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Biome-scale signatures of land-use change on raptor abundance: insights from single-visit detection-based models

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Summary

1. Declines in raptor populations often result from the transformation of natural habitats to anthropogenic land uses, but the rate of population change can vary greatly among species. Declines associated with land transformation have been linked to loss of foraging habitat, prey resources and nest sites due to expanding cultivation, overgrazing and disturbance of nests and persecution by humans.

2. We combined extensive road-survey counts of raptors, large-scale GIS data sets and a single-visit conditional likelihood *N*-mixture model to generate biome-scale projections of abundance as a function of environmental covariates while correcting for detection error and other forms of zero inflation. This approach was employed to investigate how land-use transformations in the threatened Cerrado savannas and Pantanal wetlands in Brazil have affected the populations of raptors on a large scale ($>300\ 000\ \mathrm{km}^2$). We predicted that predominance of land uses with fewer or less accessible prey and scarcer nesting sites would sustain smaller raptor populations.

3. Twelve species were encountered sufficiently to estimate abundance, while 20 others were encountered too infrequently to permit abundance estimation. Detection of all 12 species was influenced by time of day, with variable species-specific effects that followed expectations based on foraging and flight behaviour.

4. Abundance of most species was negatively influenced by conversion of natural habitats to pastures, an effect that held even for generalist species considered poor indicators of habitat quality, but was not universally impacted by urbanization and soya beans, sugarcane and Eucalyptus plantations, confirming the expectation that some species may tolerate these habitats. Spatial projections of abundance appeared realistic for most species.

5. *Synthesis and applications*. Protection of the remaining natural habitats is essential to prevent further decline of raptor populations in the Brazilian Cerrado and Pantanal, and restoration of unproductive pastures into natural habitat could prove an efficient strategy to recover diminished raptor populations. The conditional likelihood single-visit approach is a valid and useful tool for measuring population size and for making detection-corrected inferences of abundance over large geographical scales with sensible research budgets. Incorporating the approach into a multispecies framework would allow future studies to make important inferences for entire communities.

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[Correction note: Equation 4 was published with the incorrected Greek letter, $u_i \sim \mathrm{Gamma}(\mathrm{mean} = 1, \mathrm{var} = \lambda)$ instead of $u_i \sim \mathrm{Gamma}(\mathrm{mean} = 1, \mathrm{var} = \gamma)$ during first publication on 18 November this was corrected on 2 December].

Key-words: abundance, Cerrado, conditional likelihood, count data, detection error, land use, mixture models, Pantanal, raptors, single-visit methods

Introduction

Expansion of agricultural frontiers and increasing urbanization are among the main forces driving the degradation of natural habitats around the world (Margules & Pressey 2000). In South America, the Cerrado and Pantanal biomes are greatly threatened by rapid and widespread conversion to farming and ranching (Silva & Bates 2002; Harris *et al.* 2005). Although they constitute important areas for the region's biodiversity, protected areas are few (Myers *et al.* 2000; Silva & Bates 2002; Harris *et al.* 2005). In these human-dominated landscapes, the long-term persistence of many native species is highly dependent on land-use practices and a species' ability to tolerate them (Rodríguez-Estrella *et al.* 1998; Benton, Vickery & Wilson 2003; Cardador, Carrete & Mañosa 2011).

A decline in raptor populations often occurs when natural habitats are transformed to anthropogenic land uses (Sergio *et al.* 2008). Raptors are good indicators of habitat change because they are long-lived top predators or scavengers, occur across a wide spectrum of habitat disturbances, and species differ in their use of resources and habitats (Newton 1979). Raptor population declines associated with land transformation have been linked to the loss of foraging habitat, prey resources, nest sites, overgrazing, disturbance of nests and persecution by humans (Buij *et al.* 2013). Yet, impacts of these environmental changes on population size differ among species (Rodríguez-Estrella *et al.* 1998; Buij *et al.* 2013). Consequently, regional surveys that document change in the abundance of multiple raptor species over time and space are important to draw inference on the environmental factors that influence abundance, and to determine species, areas and practices of importance for conservation policy and management (Sergio *et al.* 2008).

In large-scale surveys of unmarked populations, the assumptions and sampling requirements of commonly employed detection-based analytical approaches, such as distance sampling or *N*-mixture models (Buckland *et al.* 2001; Dénes, Silveira & Beissinger 2015), are often unmet because (i) the spatial distribution of individuals relative to the observer can be biased, such as when surveys are performed along roads, rivers or paths (Marques *et al.* 2010); (ii) accurate distance measurements are difficult to obtain for fast-moving individuals (e.g. birds in flight; Buckland, Marsden & Green 2008); and (iii) visiting a site on multiple days within a sampling season increases travel costs and personnel time, which reduces the number of sites that can be surveyed for a given budget and the scale of the study (Lele, Moreno & Bayne 2012). Roadside raptor surveys are especially problematic, as birds are commonly detected either perching near roads (Meunier & Verheyden 2000) or flying, and they often occur in low densities (Donázar *et al.* 2016). Sólymos, Lele & Bayne (2012) proposed an *N*-mixture model that estimates abundance and detection probability from single-visit (SV) count data using covariates of abundance and detection. The method requires a set of covariates that affect abundance and a set of covariates that affect detection probability, and that at least one continuous covariate is unique to each set. Estimates of abundance using the SV method can be biased under certain models for detection probability (Knape & Korner-Nievergelt 2015). However, if abundance and detection probability are functions of at least one of the continuous covariates in their sets, the conditions on which the estimates are unbiased are satisfied (see Sólymos & Lele 2016 for a full description of the mathematical assumptions). By eliminating the need for repeated survey visits, the SV *N*-mixture model may increase the opportunity for monitoring populations at large spatial scales.

We apply the SV model of Sólymos, Lele & Bayne (2012) to generate biome-scale projections of abundance and examine how land-use changes in the Cerrado and Pantanal biomes of Brazil affect raptor populations. Between 2011 and 2013, we conducted SV roadside counts of raptors during wet and dry seasons over a 300 000-km^2 area to estimate patterns of abundance that we relate to measures of habitat quality derived from 1:100 000 resolution GIS maps. The extent of our target study area meant that within-season temporal replicates were unaffordable, while the large proportion of individuals detected in flight and on roadside perches made use of distance sampling inadvisable (Fig. S1, Supporting Information). These circumstances provided us with an ideal opportunity for illustrating the need and practical utility of the SV abundance model (Sólymos, Lele & Bayne 2012). We hypothesized that sensitivity to land-use change would vary among raptor species according to their dietary preferences, foraging strategies and nesting requirements (Newton 1979; Buij *et al.* 2013; Table 1). Vertebrate-hunting raptors should be more vulnerable to decreased food and nest suitability that generally follows habitat degradation than insectivore species that may more easily tolerate land-use conversion as food (e.g. termites, grasshoppers) is often still available in pastures and croplands, and opportunistic scavengers that may benefit by exploiting alternate food sources supplied by humans (e.g. refuse). When food is available, compatibility between hunting strategy and the structure of new habitats should also influence abundance responses. Hunting from perches will be difficult in land uses that are cleared of such features, and catching ground-dwelling prey in tall and dense crops (e.g. sugarcane) may be impossible. We predicted

Table 1. Species analysed, their predominant diet and foraging strategy in the study area (Ferguson-Lees & Christie 2001), the number of individuals detected in each survey and average of individuals detected per survey sample unit in the Cerrado (1006 samples) and Pantanal (204 samples) biomes

			2011		2012		2013			Mean detections/ Sample unit	
Species	Predominant diet	Foraging strategy	February	July	February	July*	February*	July*	Total*	Cerrado*	Pantanal
Family Cathartidae											
Turkey Vulture *Cathartes aura*	Scavenger	Obligate	210	318	125	260	170	244	1327	0·75	2·08
Lesser yellow-headed Vulture *C. burrovianus*	Scavenger	Obligate	14	10	25	47	71	85	252	0·09	0·73
Black Vulture *Coragyps atratus*	Scavenger	Opportunist	393	233	449	862	750	518	3205	1·09	9·24
Family Accipitridae											
Black-Collared Hawk *Busarellus nigricolis*	Aquatic	Fisher	12	6	24	19	10	10	81	0	0·40
Great Black Hawk *Buteogallus urubitinga*	Reptiles	Ground forager	4	3	24	21	20	17	89	0	0·44
White-Tailed Hawk *Geranoaetus albicaudatus*	Small birds and mammals	Aerial hunter	11	21	24	25	38	21	140	0·10	0·06
Savanna Hawk *Buteogallus meridionalis*	Small vertebrates	Perch hunter	49	64	98	135	83	103	532	0·24	1·16
Snail Kite *Rosthramus sociabilis*	Snails	Perch hunter	29	41	83	58	2	37	250	0	1·23
Roadside Hawk *Rupornis magnirostris*	Small birds and mammals	Perch hunter	34	28	54	67	33	54	270	0·13	0·55
Family Falconidae											
Southern Caracara *Caracara plancus*	Scavenger	Opportunist	147	194	224	217	331	262	1375	0·76	2·25
Aplomado Falcon *Falco femoralis*	Small birds	Aerial hunter	4	6	7	26	39	13	95	0·07	0·02
American Kestrel *Falco sparverius*	Insects	Perch hunter	37	28	58	32	52	41	248	0·19	0·09

*Includes surveys in Emas National Park (see text).

(Table S1) that predominance of land uses with fewer or less accessible prey and scarcer nesting sites (pastures, sugarcane and eucalyptus plantations, urban) would sustain smaller populations than natural habitats and other land uses (secondary vegetation).

Materials and methods

FIELD SAMPLING

We surveyed diurnal raptors (Families Accipitridae and Falconidae, Tables 1 and S2) and New World vultures (Family Cathartidae, Tables 1 and S2). We delimited nine survey transects covering c. 1740 linear km within the Cerrado (c. 1400 km) and Pantanal (c. 340 km), maximizing coverage of habitat variation in the study area (Fig. S2). Routes included natural and anthropogenic habitats, but were limited to roads drivable throughout the year. This was challenging in the Pantanal, where paved roads are scarce and unpaved roads are frequently flooded or impassable during the rainy season. Roadside counts were conducted biannually during dry (July and August) and wet (January) seasons in 2011–2013 following the protocols widely adopted for surveying raptors (Fuller & Mosher 1981; Carrete *et al.* 2009). We assume that our SV biannual surveys are independent and primary period counts of populations that are not closed between surveys. In 2012, we extended field efforts to include c. 140 km of road counts in Emas National Park (transect 9, Fig. S2) surveyed in July 2012, February 2013 and July 2013. In addition to raptors, we counted vertebrate carcasses sighted on or near roads (mostly road kills, but also dead cattle in pastures).

STUDY AREA

Fieldwork covered areas in southern Cerrado and Pantanal biomes in the Brazilian states of Mato Grosso do Sul (MS) and Goiás (Fig. S2). The Cerrado has a seasonal climate with hot wet summers and warm dry winters, a dry period that extends for three to five consecutive months between May and September (Silva & Bates 2002), and is covered by semi-deciduous to evergreen savanna vegetation that grows on deep, well-drained and nutrient-poor soils. Evergreen gallery forests with dense and low understorey often border the rivers and streams of the region, and patches of semi-deciduous, deciduous and dry forests occur in areas of richer soil. The Cerrado, a biodiversity hotspot, has been reduced to about 30% of its original area by transformation to pastures and agriculture, and only 1·2–1·6% is protected (Myers *et al.* 2000; Silva *et al.* 2006). Agriculture in the region consists mainly of annual crops, such as soya bean, maize and cotton (often alternated on the same site throughout the year), sugarcane plantations and eucalyptus forests.

The Pantanal has hot, rainy summers (November–March) and warm, dry winters (April–October), with occasional cold spells (Harris *et al.* 2005). Seasonal flooding drives ecological processes and patterns, following an annual monomodal cycle with amplitudes of 2–5 m and durations of 3–6 months. The vegetation is very heterogeneous, with different habitats, soil types and inundation regimes, resulting in a variety of patchy landscapes. The predominant formations are grassland, savanna, marshes, semi-deciduous forest, gallery forest and floating mats. Habitat loss in the Pantanal is increasing; more than 40% of the forests and savanna habitats have already been altered for cattle ranching through the introduction of exotic grass species, and only 2·5% of the upper Paraguay River basin is formally protected (Harris *et al.* 2005).

GIS DATA PROCESSING

We used a 1:100 000 resolution vegetation cover and land-use GIS (polygon layer) map of the state of MS (Silva *et al.* 2011) to extract explanatory habitat variables for models. This map has 65 vegetation and land-use categories, which we simplified into 10 habitat types (Table 2). We removed areas in the south of the state that are within the Atlantic Forest domain, and summed the different subtypes of the most representative natural and anthropogenic formations. We also calculated the amount of closed vegetation in a 100-m buffer around the survey line (road) by summing the area of habitats that hinder visibility (e.g. forest, eucalyptus forest, and sugarcane plantations). As a proxy for flooding of the Pantanal, we obtained water surface elevation at the time of surveys for the Paraguay and Miranda rivers, the major drainages in the region (ANA, 2013).

Sample units were delimited by dividing survey transects into 10-km segments over which we created a buffer of 2·5 km width on each side of the survey line. This buffer area was chosen to reflect the carrying capacity of sample units based on habitat availability because raptors have large home ranges (Newton 1979). We overlaid the buffer on the vegetation map to calculate areal proportions of each habitat for each sample unit. Preliminary analysis showed that collinearity among habitats was negligible, and proportions did not change significantly with smaller or larger buffer widths (1–10 km). Our sample size, considering repeats among the six survey trips as independent observations, was 1210 units: 1006 in the Cerrado and 204 in the Pantanal. To extract habitat data for the wider study area, we created a grid with cells of area equal to that of the sample units (50 km^2) and calculated the proportion of each of the 10 habitat types in each grid cell. GIS analysis was conducted in ARCGIS v. 10.2 (ESRI 2013).

ABUNDANCE MODELS, COVARIATES AND MODEL SELECTION

Not all raptors within 2·5 km of roads were detectable so we employed a conditional likelihood *N*-mixture approach for analysing SV count data with zero inflation and detection error (Sólymos, Lele & Bayne 2012), using the package 'DETECT' (Sólymos, Moreno & Lele 2014) in R (R Development Core Team 2016). We can write the hierarchical structure of the binomial-ZIP model as follows, where eqns 1–3 represent, respectively, zero-inflation, count process and observation process levels (Sólymos, Lele & Bayne 2012):

$$A_i \sim \text{Bernoulli}(1-\phi) \qquad \text{eqn 1}$$

Table 2. Explanatory variables used in the analysis. All covariates are continuous numeric variables (centred and scaled to unit SD), except season and year factors and road kills/carcasses

Covariate	Abundance Type	Covariate	Detection Type
Cerrado savanna	Area (proportion in sample unit)	Time	Hours
Forest	Area (proportion in sample unit)	Time^2	Hours
Chaco dry savanna	Area (proportion in sample unit)	Closed vegetation	Area (km^2) in 100-m strip
Riverine vegetation	Area (proportion in sample unit)	Carcasses[†]	Count
Pasture	Area (proportion in sample unit)		
Annual agriculture	Area (proportion in sample unit)		
Secondary vegetation	Area (proportion in sample unit)		
Urban	Area (proportion in sample unit)		
Eucalyptus forest*	Area (proportion in sample unit)		
Sugarcane plantation*	Area (proportion in sample unit)		
River surface elevation	Height (cm)		
Season	Factor: wet, dry		
Season: Annual agriculture	Interaction term		
Year	2011–2013		

*Not present in the Pantanal.

[†] Used only for Turkey, Lesser Yellow-headed and Black Vultures and Southern Caracara models.

$$N_i|A_i \sim \text{Poisson}(A_i\lambda_i) \qquad \text{eqn 2}$$

$$Y_i|N_i \sim \text{Binomial}(N_i, p_i), \qquad \text{eqn 3}$$

where N_i is the population abundance at site i ($i = 1, 2, \ldots, n$ total sites); λ_i is the rate parameter of the Poisson distribution when the species is present at site i (i.e. mean abundance); A_i is a binary random variable indicating if a site was occupied at the time of sampling, ϕ is the zero-inflation probability parameter, where $\phi = 0$ corresponds to a Poisson model for the true state; Y_i is the observed count at site i; and p_i is the probability of detecting an individual given that $N_i > 0$. p_i and λ_i and can be modelled as a function of covariates with $\text{logit}(p_i) = \alpha_0 + \alpha_1 x_i$ and $\log(\lambda_i) = \beta_0 + \beta_1 z_i$. The model can be adapted to a binomial-ZINB structure by replacing eqn 2 with:

$$u_i \sim \text{Gamma}(\text{mean} = 1, \text{var} = \gamma) \qquad \text{eqn 4}$$

$$N_i|u_i, A_i \sim \text{Poisson}(A_i\, u_i\, \lambda_i), \qquad \text{eqn 5}$$

where eqn 4 represents the overdispersion level and γ is the overdispersion parameter, whereas $\log(u_i)$ can be seen as site-level random effect on the log abundance scale. See Appendix S2 for the description of the estimation procedure for the Binomial-ZINB *N*-mixture model that is implemented in R package 'DETECT'.

Response variables were the counts of each species in each sample unit (Figs S4–S6). We used zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) distributions for the state process – instead of their non-zero-inflated counterparts – to account for the high number of zeroes in counts. We used the ZIP distribution for all species except the Turkey (*Cathartes aura*), Lesser Yellow-headed *C. burrovianus* and Black Vultures *Coragyps atratus*, Snail Kites *Rosthramus sociabilis* and Southern Caracaras *Caracara plancus*. These species are often seen in large aggregations, which cause overdispersion in the count distribution. Instead, we used the ZINB distribution because it allows the mean to vary stochastically, similar to individual random effects in a Poisson process (Cook & Lawless 2007), thus accounting for extra-Poisson variation.

We selected abundance covariates to evaluate predictions about responses to land use according to species' dietary preferences, foraging strategies and nesting requirements, and to control for seasonality and variation among years (Tables S2–S3). Detection covariates were time of day (including a quadratic term), amount of closed vegetation near roads and the number of carcasses for scavengers (Tables S2–S3). All continuous numerical covariates were centred and scaled to unit SD. We used Akaike Information Criterion scores corrected for small samples and based on the conditional likelihood (AICc, Liang, Wu & Zou 2008) for model selection, and obtained AICc-averaged parameters and unconditional SEs (Anderson 2008) across the selected models. See Appendix S3 for a detailed description of the model selection and averaging procedures.

To predict the abundance in every grid cell in the study area, we used the abundance term of each model in the 0·95 cumulative weight set. Non-habitat covariates in the abundance term (e.g. year, seasonality and river surface elevation) were set to values corresponding to the dry and wet seasons of each year with the respective river surface elevation to create a total of six prediction scenarios (Table S4). We calculated 95% prediction intervals using a Monte Carlo technique, in which we drew 500 samples of the intercepts and abundance coefficients (β) of each model from a multivariate normal distribution set with parameters from the input model. Finally, we averaged the predictions from each model for each grid cell using the AICc weights (Anderson 2008).

Results

RAPTOR COUNTS AND HABITAT COVERAGE

We detected over 8000 raptors of 32 species during the field surveys. However, only 12 species were detected in numbers that we considered *a priori* to be minimally adequate for abundance modelling ($N \geq 60$, Table 1). Snail Kite, Black-Collared Hawk *Busarellus nigricolis* and Great Black Hawk *Buteogallus urubitinga*, which occur mainly in wetland and riverine habitats (Ferguson-Lees & Christie 2001), were observed only in the Pantanal (Table 1). Due to a lack of observations of these species in the Cerrado, we restricted the abundance modelling and prediction analysis to the Pantanal. The 20 species that were not analysed (Table S2) included raptors that were naturally rare (e.g. King Vulture *Sarcoramphus papa*), migratory (e.g. Osprey *Pandion haliaetus*), only marginally occur within the study area (Black-chested Buzzard Eagle *Geranoaetus melanoleucus*) or were forest species infrequently encountered along roads (e.g. Rufous-thighed Kite *Harpagus diodon*). On average, only one to three individuals of these species were encountered per survey (median: 0–1).

Pastures dominated land use in the study area (45%), whereas savanna (25%) was the major natural habitat (Fig. S2). The relative proportion of habitat types in the sampled area did not differ significantly (Wilcoxon signed rank test $P = 0{\cdot}49$) from that of the larger study area, although anthropogenic habitats, especially agriculture, had slightly higher proportions in the surveyed areas. This was expected, as anthropogenic habitats are concentrated along roads, whereas natural habitats remain away from roads. Eucalyptus and sugarcane plantations did not occur in the sampled area in the Pantanal, so were not included as covariates for species restricted to that biome.

RAPTOR ABUNDANCE

Model-averaged mean abundance ($\hat{\bar{\lambda}}$) per occupied (i.e. $A = 1$) sample unit (50 km^2) varied between 1·068 (Roadside Hawk) and 3·113 (Black Vulture; Fig. 1, Table S5). For Snail Kite, Black-collared Hawk and Aplomado Falcon, outliers among fitted λ values resulted in skewed, unrealistic ($\hat{\bar{\lambda}}$) values; instead, we report the model-averaged medians (0·222, 1·288 and 0·716, respectively; Fig. 1, Table S5). Increased proportion of anthropogenic habitats generally exhibited moderate to strong negative effects on raptor abundance (Table S5, Figs 2 and S7–S12). Pastures negatively affected the abundance of eight species and

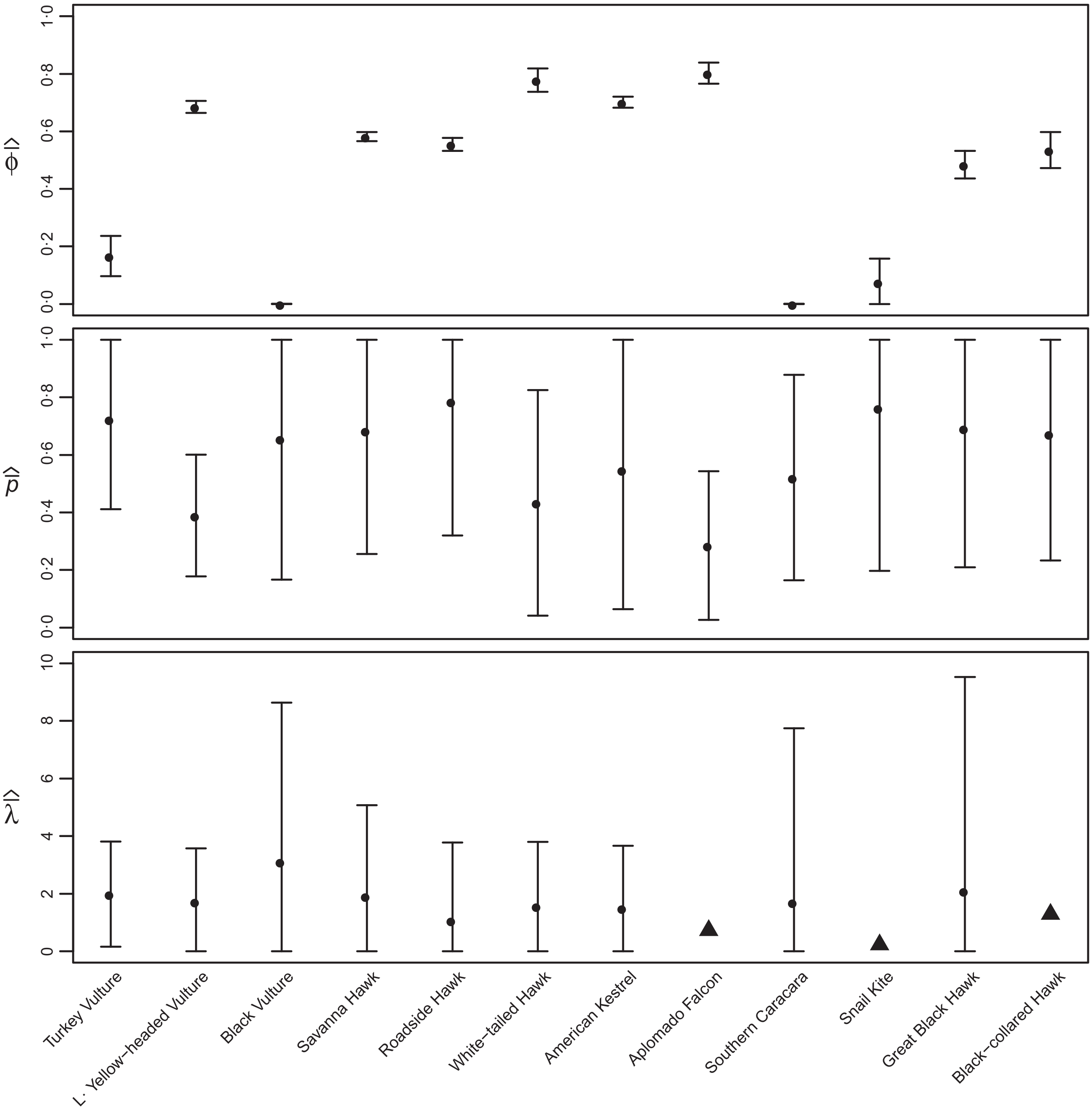

Fig. 1. Model-averaged mean detection probability ($\bar{\hat{p}}$), zero-inflation probability ($\bar{\hat{\phi}}$) and mean abundance ($\bar{\hat{\lambda}}$) parameters, with 90% CI based on unconditional SE. Circles are model-averaged parameter means, and triangles are model-averaged medians.

had no positive effects, while urban and agriculture habitats resulted in mixed responses (Table S5, Figs 2 and S7–S12). Season and river surface elevation were selected as covariates that influenced abundance for nine of the 12 species (Table S5), and the interaction between season and the proportion of agriculture was selected for five species (Table S5).

Spatial projections of abundance had reasonable, rather conservative, values for most species (Figs S13–S16). For the Aplomado Falcon (Fig. S15), however, the projections consistently attributed high values (≥20 per grid cell) to a large number of cells concentrated in the north-western region of the study area. Higher predicted abundance in the Pantanal than in the Cerrado occurred for the Lesser Yellow-headed and Black Vultures (Fig. S13) and the Southern Caracara (Fig. S15). For Savanna, White-tailed and Black-collared Hawks, Snail Kites and American Kestrels, the spatial pattern of predicted abundance varied considerably among scenarios (Figs S13–S16). In comparison, abundance predictions for the Turkey Vulture (Fig. S13), Roadside Hawk (Fig. S14) and Great Black Hawk (Fig. S16) displayed only subtle variations in space and among scenarios. Finally, we identified several small locations corresponding to cities, small towns and

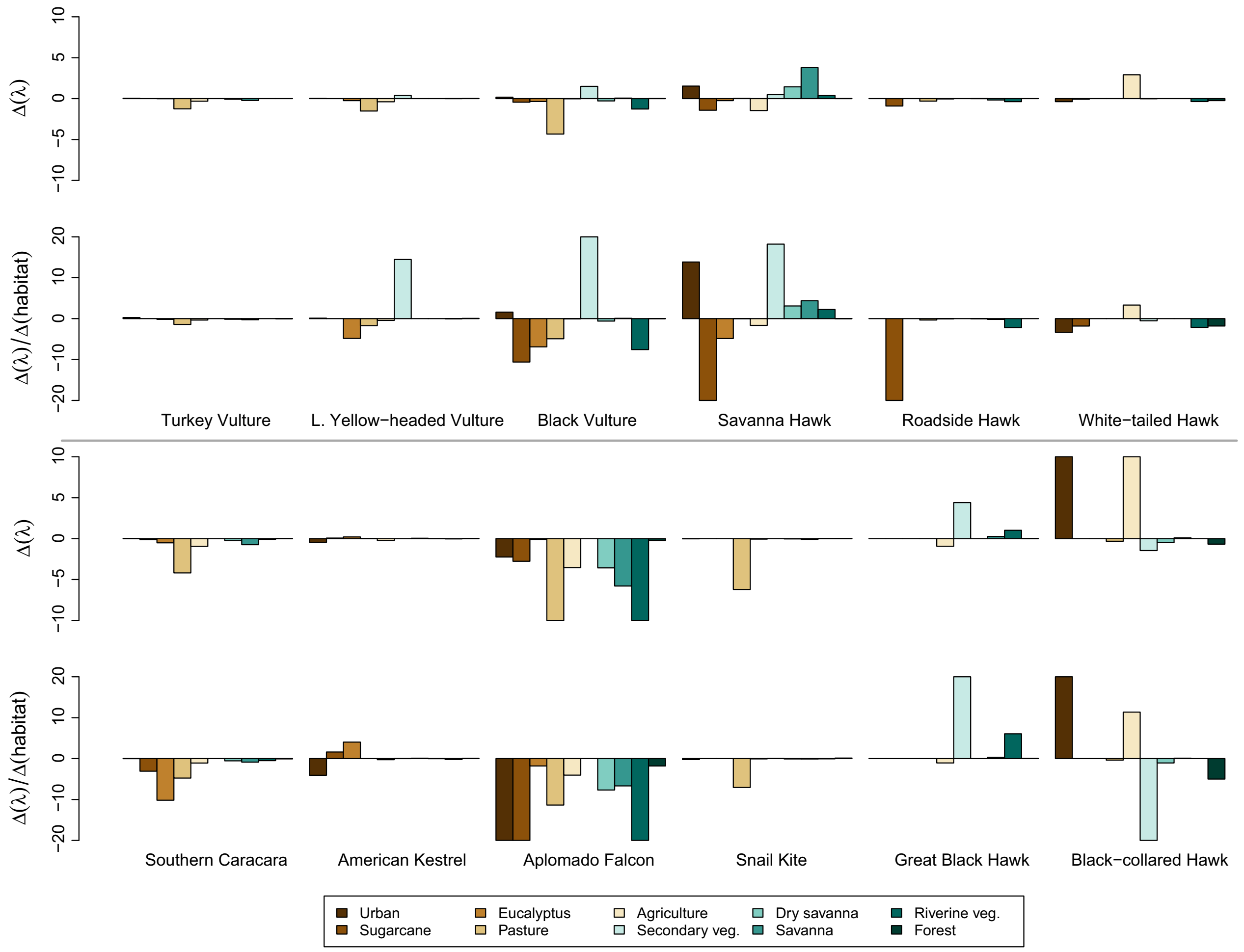

Fig. 2. Summary of habitat effects on abundance. Δ(λ) indicates changes in mean abundance as a consequence of an increase in habitat area equal to the 0·95% quantile of observed area proportions of each habitat type, Δ(habitat). Δ(λ)/Δ(habitat) shows the standardized abundance changes, that is divided by Δ(habitat), the 0·95% quantile: urban = 0–0·11; sugarcane = 0–0·04; eucalyptus = 0–0·05; pasture = 0–0·88; agriculture = 0–0·88; secondary veg. = 0–0·03; dry savanna = 0–0·47; savanna = 0–0·87; riverine veg. = 0–0·17; forest = 0–0·13. [Colour figure can be viewed at wileyonlinelibrary.com].

surrounding areas where abundance predictions seemed too high (indicated in Figs S13 and S15).

RAPTOR DETECTION AND ZERO-INFLATION PROBABILITIES

Model-averaged mean detection probabilities ($\hat{p}$) for species varied between 0·285 (Aplomado Falcon) and 0·787 (Roadside Hawk; Fig. 1, Table S5). The model-averaged zero-inflation probability ($\hat{\phi}$) varied from <0·001 (Black Vulture, Southern Caracara) to 0·802 (Aplomado Falcon; Fig. 1, Table S1).

Time of day was selected as a linear-effect covariate on detection of all species except Black Vulture, White-tailed Hawk, American Kestrel and Snail Kite, for which both linear and quadratic time-of-day effects were selected (Fig. 3, Table S5). Area of closed vegetation had sharp and moderate positive effects for the Black Vulture and Southern Caracara, respectively, and a negative effect for the American Kestrel (Fig. 3). The number of carcasses observed was not an important detection covariate for any species.

Discussion

EFFECTS OF LAND USE ON RAPTOR ABUNDANCE IN THE CERRADO AND PANTANAL OF MATO GROSSO DO SUL, BRAZIL

Raptor populations were generally negatively influenced by conversion of natural Cerrado and Pantanal habitats to anthropogenic uses (Figs 2 and S7–S12), but responses differed among species. Most species were negatively associated with increasing proportions of pasture habitat, as reported elsewhere (Carrete *et al.* 2009; Buij *et al.* 2013). Consistent with our predictions (Tables 1 and S1), they mostly shared a vertebrate diet and perch-hunting strategy, while the abundance of the insectivorous American Kestrel (Cabral, Granzinolli & Motta-Junior 2006) was not influenced. Negative impacts were also observed for

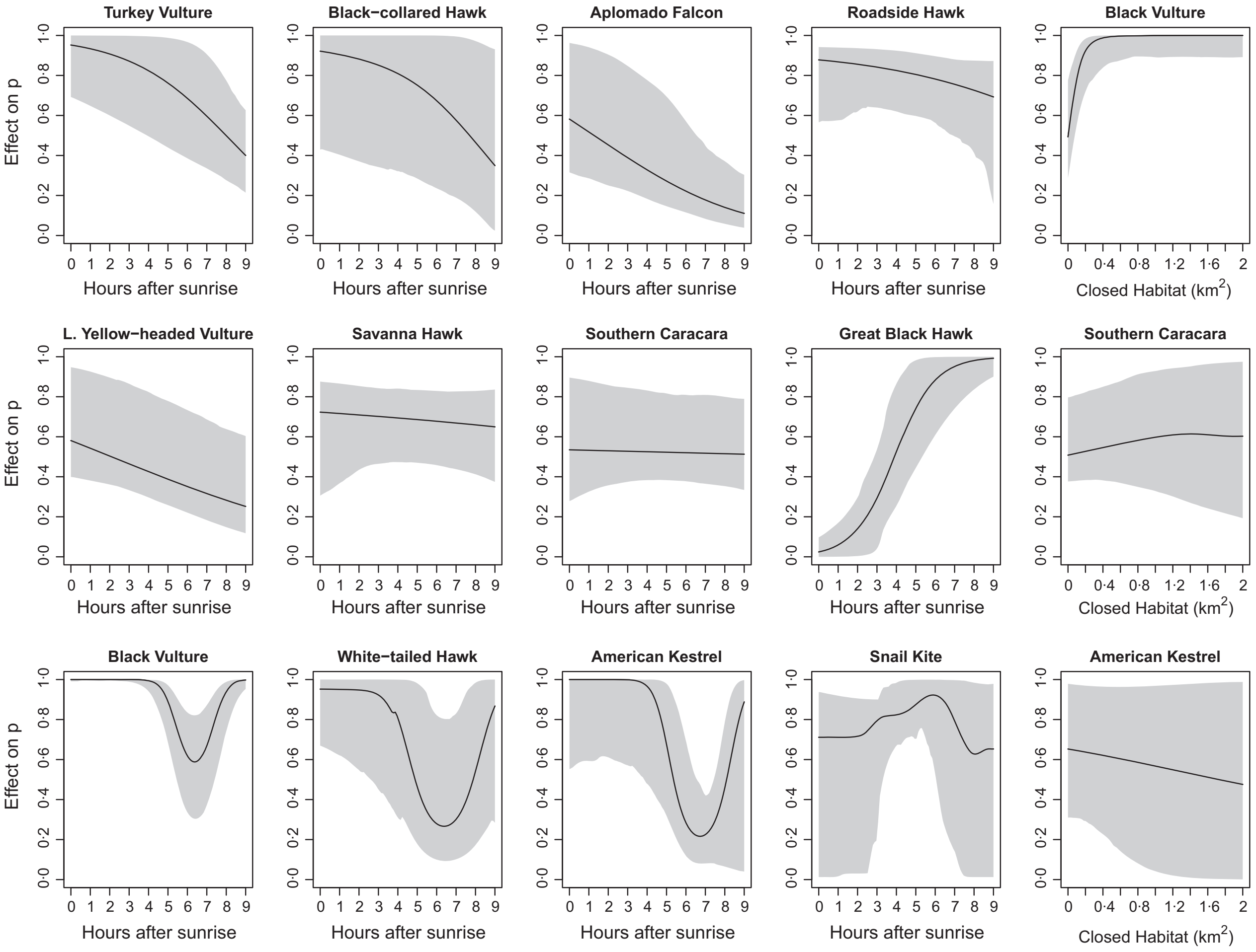

Fig. 3. Model-averaged covariate effects on detection probabilities for various species, with 90% CI based on quantiles.

scavengers, which are usually considered poor indicators of habitat quality (e.g. Black and Turkey Vultures, Southern Caracara; Rodríguez-Estrella *et al.* 1998). Half of the planted pastures in the Cerrado are degraded and support few cattle because of reduced plant cover, invasion by unpalatable plants and termite mounds (Klink & Machado 2005). These effects, combined with a similarly impoverished small vertebrate fauna and the thinning of shrub and tree cover, which reduces resources for nesting, hunting and roosting, may contribute to a reduction in raptor abundance (Fig. 2).

Urbanization, soya beans (the predominant annual crop), sugarcane and eucalyptus have become powerful threats to biodiversity in the Cerrado as a result of the expansion of agricultural frontiers, development of tolerant crop varieties, generous government subsidies and rising demand for biofuels, timber and cellulose (Fearnside 2002; Carvalho, De Marco & Ferreira 2009). Nonetheless, as reported elsewhere (e.g. Rodríguez-Estrella *et al.* 1998; Sanchez-Zapata *et al.* 2003; Buij *et al.* 2013), raptor abundance was not universally reduced in these anthropogenic land uses, confirming the expectation that some species may tolerate them. However, these habitats, as well as secondary vegetation, were underrepresented in our data set, both in terms of their overall proportion in the study area (Fig. S2) and in terms of the range of observed proportions within sample units (except for agriculture, Figs 2 and S7–S12). This shortcoming of our survey design might have influenced the ranking of habitats as predictors of raptor abundance, and contributed to unreasonable estimates (e.g. the strong positive effects of urban and agriculture habitats on abundance of Black-collared Hawk) and wide confidence intervals (Table S5, Figs 2 and S7–S12), as discussed below.

Our projections are a first attempt to generate regional maps of biome-scale raptor abundance patterns for the Cerrado and Pantanal based on roadside surveys corrected for detection error (Figs S13–S16). Numerous sources of bias intrinsic to the roadside survey method can influence raptor counts, including increased frequency of perch sites (e.g. power and telephone posts and lines, fences, road signs), food for scavengers (i.e. road kills) and edge habitats (Fuller & Mosher 1981; Meunier & Verheyden 2000). In addition, the spatial distribution of transects was limited by road availability, resulting in uneven sampling across habitats in the study area that may have influenced predictions of abundance and habitat effects. Importantly, we set the area of grid cells equal to that of sample units (2·5-km buffers) to ensure that the relationships between abundance and habitat proportions within local landscapes revealed by models were maintained. However, abundance projections may be underestimated because we infrequently detected individuals far from transect lines (>500 m). On the other hand, overestimation may result when roadside perches increase detectability. Thus, the maps presented in Figs S13–S16 should be viewed as depictions of the relative differences in spatial and seasonal variation of abundance, rather than representations of the actual numbers of individuals occurring in the region.

RAPTOR DETECTION PATTERNS: UNDERLYING PROCESSES

The probability that a raptor was detected during a survey can be considered as the product of four conceptually different components (Nichols, Thomas & Conn 2009). The first two components – the probability that its home range or territory partly overlaps a sampling unit (spatial sampling) and the probability that it is present during the survey (presence) – are related to spatial coverage. These probabilities likely contributed to the high frequency of zeroes in our observed counts (Figs S4–S6), which we modelled using zero-inflated distributions. However, they may also have affected observations where at least one individual was counted, and this effect cannot be disentangled from our abundance estimates.

The other two components affecting raptor detection are the probability that an individual present at the time of survey gave a visual or auditory cue and was therefore available for detection (availability), and the conditional probability that the available birds were detected (perceptibility). Their product is the overall detection probability (P), which we modelled as a function of time of day, visibility (with covariate closed habitat) and the number of carcasses on roads. Detection of raptors is often linked with activity patterns, which in turn vary throughout the day as a result of changes in prey availability or flight requirements (Bunn, Klein & Bildstein 1995; Table S2). For example, species that prey on small mammals and birds are more active in the early morning than in the late morning or afternoon, because activity of their prey usually peaks around sunrise (Vieira & Baumgarten 1995), while raptors that hunt reptiles have a delayed activity peak (Blair 2009). Vultures and other large raptors that require thermals and updrafts to soar face difficulty in flying in the early morning, and are more active later in the day (Fuller & Mosher 1981).

Our patterns of detection support the above generalizations for several raptors (Fig. 3). We found a negative effect of time of day on detection for the Savanna Hawk, Roadside Hawk and Aplomado Falcon, all of which feed on small mammals, reptiles or birds. The diet of the American Kestrel in the Cerrado is dominated by diurnal and nocturnal arthropods, suggesting that it forages in crepuscular hours (Cabral, Granzinolli & Motta-Junior 2006). Great Black Hawk detections increased with time of day; most of its diet consists of ectothermic reptiles, amphibians and large insects (Carvalho Filho, Canuto & Zorzin 2006), which should be more active later in the day. In contrast, Snail Kite detection was highest during midday and early afternoon, when perching behaviour peaks for this species (Beissinger 1983). Thus, behaviours that increase exposure and consequently detection are not necessarily linked to higher mobility. A similar pattern was observed for the Black-collared Hawk, which feeds mainly on fish. Conversely, time of day did not affect the detection of vultures, Southern Caracara and White-tailed Hawk as expected (Fig. 3). Turkey and Lesser Yellow-headed Vultures were more likely to be seen earlier than later in the day; detection of Black Vulture and White-tailed Hawk was lowest in the middle of the day; and detection was nearly constant throughout the day for Southern Caracaras. A shift of activity to an earlier period could be a consequence of thermals occurring earlier in the day than where previously studied (Bunn, Klein & Bildstein 1995; Vergara 2010). Increasing vulture and Southern Caracara detections during the day could also be due to detections of large aggregations at communal roosts, feeding on carcasses or scavenging in ploughed fields.

Surprisingly, the amount of closed vegetation near roadsides was an important detection covariate for few species. Detections of Black Vulture and Southern Caracara were positively affected and American Kestrel negatively affected by forest cover near roads (Fig. 3). Although visibility through closed habitat decreases (Fuller & Mosher 1981), perches often associated with road borders are commonly used by raptors for resting, roosting, still-hunting and maintenance activities. They may be responsible for increased detections associated with forests compared with other habitats, such as fields and pastures, without such features.

The amount of carcasses was not an important detection covariate for species with obligate or facultative scavenging habits. While this resource may offer feeding opportunities, it can also act as an ecological trap. Vultures and other large raptors that land on roads are sometimes unable to avoid oncoming vehicles. Indeed, carcasses of four Black Vultures, two Turkey Vultures and six Southern Caracaras were encountered during the surveys, apparent victims of highway mortality.

APPLICATION OF THE SINGLE-VISIT MODEL TO RAPTOR ABUNDANCE SURVEYS

Large-scale field surveys often balance a trade-off between the extent of area sampled and the financial costs associated with repeated sampling of sites. This trade-off can impose serious sample-size constraints on studies of abundance that seek to account for imperfect detection, whether by attempting to control effects with careful sampling design (Banks-Leite *et al.* 2014) or by modelling detection probabilities (Dénes, Silveira & Beissinger 2015). In addition, rarity, patchy distribution, large home ranges, high mobility and elusiveness of species surveyed can make such studies even more challenging (Dénes, Silveira & Beissinger 2015). Our SV survey methodology combined extensive road-survey counts, large-scale GIS data sets and the conditional likelihood *N*-mixture model (Sólymos, Lele & Bayne 2012) to sample raptor abundance at a regional scale as a function of environmental covariates while accounting for detection error.

We were unable to analyse count data of 20 species of raptors that were infrequently encountered (Table S1) with our SV methods because likelihood-based inference is not a small-sample procedure (Royle & Nichols 2003), which is an important shortcoming of any similar analytical approach. Further methodological development, such as incorporation of the SV approach into a multispecies framework (Iknayan *et al.* 2014), could allow future studies to make important detection-corrected inferences of abundance for entire communities at large geographical scales and with sensible research budgets. For example, in our study Turkey, Lesser Yellow-headed and Black Vultures, Southern Caracara, Aplomado Falcon and Snail Kite demonstrated a linear decline in abundance with increased pasture area (Figs 2 and S7–S11), and to the extent that other less frequently encountered species behaved similarly, this common pattern could be exploited in a multispecies analysis.

CONCLUSIONS

Raptor populations in the Cerrado and Pantanal were mostly negatively affected by expansion of anthropogenic habitats, especially pastures, even for species considered habitat generalists. Thus, protection of the remaining natural habitats is essential to prevent further decline of raptor populations in these biomes. Moreover, given the pervasive negative effects of pastures on the raptor community, the restoration of unproductive pastures into natural habitat could prove an efficient strategy to recover diminished raptor populations in the region. Although none of the raptors we investigated are classified as endangered, we encountered 20 other species, including the rare King Vulture, the endangered Chaco Eagle *Buteogallus coronatus* and long-distance migrants such as Osprey *P. haliaetus* and Peregrine Falcon *Falco peregrinus* that were recorded in numbers too small to allow inclusion in our analysis. They are likely to be subject to similar pressures in this region.

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Data accessibility

The full data set with species counts and explanatory variables for all observations is uploaded as online supporting information (Appendix S4).

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Supporting Information

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

Fig. S1. Percentage of individuals of the twelve analysed species detected while flying.

Fig. S2. Study area and survey transects.

Fig. S3. Proportion of natural and anthropogenic habitats in the sampled and study areas.

Figs. S4–S6. Count frequency plots of various species.

Figs. S7–S12. Model-averaged habitat effects on mean abundance various species.

Figs. S13–S16. Abundance predictions of various species in the Cerrado and Pantanal in MS.

Table S1. Explanation of predictions between model covariates and raptor abundance and detection.

Table S2. Species detected but not analysed due to low number of individuals.

Table S3. Predictions of covariate effects on abundance and detection of each of the twelve species analysed.

Table S4. Prediction scenarios used for spatial projections of abundance.

Table S5. Model averaged results.

Appendix S1. Legends for Figures S1–S16.

Appendix S2. Binomial – Zero-inflated negative binomial (B-ZINB) model for abundance.

Appendix S3. Description of the model selection and averaging procedure.

Appendix S4. Dataset with species counts and explanatory variables for all observations.

Appendix S5. Description of dataset in Appendix S3.