSTRACT

During recent years, predictive modelling techniques have been increasingly used to identify regional patterns of species spatial occurrence, to explore species–habitat relationships and to aid in biodiversity conservation. In the case of birds, predictive modelling has been mainly applied to the study of species with little variable inter-annual patterns of spatial occurrence (e.g. year-round resident species or migratory species in their breeding grounds showing territorial behaviour). We used predictive models to analyse the factors that determine broad-scale patterns of occurrence and abundance of wintering Swainson's hawks (*Buteo swainsoni*). This species has been the focus of field monitoring in its wintering ground in Argentina due to massive pesticide poisoning of thousands of individuals during the 1990s, but its unpredictable pattern of spatial distribution and the uncertainty about the current wintering area occupied by hawks led to discontinuing such field monitoring. Data on the presence and abundance of hawks were recorded in 30 × 30 km squares ($n = 115$) surveyed during three austral summers (2001–03). Sixteen land-use/land-cover, topography, and Normalized Difference Vegetation Index (NDVI) variables were used as predictors to build generalized additive models (GAMs). Both occurrence and abundance models showed a good predictive ability. Land use, altitude, and NDVI during spring previous to the arrival of hawks to wintering areas were good predictors of the distribution of Swainson's hawks in the Argentine pampas, but only land use and NDVI were entered into the model of abundance of the species in the region. The predictive cartography developed from the models allowed us to identify the current wintering area of Swainson's hawks in the Argentine pampas. The highest occurrence probability and relative abundances for the species were predicted for a broad area of south-eastern pampas that has been overlooked so far and where neither field research nor conservation efforts aiming to prevent massive mortalities has been established.

Keywords

***Buteo swainsoni*, conservation planning, long-distance migrant, predictive modelling, Swainson's hawk, wintering grounds.**

INTRODUCTION

Conservation of biodiversity requires basic information on species spatial distribution. However, gathering this data for migratory birds has posed a continuing challenge for wildlife biologists, especially when trying to delimit the geographical areas occupied by migratory birds during the non-breeding or 'wintering' season located in many cases thousands of kilometres away from their breeding areas. This is a task of special concern for species conservation because migratory bird populations are limited by their need of quality habitats in which to maintain high fecundity in summer in addition to high survival in winter (Sherry & Holmes, 1995; Newton, 2004). Population declines of many Neotropical migratory species are suspected to be related to habitat loss and fragmentation, affecting bird populations in their wintering grounds (Robbins *et al.*, 1989). Thus, reducing vague or fragmentary knowledge on the area occupied by migratory species during winter, particularly on the sites where the bulk of wintering populations are located, would help to focus conservation efforts in specific areas and to target conservation resources efficiently.

The Swainson's hawk, *Buteo swainsoni* Bonaparte 1838, is a Neotropical migratory species that has attracted conservation

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efforts in its wintering area in recent years. These efforts have involved cooperative work among researchers, NGOs, and government agencies from both extremes of the species distribution. This raptor breeds throughout western North America in grasslands, shrub-steppes, and agricultural areas and its breeding populations have been reported as declining in California (more than 90% decrease in during the last century), Oregon, and Nevada (England *et al.*, 1997). Until the 1990s, there was very little information on the wintering area used by Swainson's hawks in South America, and records of the Swainson's hawk's austral destinations were limited to scattered band recoveries and anecdotal field observations from the Argentine pampas (White *et al.*, 1989). During the 1995 and 1996 austral summers, more than 5000 hawks were found dead due to the ingestion of grasshoppers treated with the organophosphate pesticide monocrotophos (MCP) in a total of 19 mortality incidents in Argentina (Woodbridge *et al.*, 1995; Goldstein *et al.*, 1996, 1999a). The final estimation of the total number of hawks poisoned in this area was about 20,000 birds, approximately 5% of the world population (Goldstein *et al.*, 1996).

Following the mortality incidents, an international multidisciplinary project was initiated that aimed to understand and prevent Swainson's hawk mortalities in an area of 2250 km^2 in northern La Pampa province where MCP was excluded (Hooper *et al.*, 1999). Although new mortalities were not recorded in this area (Goldstein *et al.*, 1999b), this research provided some insights into Swainson's hawks habitat use and selection at a landscape level (Canavelli *et al.*, 2003). Nevertheless, new questions arose about the pattern of the species' distribution and the factors associated with hawk movements at a regional scale in its wintering grounds. During the 1997 austral summer, few hawks were sighted in the same area where mortalities occurred and where thousand of hawks wintered during the previous season (Canavelli, 2000). Proximate causes for this abrupt change in abundances of Swainson's hawks were linked to the occurrence of El Niño in 1997–98 that resulted in rainfall 2.5–4.0 times above mean records for the region (Canavelli, 2000). This may have affected the occurrence of grasshopper outbreaks, the staple prey in the diet of wintering hawks. Nowadays, however, the rainfall of the region has dropped back to its normal values but Swainson's hawks abundances in this area have not recovered to the levels observed in 1996 and before. Uncertainty about the current wintering area occupied by Swainson's hawks in the Argentine pampas has led to a discontinuation of the field monitoring and educational efforts focused on this species.

The aim of this study was to investigate the factors that determine the distribution and abundance of Swainson's hawks in the Argentine pampas. Due to the variable annual patterns of local abundance and the imprecise knowledge of the locations currently used by the bulk of wintering populations of Swainson's hawks in this area, we planned and conducted intensive, regional scale surveys that allowed us to model the factors that determine the occurrence and abundance of the species in this region. We built predictive maps that should become valuable for the implementation of a regional monitoring and conservation program aiming to minimize the negative impacts of agricultural practices on Swainson's hawks populations wintering in Argentina.

METHODS

Study area

Our study was carried out in the region thought to be the main wintering area for Swainson's hawks (England *et al.*, 1997; Fuller *et al.*, 1998) in the pampas of Argentina (Fig. 1). This region covers approximately 45 million ha encompassing *c.* 140 counties and four provinces (i.e. Buenos Aires, Santa Fe, Córdoba, and La Pampa). The climate of the region is oceanic and includes a wide range of types, from dry subhumid in the west to humid in the east (Soriano, 1992).

As with other lowland regions in the world, the Argentine pampas have been highly transformed by humans throughout the 20th century (Soriano, 1992; Viglizzo *et al.*, 1997). The regional change happened both in terms of the conversion of natural grasslands into arable lands and the gradual intensification of agriculture on land already cultivated (Viglizzo, 1994). Current land use is devoted to annual crops such as wheat, corn, sunflower, and soybean. However, in some areas, cattle and crop production activities are combined in different proportions in

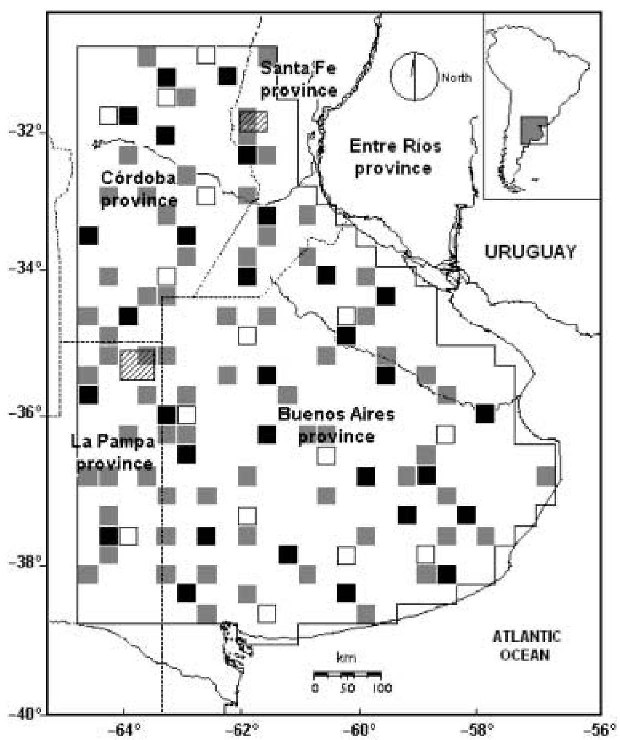


Figure 1 Study area (polygon delimited by a continuous line) and location of the surveyed squares (white, grey, and black squares were surveyed in 2001/02, 2002/03, and 2003/04, respectively) in the Argentine pampas. Dash-filled polygons in Santa Fe and La Pampa provinces represent the areas where field research and educational programs on Swainson's hawks and the correct use of pesticides have been previously conducted (Canavelli *et al.*, 2003).

response to environmental constraints (Viglizzo *et al*., 1997), resulting in the use of broad areas for the cultivation of perennial and annual pastures such as alfalfa and oats for direct grazing or hay production.

Swainson's hawk data

In the austral summers of 2001/02, 2002/03, and 2003/04, we drove more than 30,000 km of roads to determine regional distribution and abundance of Swainson's hawks in the Argentine pampas. Surveys were conducted during mid-December to mid-February each year, totalling 115 squares without repetition (15, 70, and 30 squares surveyed each of the three austral summer seasons in the study, respectively; Fig. 1). Square size (30 × 30 km in the Universal Transverse Mercator (UTM) grid) was defined on the basis of the seasonal, mean activity area for wintering hawks estimated by Canavelli (2000) in *c.* 1000 km^2. In order to avoid hawk migratory movements during field surveys that would bias presence/absence and abundance data recording, field surveys were carried out half-way through the wintering season of Swainson's hawks in Argentina (mid-November to mid-March; England *et al.* 1997). Surveyed squares were selected with a stratified random sampling from the total of 506 squares that comprised the study area. Aiming to obtain a homogeneous distribution of the squares to be surveyed through the study area, we first split the entire region into 10 zones with the single condition that each of them except one would comprise the same number of squares, upon which we then randomly selected the sampled squares.

We employed a mixed survey design (Canavelli *et al*., 2003) that included both road transects and point counts to record presence/absence and abundance of hawks in each square. We chose this methodology to maximize the probability of detection of hawks even at different times of the day or under different detection probabilities related to hawk daily activities (Sarasola & Negro, 2005). During surveys, 70 km were driven at low speed (approximately 40 km h^{-1}) in each square. Surveys in each square started with a point count of 15 min that was repeated every 10 km of road surveys, resulting in a total of seven transects 10 km long and eight point counts per square. The distance to be driven in the squares during road surveys was chosen and standardized for all sampled squares based on the typical availability of roads and tracks in good condition for a car.

Variables considered

To build models to predict the distribution and abundance of the species, we chose and tested 16 broad-scale variables as predictors of distribution and abundance of Swainson's hawks (Table 1): eight land-use/land-cover variables derived from the 2002 Agriculture National Census conducted by the Instituto Nacional de Estadísticas y Censos of Argentina (data available at http://www.indec.mecon.org), two topographical variables (altitude and slope) derived from a digital elevation model (DEM) obtained for the study area, and six variables derived from the Normalized Difference Vegetation Index (NDVI) obtained from the Vegetation sensor on board of the SPOT4 satellite.

Land-use/land-cover variables from the Agriculture National Census were at the resolution of county level. Because our data base on presence/absence and abundance of Swainson's hawks was in 30 × 30 km UTM squares, we first estimated land-cover/land-use data in each square. When the square was completely

Table 1 Predictive variables measured for each of the 30 × 30 km Universal Transverse Mercator (UTM) squares tested in the models of occurrence and abundance of Swainson's hawks in the Argentine Pampas.

Predictor	Description	Source
PSPR	Mean NDVI from September to November of the previous year (previous spring)	VEGETATION images
PSUM	Mean NDVI from December to February of the previous year (previous summer)	VEGETATION images
WINT	Mean NDVI from May to July of the previous year (previous winter)	VEGETATION images
SPRG	Mean NDVI from September to November for the same year of field census (spring)	VEGETATION images
SUMM	Mean NDVI from December to February for the same year of field census (summer)	VEGETATION images
NDVI	Mean NDVI for the period 1998–2003	VEGETATION images
ALT	Mean altitude (m)	Digital elevation model
SLO	Mean slope (SD of the altitude measures contained in each 30 × 30 km square)	Digital elevation model
CEREAL	Percentage of cereal crops (mainly wheat; also rye and barley)	INDEC*
OLEA	Percentage of oleaginous crops (mainly soy bean; also sunflower and corn)	INDEC
GRASS	Percentage of natural grasslands (remains of native grasslands)	INDEC
PPAS	Percentage of perennial pastures (pastures based in alfalfa made 80% of this category; plots with this type of pastures are implanted for a 3- to 5-year period and rotated to crops).	INDEC
APAS	Percentage of annual pastures (e.g. oat, sorghum; implanted for direct grazing or hay production during summer or winter)	INDEC
FOR	Percentage of natural forests (remains of forest areas of native tree species mainly located in ecotone areas surrounding the pampas region).	INDEC
GROV	Percentage of implanted forest (groves of exotic trees, mainly *Eucalyptus*)	INDEC

*INDEC, Instituto Nacional de Estadísticas y Censos de Argentina; NDVI, Normalized Difference Vegetation Index.

included in a single county, then the percentage of each land-use type for the county was assigned to the square. When more than one county was represented in the surveyed square we calculated the percentage of each land-use type for the square as the product between the percentage of land-use type assigned to the county and the proportion in which that county was represented in the square.

Topographical variables were estimated from a digital elevation model (DEM) obtained for the study area from digital cartography provided by the Shuttle Radar Topography Mission (SRTM) of the National Imagery and Mapping Agency (NIMA) and the National Aeronautics and Space Administration (NASA) (see http://seamless.usgs.gov for further details). This mission produced digital cartography with 3-arc-second spatial resolution (*c.* 90 m) with images covering 1×1 geographical degree area. Using these, we composed a single image for our study area and extracted values with a spatial resolution of 1 km (pixel size) using Idrisi32 Release 2 (Eastman, 2001). The topographical variables chosen were the mean altitude and terrain ruggedness for each 30×30 km square ($n = 900$, 1 km pixels), the later measured as the standard deviation of the altitude for the pixels in the sample.

The NDVI was included in the models as a surrogate of rainfall at the regional-scale analysis. NDVI is an index describing 'greenness' of land cover and derived from the red and infrared reflectance recorded by multispectral sensors onboard of resource mapping satellites. One of the main features of this index is the linear relationship that it exhibits when compared with total energy intercepted by vegetation canopy (Monteith, 1981), making NDVI a valuable tool in studies of ecosystems functioning by using it as a surrogate of ecosystem carbon uptake (e.g. Myneni *et al.*, 1997; Jobbágy *et al.*, 2002). However, a regional analysis of NDVI responses to climatic and land-use changes in the Argentine pampas has also shown that most of the 80% of the spatial variability of NDVI measured over this area is accounted by precipitation (Guerschman *et al.*, 2003). This direct and positive relationship between NDVI and precipitation, added to NDVI coarse spatial resolution (1 km), makes NDVI a reliable measure of precipitation and adequate for monitoring the spatial variability of this climate variable in the Argentine pampas. We derived NDVI values from the Vegetation (VGT) sensor onboard the SPOT-4 satellite which allows a daily monitoring of terrestrial vegetation cover. The VGT products (provided by http://free.vgt.vito.be) are 10-day syntheses with 1.15 km of spatial resolution at nadir. All the images of this period were compared pixel by pixel to pick out the 'best' ground reflectance values. Three 10-day syntheses are made during a month: synthesis from the 1st to the 10th day of the month, synthesis from the 11th to the 20th day of the month, and synthesis from the 21st day to the end of the month.

The images were imported to Idrisi32 Release 2 (Eastman, 2001) and corrected for pixels without information (e.g. clouds or water bodies). We estimated the mean NDVI value in five periods: (1) previous spring: September to November on the year before the field survey; (2) previous summer: December to February on the year before the field survey; (3) previous winter: June to August previous to the field survey; (4) current spring: September to November on the year of the field survey; and (5) current summer: December to February on the year of the field survey. By splitting NDVI data into delimited time periods we aimed to take into account seasonality effects that would affect prey populations throughout their life cycle, specially during the time when grasshoppers laid their eggs (late summer and fall), the eggs' diapause period (winter), and the time in which eggs hatch (spring) (Preston-Mafham, 1990). A final image, containing the mean NDVI for the period 1998–2003 with all seasons and years pooled together, was also obtained and included in the set of explanatory variables as a global measure of NDVI, irrespective of seasonal effects.

Statistical analysis

We built generalized additive models (Hastie & Tibshirani, 1990) of occurrence and abundance of Swainson's hawks in 30×30 km squares. To model the occurrence of Swainson's hawks, the response variable was presence/absence of hawks in the squares and we used a binomial error and a logistic link. We started with a model containing all the predictive variables introduced as smooth terms (a smoothing spline with 3 d.f.) and made a backward–forward stepwise search of the best subset model using the step.gam directive of S-PLUS 2000 (MathSoft, 1999). The step.gam is an automatic procedure that searches for the best model in terms of Akaike's Information Criterion (AIC, the lower the AIC, the better the model), which takes into account both the information explained by the model and its complexity in terms of number of estimated parameters (Sakamoto *et al.*, 1986). We then used the methodology proposed by Burnham & Anderson (2002) to compare models that were as good as the best model in terms of AIC after setp.gam. We considered as competing models those with AIC values less than four points compared with the model with the lowest AIC. For this set of models, we first calculated the second-order AIC (AICc), which is similar to AIC but corrected for small sample size, the ΔAICc (the differences in AICc with respect to the AICc of the best candidate model), and AICc weight (the relative model likelihood). This last measure was examined to look for the support of data towards the best model selected after applying the step.gam procedure.

Spatial autocorrelation, i.e. spatial dependence of observations in which values of a variable in neighbouring locations are more similar or less similar than expected for locations randomly distributed, can be a statistical problem when modelling species–habitat relationships (Legendre, 1993). Ignoring this effect may lead to overestimation of the importance of covariates in the models and include in them variables that have little relevance in the response variable. We examined the extent of spatial correlation both for the response variable and for the residuals of the model by using the Moran's index (I) (Legendre & Legendre, 1998). This index is in the range from 1 (maximum positive spatial autocorrelation) to –1 (maximum negative spatial autocorrelation) with values of I being approximately equal to zero when data arrangement is random. Moran's I statistics were computed for a lag distance of 30 km using the program ROOKCASE (Sawada, 1999), while *P*-values for the calculated index were obtained after performing 999 Monte Carlo permutations of the original data.

To model abundance we considered only those squares where Swainson's hawks were recorded during surveys ($n = 62$). Abundance models were fitted using a Poisson error and an identity link. For modelling purposes, we use the total number of point counts and 10-km road transects in the square in which Swainson's hawks were observed (maximum value = 15) as a proxy of relative abundance of hawks in each square. By using this index instead of the absolute number of observed birds, we minimized the biases associated with double counting and the gregariousness of the hawk (the point/transect was considered as having hawks independently of the number of birds/groups observed). Swainson's hawks are highly gregarious during winter, and group size, affecting detection probability, relates to activities such as foraging and roosting, that are in turn affected by the time of the day (Sarasola & Negro, 2005) or weather conditions. Our abundance index minimized such effect and at the same time partially reflected absolute abundances since this index correlated significantly with the total number of hawks in the squares ($r_s = 0.69$, $t = 7.35$, $P < 0.0001$).

Model validation and discrimination ability

We used a data splitting or five-fold cross-validation strategy for model validation. The original data set was divided into five groups drawn at random from across the data set and representing all the geographical range of the study area. Each group ($n = 23$) was dropped in turn and the remaining four constituted the training set, used to fit the model. Then predictions were made for the group that had been dropped (20% of data squares, the test set). The procedure was repeated for the five groups, dropping different groups each time. Then data were reshuffled and the procedure repeated 10 times. This technique is more robust than the similar jackknifing or leave-one-out assessment because it produces a higher perturbation of the model by dropping a group of observations instead of a single observation and gives a better reflection of model performance on the new data (Fielding & Bell, 1997). We did not re-select the best model at each fold of the cross-validation. This may result in a slight overestimation of out-of-sample predictive performance as the model was selected in part using the data with which it is being tested.

To assess the discrimination ability of the cross-validated occurrence model, we used Cohen's kappa statistics (Titus *et al.*, 1984) and the area under the curve (AUC) of receiver-operating characteristic (ROC) plots (Pearce & Ferrier, 2000). The Cohen's kappa is commonly used to estimate correct classification rates adjusted by chance and requires a user-defined probability threshold above which to consider the species as present. We chose the threshold to be the mid-point between the mean estimated probability for presences and the mean estimated probability for absences (Fielding & Haworth, 1995). The final value of kappa statistic was obtained by averaging values for each of the folds of the cross-validation procedure. The AUC measures the proportion of all possible pair of squares, one with presence and other with absence of hawks, in which the square with presence has a higher probability of presence than the square with absence. This procedure is considered as more adequate than Cohen's kappa to evaluate the discrimination capacity of the models since it does not require the arbitrary choice of a decision threshold and it is independent of species prevalence (Pearce & Ferrier, 2000). We used the percentage of explained deviance (i.e. null deviance minus residual deviance, divided by null deviance, multiplied by 100) as a measure of the amount of variation in occurrence and abundance explained by the model but the Spearman correlation (r_s) to analyse the agreement between observed abundances and those predicted by the single-best model (Seoane *et al.*, 2003).

RESULTS

A total of 14,463 Swainson's hawks were recorded in 62 (54%) of the surveyed squares. As expected from the gregarious habits of these hawks, most of the records (70%) were of individuals grouped in flocks (> 5 individuals), but with a highly variable flock size with a mean (± standard deviation – SD) of 343 (± 921) hawks per flock. The mean number of hawks per occupied square and the mean number of hawks per transect/point count were also variable with mean (± SD) values of 233 (± 772) and 72.6 (± 340) individuals, respectively.

Occurrence model

The occurrence model containing land-cover/land-use, topographical and NDVI variables was highly significant ($P < 0.0001$) and included six of 16 variables of the original set (Table 1). This selected model was more than two times better supported than the following model according to its AIC weight value (0.34 vs. 0.15 for first and second ranked models, respectively). In addition, seven of the subset of nine competing models included those six explanatory variables retained in the best candidate model, accounting all these models together for about 90% of the AIC weight (Table 2). Moran's index was not significant, neither for the response variable ($I = 0.27$, $P = 0.11$) nor for the model residuals ($I = -0.13$, $P = 0.29$) after Monte Carlo permutations, indicating little evidence of spatial autocorrelation in our data set.

Swainson's hawk probability of occurrence had a positive relationship with the percentage of perennial pastures (PPAS, Fig. 2) and cereal crops (CROP). For cereal crops, however, such a relationship is observed only for values beyond 20% (Fig. 2). Altitude showed an optimum-like relationship for the probability of occurrence of hawks, so that maximum probabilities are obtained for altitudes around 200 m a.s.l. (Fig. 2). The model showed a decrease in the probability of occurrence when increasing the percentage of land devoted to annual pastures (APAS) and oleaginous crops (OLEA). Occurrence probability was also high for low values of mean NDVI during spring (SPRG), i.e. the time in which hawks arrived to the wintering grounds, decreasing at intermediate values before showing a slight increase at maximum NDVI values (Fig. 2).

Because model data came from surveys conducted during three different years, we tested whether there were significant differences among years in the occurrence of Swainson's hawks.

Table 2 Competing models for Swainson's hawk distribution in the Argentine pampas. For each model, the corrected Akaike's Information Criterion (AICc), the difference on AICc between the current model and the best model (Δ AICc), and the Akaike weights (*w*) are given. Variables in those models that included all the six variables retained in the best candidate model are in bold.

Model/Variables	AICc	Δ AICc	*w*
PPAS + ALT + CEREAL + APAS + SPRG + OLEA	124.85	0.00	0.34
PPAS + ALT + CEREAL + APAS + SPRG + OLEA + WINT + GRASS	126.56	1.71	0.15
PPAS + ALT + CEREAL + APAS + SPRG + OLEA + GRASS + NDVI	126.89	2.04	0.12
PPAS + ALT + CEREAL + APAS + SPRG + OLEA + SLO + GRASS	127.20	2.35	0.11
PPAS + ALT + CEREAL + APAS + SPRG + GRASS	127.21	2.36	0.11
PPAS + ALT + CEREAL + APAS + SPRG + OLEA + PSPR + GRASS	127.82	2.97	0.08
PPAS + ALT + CEREAL + APAS + OLEA + GRASS	127.28	2.43	0.10
PPAS + ALT + CEREAL + APAS + SPRG + OLEA + GRASS + SUMM	128.30	3.45	0.06
PPAS + ALT + CEREAL + APAS + SPRG + OLEA + GRASS + PSUM	129.03	4.18	0.04

Table 3 Competing models for Swainson's hawk abundance in the Argentine pampas. For each model, the corrected Akaike's Information Criterion (AICc), the difference on AICc between the current model and the best model (Δ AICc), and the Akaike weights (*w*) are given. Variables in those models that included all the seven variables retained in the best candidate model are in bold.

Model/Variables	AICc	Δ AICc	*w*
PSUM + SPRG + CEREAL + APAS + PPAS + GROV + GRASS	106.39	0.00	0.31
PSUM + SPRG + CEREAL + APAS + PPAS + GROV + GRASS + ALT	108.27	1.89	0.12
PSUM + SPRG + CEREAL + APAS + PPAS + GROV + GRASS + WINT	108.85	2.47	0.09
PSUM + CEREAL + APAS + PPAS + GROV + GRASS	108.89	2.50	0.09
PSUM + SPRG + CEREAL + APAS + PPAS + GROV + GRASS + NDVI	109.44	3.06	0.07
PSUM + SPRG + APAS + PPAS + GROV + GRASS	109.23	2.84	0.08
PSUM + SPRG + CEREAL + APAS + PPAS + GROV + SUMM + ALT	109.85	3.46	0.06
PSUM + SPRG + CEREAL + APAS + PPAS + GROV + ALT	109.80	3.41	0.06
PSUM + SPRG + APAS + PPAS + GROV + GRASS + ALT	110.18	3.79	0.05
PSUM + SPRG + CEREAL + APAS + PPAS + GROV + GRASS + SUMM + ALT	110.96	4.57	0.03
PSUM + SPRG + CEREAL + APAS + PPAS + GROV	110.12	3.74	0.05

We included year as a factorial term along with its interaction with the NDVI value for spring (the single year-to-year variable included in the model) and tested its significance using chi-square test. Neither year nor the interaction year*SPRG was significant ($P = 0.12$ and $P = 0.06$, respectively, with statistical power or 1-(β) equal to 0.40 and 0.38 for each of the hypothesis tested), indicating that pooling survey results through different seasons was adequate. The inclusion in the model of the NDVI for each of the springs in accordance with dates in which surveys were carried out was also tested against a more simple approach of considering for each of the squares a single, 3-year mean spring NDVI. The 3-year mean NDVI had a non-significant improvement of the model when included in the model containing SPRG ($P = 0.61$); however, SPRG had a significant improvement of the model when included in the model containing the 3-year mean NDVI ($P < 0.05$). This indicates that each year values of spring NDVI explain a major fraction of spatial variability in Swainson's hawk occurrence, and that is a better predictor than an interannual mean for this variable.

The environmental model had a good discrimination ability when considering both the AUC (0.84, i.e. some eight of 10 pairs of squares were correctly rated) and the correct classification rate ($r = 0.74$), which is almost 50% more than expected by chance as estimated by Cohen's kappa statistic (0.49, range = 0.10–0.81). Furthermore, the model explained a high percentage of the variability of the data (45.7% of deviance explained by the model).

Abundance model

The abundance model was highly significant ($P < 0.001$) and included seven of the 16 original environmental variables (Table 3). This final model was almost two and a half times better supported for the data than the closest competing model in terms of AIC weight (Table 3). The model had a good predictive ability for the abundance of Swainson's hawks ($r_s = 0.79$, $t = 10.0$, $P < 0.0001$) and it could explain about 54.6% of the variability of data. Moran's index was not significant, neither for the response variable ($I = -0.10$, $P = 0.40$) nor for the model residuals ($I = -0.30$, $P = 0.17$).

As in the case of the occurrence model, the mean NDVI for the spring (SPRG) and the percentage of land devoted to cereal crops

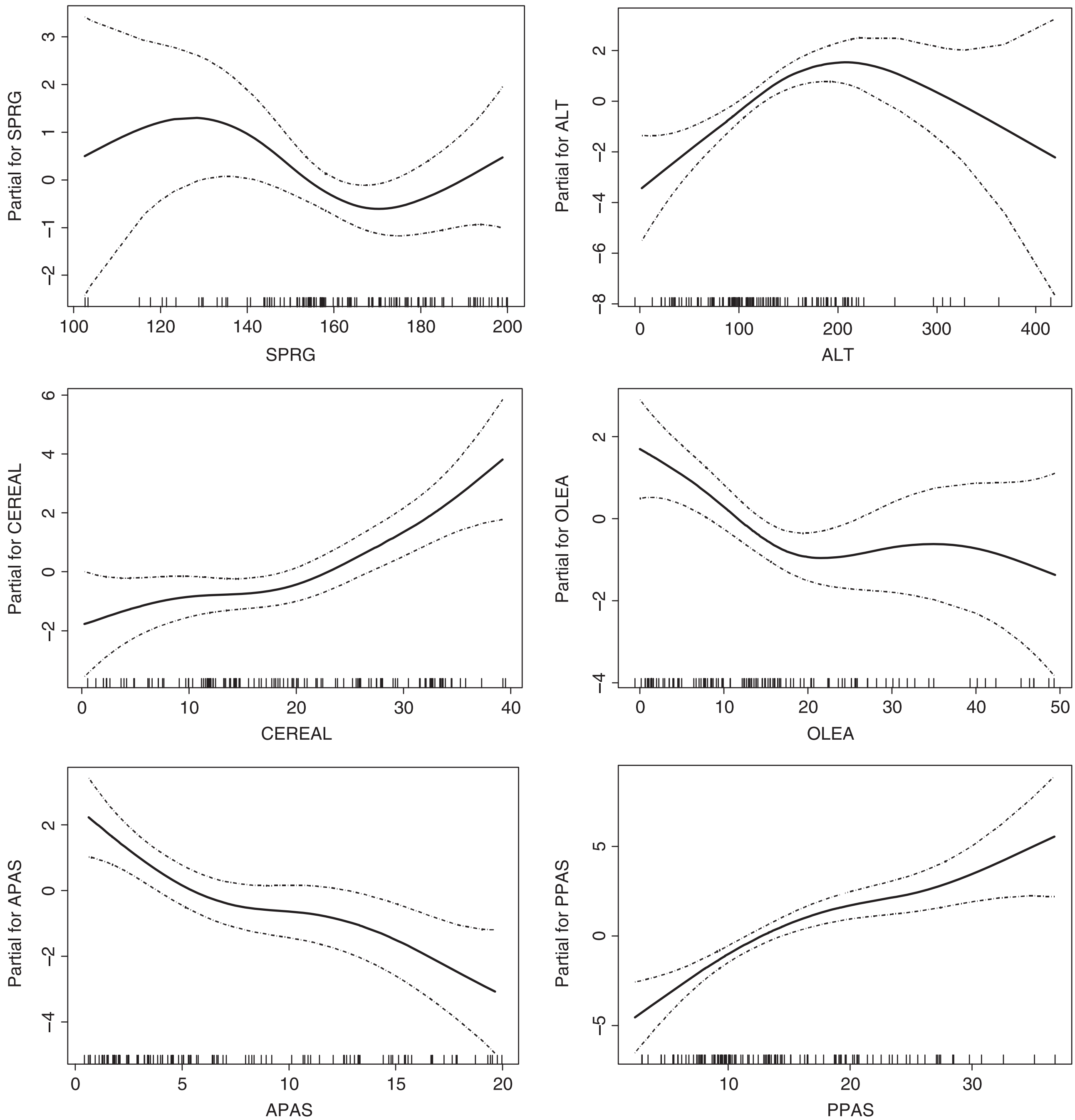
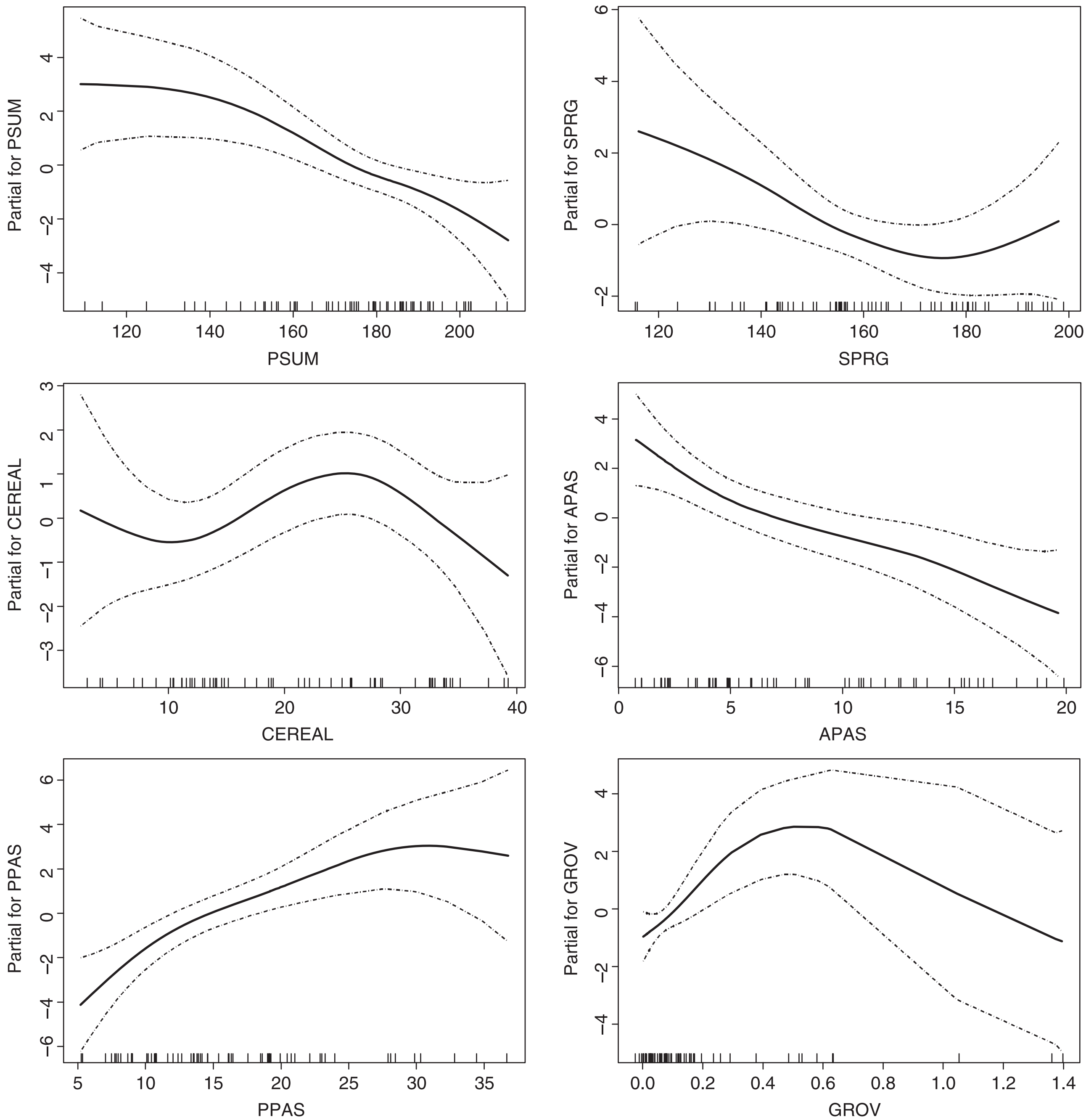


Figure 2 Partial effects of each environmental variable in the occurrence models for wintering Swainson's hawks. Dashed lines represent 95% confidence intervals and *Y*-axis is the logit of the probability of occupancy. SPRG – Normalized Difference Vegetation Index (NDVI) for current spring; ALT – altitude; CEREAL – percentage of land devoted to cereal crops; OLEA – percentage of land devoted to oleaginous crops; APAS – percentage of land devoted to annual pastures; and PPAS – percentage of land devoted to perennial pastures.

(CEREAL), annual pastures (APAS), and perennial pastures (PPAS) were retained in the final model for Swainson's hawk abundance. The remaining variables in the model were the mean NDVI for the summer previous to the arrival of hawks (PSUM), the percentage of land implanted with exotic trees (GROV), and the percentage of land with natural grasslands (GRASS).

Roughly speaking, the percentage of land devoted to annual and perennial pastures showed a similar relationship with the predicted abundance of hawks than the observed for occurrence probability in the occurrence model (i.e. positive and negative for PPAS and APAS, respectively, Fig. 3). The abundance of Swainson's hawks was inversely related to PSUM (mean NDVI for the previous summer) while Swainson's hawk predicted abundance was greatest in squares with 0.5–0.6% and 20–30% of the area implanted with groves of exotic trees and cereal crops, respectively (Fig. 3).



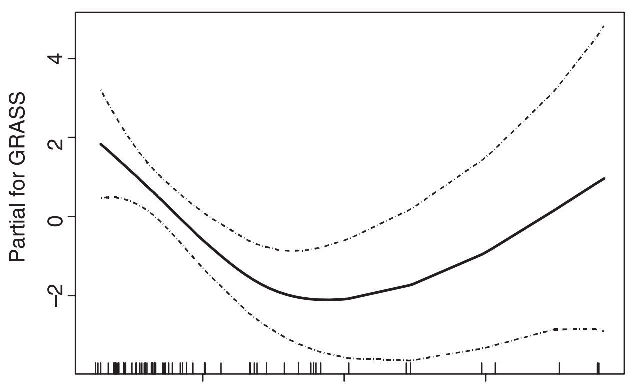


Figure 3 Partial effects of each environmental variable on the abundance model for wintering Swainson's hawks. Dashed lines represent 95% confidence intervals and *Y*-axis is the logit of the probability of occupancy. PSUM – Normalized Difference Vegetation Index (NDVI) for previous summer; SPRG – NDVI for current spring; CEREAL – percentage of land devoted to cereal crops; APAS – percentage of land devoted to annual pastures; PPAS – percentage of land devoted to perennial pastures; GROV – percentage of land implanted with groves of exotic tree species; GRASS – percentage of land with remaining natural grasslands.

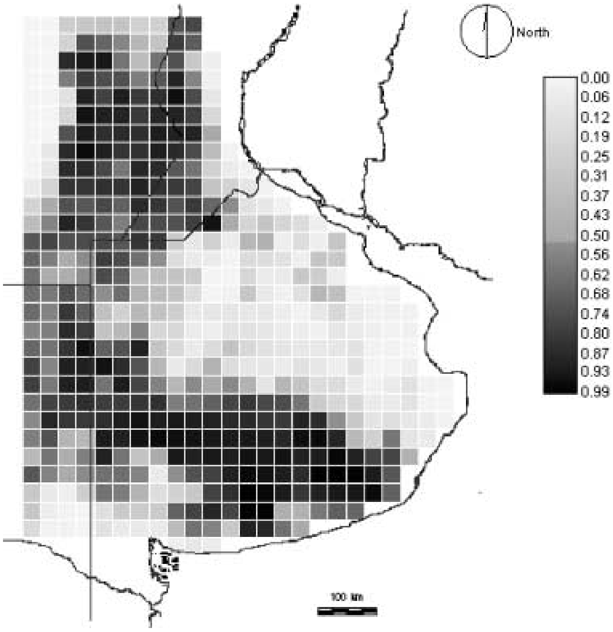


Figure 4 Predictive map for the occurrence of Swainson's hawks in the Argentine pampas. The final map was obtained after averaging occurrence probability for each square through 2001–03 austral summers. Presence of hawks is positively predicted using a threshold of $P > 0.52$.

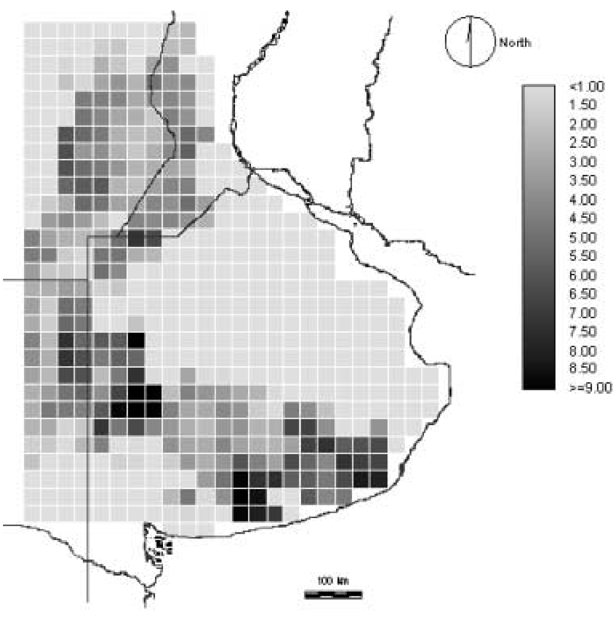


Figure 5 Predictive map for the mean relative abundance of Swainson's hawks for 2001–03 austral summers. The final map was obtained after averaging predicted abundances for each square through 2001–03 austral summers with abundance considered as the number of point count and transect lines in each square (maximum value = 15) in which hawks were recorded.

Predictive maps

According to the inclusion of temporal, yearly variable terms into the occurrence model (i.e. the mean NDVI for spring), we built three maps for the probability of occurrence of Swainson's hawks in the Argentine pampas that were averaged over the three seasons (Fig. 4). As shown by the distribution of squares with highest probabilities of occurrence, Swainson's hawk occurrence in the area resulted in a 'C' shaped distribution. As a result of mapping predicted abundances for the three seasons and the mean abundances of the predictions for the whole study period (Fig. 5), highest Swainson's hawk abundances were predicted for two areas in the Argentine pampas located in western and south-eastern Buenos Aires province.

DISCUSSION

Factors affecting Swainson's hawk distribution

Topography, land-use/land-cover variables, and climate for the period prior to the arrival of birds to wintering grounds predict the pattern of occurrence of Swainson's hawks in the Argentine pampas. Despite the general acceptance that the Argentine pampas is the main wintering area for Swainson's hawks, our occurrence model shows that this broad region is not all equally suitable for the species and about half of the territory is not predicted to be used by the hawks every year.

Altitude was the only topographical variable included in the occurrence model. Although the pampas is considered to be a flat region of uniform physiognomy and topography, several units are recognized according to geomorphology, drainage, soils, and vegetation. The major areas avoided by Swainson's hawks could be included in the 'rolling' and 'flooding' pampas (Soriano, 1992). The former comprises a distinct network of fluvial valley tributaries of the Río de la Plata and Río Parana while the flooding pampas comprise lowlands with interconnected natural ponds in the basin of the Río Salado also featured by their slight slope and recurrent flood episodes. In addition, Swainson's hawks did not occur in the northern pampas where the altitudes gradually increase westward due to the proximity of the hill systems in the Córdoba province. The ultimate cause for the low predicted occurrence of hawks in the lowland areas may be their soil features and humidity, which made them less suitable for the occurrence of grasshopper outbreaks (Schell & Lockwood, 1997).

The inclusion of perennial pastures and cereal crops in the final model was congruent with previous analyses of habitat use and selection of Swainson's hawks at a landscape scale (Canavelli *et al.*, 2003) and with the association of the most abundant grasshopper species to these land-use types (Torrusio *et al.*, 2002). Canavelli *et al.* (2003) found that in both their study areas in La Pampa and Santa Fe provinces, Swainson's hawks heavily selected for foraging pasturelands that are not rotated in an annual basis (perennial pastures that remain implanted during several years) over other land-use types. Furthermore, wheat fields in the Argentine pampas are linked to permanent pastures and cattle grazing, since wheat crops are mostly grown in a agriculture–pasture (annuals or perennials) rotation system (Verón *et al.*, 2004).

Variables derived from satellite imaginary and used as surrogate of climate variables had proved to be useful when trying to improve the predictive and discrimination ability of species distribution models (Suárez-Seoane *et al.*, 2004). In this case, Swainson's hawk occurrence probability was related to total rainfall previous to the wintering seasons as indicated by the inclusion of mean NDVI for spring in the final model. This variable showed an inverted-bell or 'U' shaped relationship with mean NDVI for spring, with maximum probabilities for lowest and highest values for this variable. Ultimate causes for this type of response of hawks to NDVI could be due to the interaction of NDVI with different land-use types such as observed by Guerschman *et al.* (2003) when comparing high- and low-impacted vegetation areas on an annual NDVI composite basis. Thus, rainfall levels during the months previous to the arrival of Swainson's hawks to their wintering areas could affect differentially the pattern of occurrence of this species throughout the Argentine pampas depending on the dominant vegetation type or crop in a given area.

Factors explaining Swainson's hawk abundance

The abundance model was as good as the occurrence model when considering the proportion of explained variability of the data. Land-use/land-cover variables and climate seem to be responsible for Swainson's hawk abundance in its wintering grounds. The abundance model agrees with the general pattern described by the occurrence model as denoted by the positive correlation between predicted values for each of them (i.e. squares with low and high abundances had lower and highest probability of occurrence, respectively) but also for the agreement in the type of land-use and climate variables that were finally included in both models. In addition to these variables, the abundance model considers also precipitation from the previous year as affecting negatively the abundance of hawks during the austral summer (i.e. moister summers will result in lower abundances of hawks in the following season). As expected, weather, and particularly precipitation, seems to play an important role in local Swainson's hawk abundance. Proximate causes for this link between weather conditions as long as 1 year before the arrival of the hawks to the wintering ground would be found in the life-cycle of grasshoppers in the region. In temperate areas such as Argentina, most grasshopper species emerging in any given year laid their eggs during the previous summer (Preston-Mafham, 1990). Thus, local insect abundance would be a consequence not only of current weather conditions but also of past weather that sustained large reproductive populations of grasshoppers at the time of egg laying.

The percentage of land planted with exotic trees was also included in the abundance model. These small areas implanted with exotic trees play a vital role in Swainson's hawk ecology during wintering, since these are the only structures used by Swainson's hawks to roost (Sarasola & Negro, 2006). However, and although included in the abundance model, this land-use type was not selected for the occurrence model, indicating that presence of groves would not be determining the selection of specific wintering areas by hawks but, on the other hand, that its availability would be modulating local abundances of wintering birds. Natural grassland was included in the abundance models, indicating that, despite the adaptive potential of Swainson's hawks to human-made environments, natural habitats remaining after a century of transformation of the Argentine pampas are also responsible for the current pattern of spatial abundance of Swainson's hawks in this region.

Considerations on conservation planning

Predictive modelling of species distribution has become a valuable tool for biodiversity conservation (e.g. Ortega-Huerta & Peterson, 2004; Rodríguez *et al.*, 2007). In addition, these methodological techniques have allowed a more adequate representation of large-scale species distribution for sustainable use (Travaini *et al.*, 2007) or conservation (Muñoz *et al.*, 2005). However, and even considering the advantages of this management and conservation tool, depiction maps resulting from a modelling process such as the one we have conducted here should be taken with caution and considered as 'working models' but not as 'truth'. That is especially certain for highly dynamic and changing landscapes such as the Argentine pampas (Viglizzo *et al.*, 1997), where active land-use changes would make necessary a periodic update of maps to track the possible changes in the occurrence and abundance patterns of Swainson's hawks.

Our predictive maps have shown a broad area in south-eastern Argentine pampas where Swainson's hawks winter at a relatively high abundance. This area was previously overlooked as a core area. Furthermore, the impact of insecticides on Swainson's hawk populations has never been assessed in this area, which also comprises the zones less variable in terms of hawk prevalence and mean relative abundance over the years and hence the most suitable for the establishment of a long-term field monitoring and ecotoxicological assessment of wintering hawk populations. Future field-monitoring and conservation actions therefore should be focused in these areas, taking into account information and educational programs on the correct use of agrochemical compounds by local landowners. Although the organophosphate pesticide identified as the responsible of massive mortalities of Swainson's hawks in the past (monocrotophos, MCP; Goldstein *et al.*, 1999a) was banned in Argentina in 1999 (Resolution no. 182/99 from SAGPYA/SENASA, Argentina), other highly toxic organophosphate compounds have replaced it (Goldstein *et al.*, 1999b; Hooper *et al.*, 1999). Furthermore, during 1996–97 one Swainson's hawk mortality incident (24 birds affected) was recorded in Cordoba province outside of the MCP exclusion zone delimited in northern La Pampa province, although samples were not adequate to determine the cause of mortality (Goldstein *et al.*, 1999b). Consequently, it is unclear if the absence of new cases of mortality being reported in the Argentine pampas is due to insecticide regulatory measures, the effectiveness and geographical extent of educational programs, or just to the less favourable weather conditions for pest outbreaks. An alternative and more refined approach should be to map the spatial extent of the use of agrochemical compounds in Argentine pampas, considering the type of product and its relative toxicity for wildlife. These maps should be then overlapped with occurrence and abundance maps obtained for Swainson's hawks to detect those hot-zones where the probability of occurrence of massive mortalities could be greater and where field monitoring should be intensified.

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