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Distribution and habitat use of the endemic Yungas Guan *Penelope bridgesi* in the Southern Yungas of Argentina

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Summary

Identifying the factors that determine the spatial distribution and habitat use of species of conservation importance is essential to developing effective conservation and management strategies. As seed dispersers, guans play a key role in the regeneration of forests in South America and are threatened mainly by habitat loss and hunting pressure. The Yungas Guan *Penelope bridgesi*, an endemic species restricted to the Southern Yungas of Argentina and Bolivia, has been recently recognized as a separate species. To determine the conservation status of Yungas Guan, information on its distribution and habitat use is urgently needed. The objectives of our work were to 1) determine the potential distribution of the Yungas Guan in the Southern Yungas of Argentina and 2) assess the influence of environmental and anthropogenic covariables on habitat use of the species. We used records of Yungas Guan to model the potential distribution of the species with MaxEnt software and developed occupancy models to determine habitat use and influential elements of the landscape (puestos, urban areas, roads, rivers, and elevation). We obtained data on the presence of Yungas Guan with camera traps, with an effort of 6,990 camera trap-days. The total potential distribution of the species was 21,256 km^2. We found that the habitat use by Yungas Guan increased with proximity to rivers and streams. The probability of habitat use was 0.27, with a range of 0.02–0.42. Of the total potential distribution area, 15,781 km^2 (81%) had a probability of habitat use greater than 0.2. This study is the first in determining the potential distribution of Yungas Guan in the Southern Yungas of Salta and Jujuy provinces in Argentina and highlights the importance of conducting analyses with occupancy models to assess the influence of environmental and anthropogenic variables and threats to cracid species.

Keywords: Occupancy, Yungas Guan, Southern Yungas, Potential distribution

Introduction

Frugivorous birds are important seed dispersers of various plant species (Loiselle and Blake 1991) and play a fundamental role in the maintenance of plant diversity, especially in tropical forests

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(Fleming *et al.* 1987). The extinction or decline of frugivorous bird populations may have severe effects on forest vegetation, producing changes in plant abundance, dominance, and diversity (Da Silva and Tabarelli 2000). The Cracidae is a Neotropical seed-dispersing bird family comprising 55 described species (BirdLife International 2021), particularly guans and chachalacas. This family is of special interest since it includes large individuals that play an important role in the regeneration of tropical forests (Brooks and Strahl 2000, Thornton *et al.* 2012). Cracidae is one of the most threatened bird families worldwide due to habitat loss and hunting pressure (Del Hoyo 1994, Brooks and Strahl 2000). The Southern Yungas of Argentina are home to two cracid species, *Penelope dabbenei* and *P. bridgesi*.

The Yungas Guan *Penelope bridgesi*, a cracid endemic to the Southern Yungas ecoregion of Argentina and Bolivia, was recently split from Dusky-legged Guan *Penelope obscura* and recognized as a new species (Evangelista-Vargas and Silveira 2018, Remsen *et al.* 2021). This recent change in taxonomy at the species level shows the urgent need to assess the conservation status of the Yungas Guan; this is especially important, since this endemic species, like many Guans, could be threatened by hunting pressure and habitat loss. The Yungas Guan has been recorded from 700 to 2,200 m asl (BirdLife International 2021), although it is rarely found above 1,000 m (Chalukian 1997). Ecological and habitat information for the Yungas Guan is almost inexistent. It feeds on leaves, flowers and, in the winter, mainly on fruits of *Celtis iguanea*, *C. pubesccens*, *Smilax campestris* and *Acacia aroma* (Chalukian 1997). Although the home range size is not known for the Yungas Guan, there is information for *Penelope superciliaris jacupemba*, a Guan of similar size (De la Peña 1992, Del Hoyo 1994) that has an estimated home range of 11 ha (Guix and Ruiz 1997), and both species could have similar habitat and home range requirements. Information for the related Dusky-legged Guan in the Paraná River shows that it is associated with forests, mainly along rivers and streams (Malzof *et al.* 2012).

The Southern Yungas is a mountain forest distributed along the eastern slopes of the Andes, from southern Bolivia to north-western Argentina (Tortorelli 1956, Hueck 1978). This ecoregion harbours endemic and threatened species at the global and national levels and is considered a biodiversity hotspot at a global scale (Myers *et al.* 2000). In addition, these forests provide ecosystem services, such as water provision for urban centres and crops (Politi and Rivera 2019). In Argentina, the Southern Yungas covers an area of approximately 5,000,000 ha, of which about 30% have already been transformed to other land uses (Malizia *et al.* 2012). The most common human activities in these forests are logging and extensive livestock farming. Many threatened and endemic species have suffered reductions in their abundances mainly due to the transformation and degradation of the forest by anthropogenic activities (Perovic *et al.* 2015, Pidgeon *et al.* 2015).

Despite the important ecological role of the Yungas Guan and its potential importance as a source of protein for people, basic information on its abundance, distribution, and habitat use is not available. The objective of our work was to determine the potential distribution and assess the influence of environmental and anthropogenic covariables on habitat use of the Yungas Guan in the Southern Yungas of Argentina, in the provinces of Salta and Jujuy.

Methods

Camera trap occurrence records provide essential input for species distribution modelling (SDM) (Paglia *et al.* 2012). Species distribution models allow estimates of potential geographical distribution of a species and are fundamental for ecological studies (Bezerra *et al.* 2019). Occupancy modelling allows inferences to be made about the spatial distribution and habitat use of rare or elusive species whose behaviour hinders their detection, as is the case of cracids (MacKenzie *et al.* 2006, O'Connell and Bailey 2011). These models estimate the probability of occupancy and detection of a species at a site through repetitive sampling (MacKenzie and Royle 2005, MacKenzie *et al.* 2006). Our approach was similar to a hierarchical framework (Pearson and Dawson 2003) and consisted of fitting a model at a larger scale to define potential habitat for the species based on bioclimatic variables and with low resolution in Maxent (Phillips *et al.* 2006), followed by

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occupancy modelling that includes environmental and human influence co-variables at a local scale and with a higher resolution (MacKenzie *et al.* 2006).

Study area

We carried out the study in the Southern Yungas of Argentina, in the provinces of Salta and Jujuy. The Southern Yungas in Argentina extends latitudinally between 22° and 29°S and altitudinally between 400 and 2,500 m (Cabrera 1976) on the eastern slopes of the Andes Mountains. The climate is subtropical, with a marked dry season (April to October) and occasional snowfall in the cold months. Three national parks (Baritu, Calilegua, and El Rey) protect the high biodiversity of these forests, although human activities have already transformed 75% of the lower and flatter parts of the forests into agriculture (Brown and Malizia 2004).

Camera trap records

To determine the locations of individual Yungas Guans, we placed 233 camera traps (BUSHNELL, Model Trophy Camera Aggressor) along the latitudinal distribution of the Southern Yungas of the provinces of Salta and Jujuy, including private properties and national protected areas (Fig. 1). We deployed camera traps along forest trails used by animals. We georeferenced the location of each camera trap with a Garmin etrex® model geo-positioner. The mean distance from a camera-trap to its nearest one was 1.69 ± 0.77 km. Because the Yungas Guan is associated with forests, we placed the camera traps inside continuous forests with a mimimum distance of 100 m from forest edges. We attached camera traps to a tree at a height of 30 cm from the ground and set them to take photos 24 hours a day; cameras remained active for 30 consecutive days between May and October in 2016, 2017 and 2018. We conducted sampling in blocks of 5–20 camera traps, and then relocated them within the study area. We analyzed the photographs to identify individuals of the Yungas Guan.

Potential habitat distribution

We used MaxEnt software version 3.4.1 (Phillips *et al.* 2006) to generate a map of the potential distribution of Yungas Guan. We used the occurrence data from camera traps as presence data in the model. To minimize the sample bias due to double counting of individuals, we used only the records of Yungas Guans that were more than 2 km apart with the assumption that the home range of *P. bridgesi* would be similar to that of *P. superciliaris* (Guix and Ruiz 1997). We carried out a correlation analysis of 19 bioclimatic variables (Table S1 in the online supplementary material) of 1-km resolution, representing the conditions between 1970 and 2000 (Hijmans *et al.* 2005). Only five variables were retained and used as predictors: mean diurnal range (mean of monthly max temp-min temp) (BIO 2), temperature seasonality (BIO 4), temperature annual range (BIO 7), precipitation of wettest month (BIO 13), and precipitation of warmest quarter (BIO 18). We did not include topographic data in the species model because climate and elevation are often highly correlated (Martinuzzi *et al.* 2018). We generated data for model training in MaxEnt with 10,000 pseudo-absences and selected 50 km for pseudo-absence locations because at that buffer distance the model produced the most accurate and biologically significant results compared to other buffer sizes (VanDerWal *et al.* 2009, Martinuzzi *et al.* 2018). When running MaxEnt, we set all the other options to default (Schank *et al.* 2015) and evaluated the performance of the model using the bootstrap technique (Bateman *et al.* 2012) and the area under the receiver operation curve (AUC). AUC measures the ability of a model to discriminate between sites where a species is present and those where it is absent (Hanley and McNeil 1982). The AUC ranges from 0 to 1, with 1 indicating perfect discrimination and 0.5 a predictive discrimination that is no better than a random guess (Elith *et al.* 2006). AUC values can be interpreted as indicating the probability that, when a presence site and an absence site are drawn at random from the population, the former will have a higher predicted value than the latter (Elith *et al.* 2006). Additionally, we used the test of

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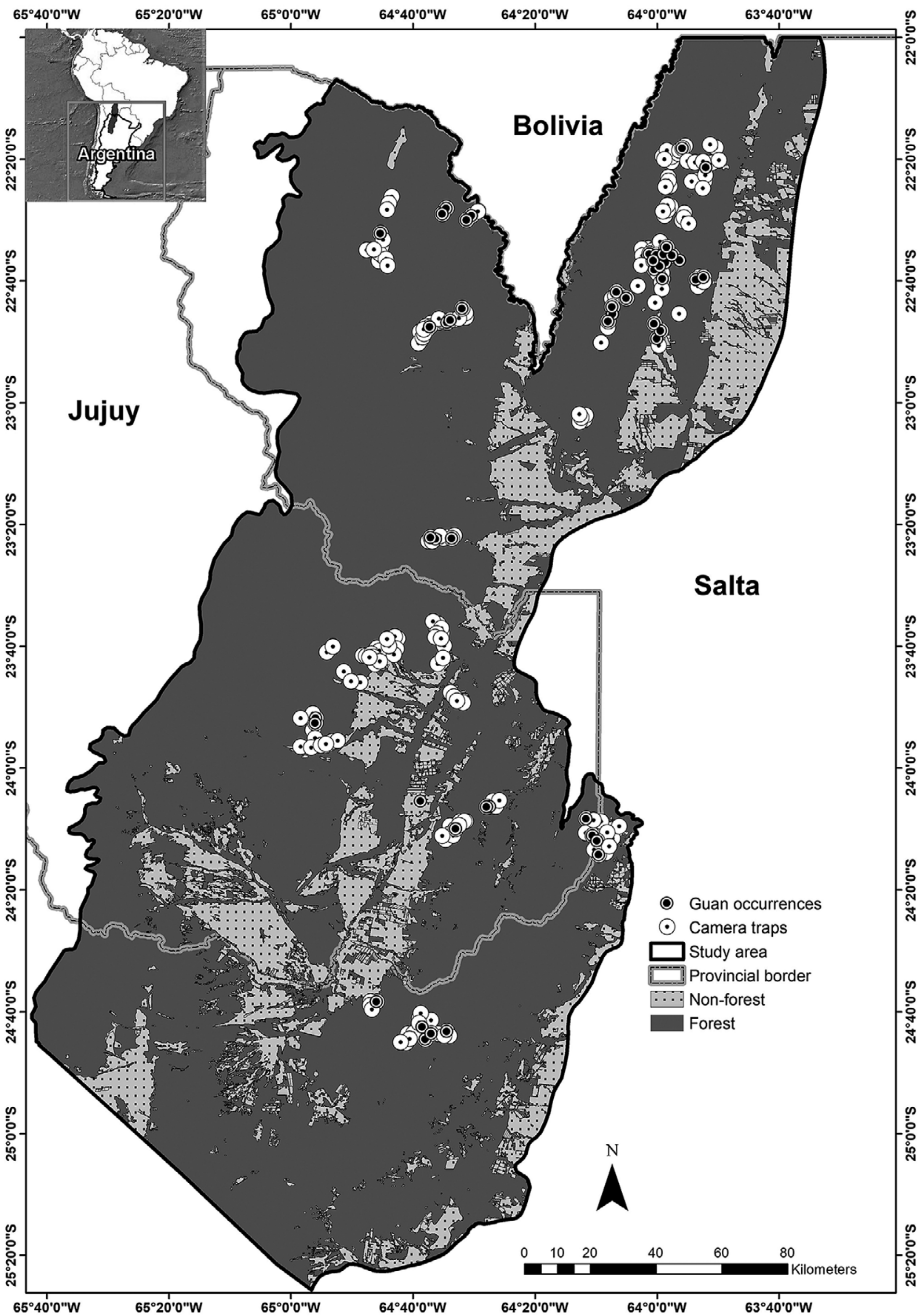

Figure 1. Location of camera traps with presence of Yungas Guan (black circles) and without presence of the species (white circles) in the study area within the Southern Yungas of Argentina.

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binomial probabilities to assess ommission rates for the models. These are 1-sided p-values for the null hypothesis that test points are predicted no better than by a random prediction with the same fractional predicted area (Phillips 2017). We transformed the MaxEnt predictions using the logistic threshold for the presence of the tenth percentile into a suitable versus inadequate binary habitat map to create a potential distribution map of the species. Since the Yungas Guan is a forest-associated species, we removed the transformed non-forest areas from the potential distribution map of the species, by overlapping the potential distribution maps with a land cover map (Martinuzzi *et al.* 2018). Then, we calculated the total area of potential habitat available for the species in the study area.

Occupancy models

We performed an occupancy analysis to estimate the proportion of area occupied by the Yungas Guan (MacKenzie *et al.* 2006). Because close cameras may record the same individual, producing non-independent records, we consider that occupancy (ψ) represents habitat use of the species (MacKenzie *et al.* 2006). Occupancy analyses require successive sampling at points over short periods within which the population is considered demographically closed (MacKenzie *et al.* 2006). To meet this condition, we partitioned the detection history of each 30-day camera-trap period into 5-day blocks, producing a maximum of six repeated surveys at each site. We included the following environmental and anthropogenic variables that may influence the detection and occupancy of cracid species in the occupancy models: distance to rivers, elevation, distance to small human households, distance to urban areas, distance to roads, and distance to transformed areas (Chalukian 1997, Pereira-Ribeiro *et al.* 2018, Zalazar *et al.* 2018). We obtained spatial data sets on human settlements, roads, and rivers from government databases in Geographic Information Systems (IGN 2016). We obtained data on transformed areas from Martinuzzi *et al.* (2018). Human settlements were of two types: "puestos", i.e. isolated small households inhabited by one person or a few people, in some cases inhabited only seasonally, and urban areas (IGN 2016). To assess the probability of detection, we used the Occasion variable (Dias *et al.* 2019), which was defined as the follow-up period in consecutive 5-day blocks, totalling six blocks (Occasion 1-6). We calculated the linear distance (km) from the camera traps to urban areas, transformed areas, roads, rivers and puestos in ArcGIS 10.4.1 and normalized the variables by converting them to Z values (Donovan and Hines 2007). To avoid collinearity between covariates, we calculated the Pearson's correlation coefficient and did not include distance to transformed areas in the rest of the analyses, since it presented a correlation >0.65 with urban areas (Figure S1) (McDonald *et al.* 2015, Steenweg *et al.* 2016). We developed 16 *a priori* hypotheses or models to estimate the influence of the variables on the habitat use of the Yungas Guan (Table S2). We evaluated two parameters in the occupancy models (MacKenzie *et al.* 2006): detectability (p) and probability of occupancy (ψ). To run the analyses, we used packages "Unmarked" (Fiske *et al.* 2013), "AICcmodavg" (Burnham and Anderson 2002), MuMIn, and "Lubridate" (Garrett and Hadley 2011), in the R program version 3.5.0 (R Core Team 2018). The 16 models with the occupancy and detection covariates included null and full models. We evaluated the degree of fit of the full occupancy model using the MacKenzie and Bailey (2004) goodness-of-fit test. Instead of choosing a single model with the lowest ΔAIC value, we estimated the average of the first eight models that summed an Akaike Information Criterion relative model weight (AIC wt) of 0.95 as an acceptable maximum cutoff to select models (Barton 2013). We also evaluated the relative importance of each covariate and the magnitude of their effect on the probability of occupancy. We calculated the 95% confidence intervals of the β coefficients through the adjustment function "model.avg" of the "MuMIn" package (Burnham and Anderson 2002) and the "confint" function. When the confidence interval did not include zero, we considered the effect of the covariate as significant (Manly *et al.* 2002). We constructed a spatially explicit map of the likelihood of habitat use of the Yungas Guan, based on model averaging. To generate the map of habitat use probability, we established a grid of hexagonal cells of 0.5 km apothem length over the study area to determine

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the distance between the centroid of the cell and the explanatory variables and to allocate a probability value to the cell. With these values, we built a matrix of 48,719 cells for the study area and predicted the occupancy for each cell using the predict function (Burnham and Anderson 2002). We overlapped the spatially explicit map of habitat use with the potential habitat distribution map of the species.

Results

The sampling effort produced 88 independent photographic records of Yungas Guan from 6,990 camera trap nights. The mean distance from the camera traps to the nearest urban area, road, puesto and river was 24.53 ± 18.07 km, 5.20 ± 3.50 km, 7.41 ± 3.50 km, and 1.35 ± 1.63 km, respectively. Camera traps were deployed along an elevation range of 372–2,148 m asl. The Yungas Guan was recorded within an elevation range of 410–2,148 m.

Potential habitat distribution of Yungas Guan

We used 44 records of the Yungas Guan to model its potential distribution. The AUC value of the potential distribution model of the Yungas Guan was 0.91. The average binomial test of omissions ($P = 0.0037$) showed the statistical significance of the predictions. Three variables contributed 90.1% of the explanatory power of the potential distribution model of Yungas Guan: 45.4% precipitation of warmest quarter (BIO 18); 37% mean diurnal range (mean of monthly (max temp-min temp)) (BIO 2), and 7.7% temperature seasonality (BIO 4). The total area of Yungas Guan potential distribution was 21,256 km^2 (Figure S2). Of this area, 9% of the potential habitat was transformed to another type of land cover, resulting in 19,344 km^2 of current potential distribution (Fig. 2).

Habitat use of Yungas Guan

The estimated naive occupancy of Yungas Guan was 0.21. Our single-season model produced an estimated habitat use by the Yungas Guan for the entire study area of $\Psi = 0.44$ ($\beta \pm SE = -0.56 \pm 0.24$), with a probability of detection of $p = 0.44$ ($\beta \pm SE = -0.34 \pm 0.14$). For the best model, habitat use (Table 1) ranged from 0.02 to 0.42, with an average of 0.27. The full model was not the most parsimonious (Table 1) and the c-hat estimator presented a value of 3.15. The variables that were included in the averaged model were distance to rivers, distance to puestos, distance to urban areas, distance to roads, elevation and Occasion. The variable that was most strongly associated with probability of habitat use was distance to rivers (Table 2). The probability of habitat use by the Yungas Guan decreased significantly with increasing distance from rivers (Fig. 3, Table 2). The probability of detection (p) was significantly and positively associated with the variable Occasion (Table 2).

The spatially explicit map of estimated habitat use showed that 81% of the species' potential distribution (i.e., 15,781 km^2) has a probability (0.20–0.42) of habitat use near rivers (Fig. 4).

Discussion

The Yungas Guan is strongly associated with rivers in the Southern Yungas. Riparian forests are restricted habitats, with high levels of food resources that may be important for the reproduction and movement of numerous bird species (Palmer and Bennett 2006, Gomez *et al.* 2016). A similar pattern of association with riparian forests was recorded for the Dusky-legged Guan in the Paraná River Delta, in central-eastern Argentina (Malzof *et al.* 2012), for *Penelope superciliaris* in the Atlantic Forest of Brazil (Pereira-Ribeiro *et al.* 2018), and for other cracid species (Luna-Maira *et al.* 2013). Studies on *Crax globulosa* suggested that the strong association with water might reflect feeding dependency on the seasonal availability of small fish, insect larvae and crustaceans

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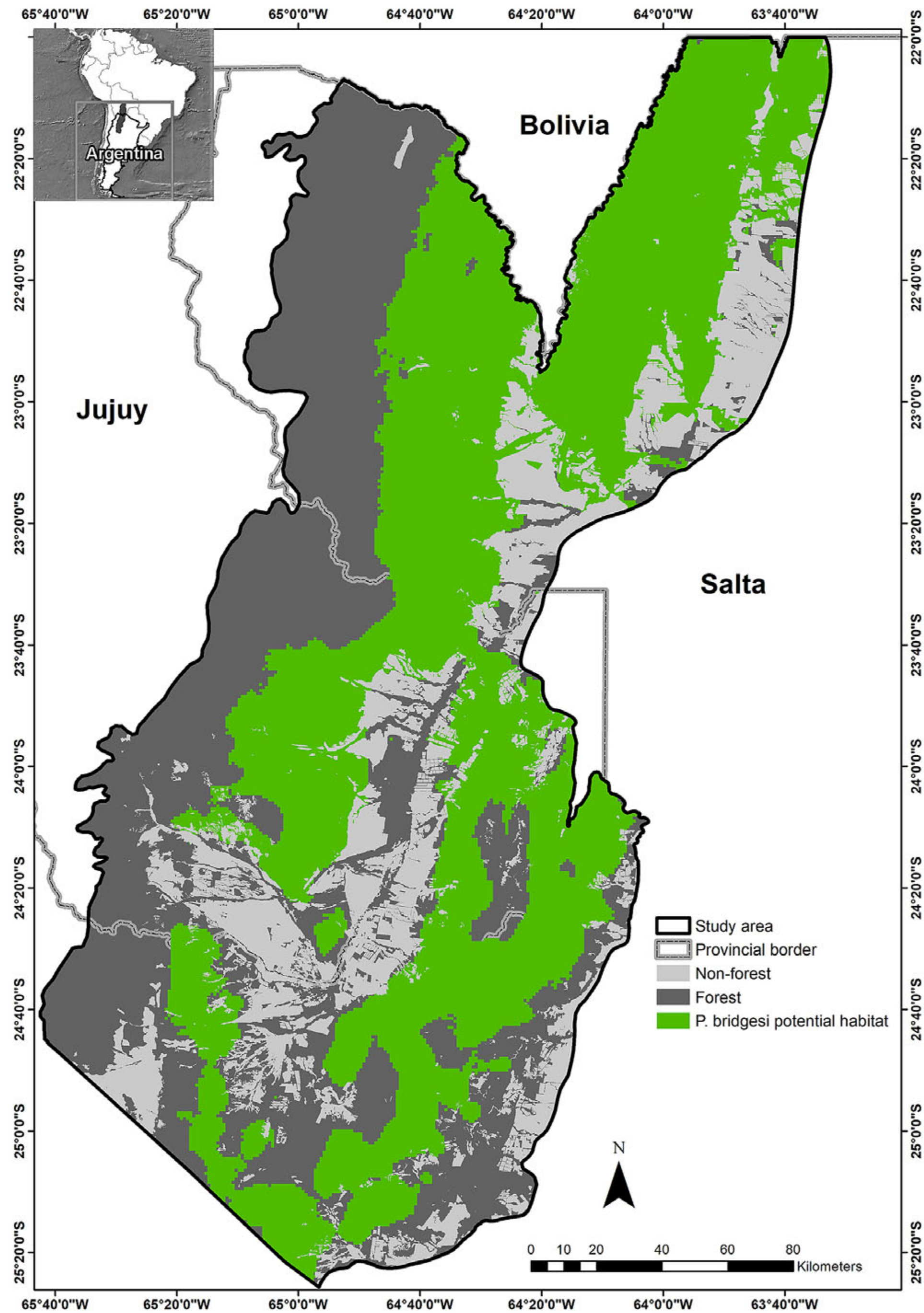

Figure 2. Distribution of the potential habitat of the Yungas Guan in the Southern Yungas of Argentina.

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Table 1. Models used to determine the habitat use of the Yungas Guan in the Southern Yungas of Argentina.

Models	AIC	ΔAIC	AICwt	cumltvWt	K
p(Occasion)psi(Rivers)	584.01	0	0.44	0.44	4
p(Occasion)psi(Rivers + Urban areas)	585.14	1.14	0.25	0.69	5
p(Occasion)psi(Rivers + Urban areas + Roads)	586.49	2.49	0.13	0.82	6
p(.)psi(Rivers)	587.36	3.35	0.08	0.90	3
p(Occasion)psi(.)	589	4.99	0.04	0.94	3
p(Occasion)psi(Puestos + Rivers + Urban areas + Roads + Elevation)	589.89	5.86	0.02	0.96	8
p(Occasion)psi(Urban areas)	589.9	5.89	0.02	0.99	4
p(Occasion)psi(Puestos)	590.78	6.78	0.02	1.00	4

Abbreviations: AIC = Akaike Information Criterion, ΔAIC = difference in AIC from the highest ranked model, AIC wt = relative model weight, k = number of model parameters, cumltvWt: cumulative weight. Ψ: probability of habitat use; p: probability of detection; Urban areas: distance from the camera trap to the closest city or town, Roads: distance from the camera trap to the nearest road, Rivers: distance from the camera trap to the nearest river, Puestos: distance from the camera trap to the nearest small household, Elevation: vertical distance of a point on earth from sea level, Occasion: time calculated in five-day periods.

Table 2. Beta values of the model averaging, standard errors, and 95% confidence intervals for the variables that affected the probability of habitat use (ψ) and the probability of detection (p) of Yungas Guan in the Southern Yungas of Argentina.

Variable	Parameter estimates	Standard error	z-value	95% confidence interval	
				Upper limit	Lower limit
p(Int)	**-1.34**	0.20	6.85	-1.73	-0.96
p(Occasion)	**0.32**	0.15	2.19	0.03	0.61
ψ(Int)	**-0.97**	0.22	4.36	-1.41	-0.53
ψ(Rivers)	**-0.56**	0.24	2.32	-1.03	-0.09
ψ(Urban areas)	0.17	0.18	0.98	-0.17	0.51
ψ(Roads)	-0.17	0.20	0.83	-0.56	0.23
ψ(Puestos)	0.14	0.21	0.64	-0.28	0.56
ψ(Elevation)	0.02	0.20	0.09	-0.37	0.40

Ψ : probability of habitat use; p: probability of detection; Urban areas: distance from the camera trap to the closest city or town, Roads: distance from the camera trap to the nearest road, Rivers: distance from the camera trap to the nearest river, Puestos: distance from the camera trap to the nearest small household, Elevation: vertical distance of a point from the earth to the sea level, Occasion: time calculated in five-days periods. Terms in bold indicate 95% confidence intervals that do not include zero.

(Bennett and Franco-Maya 2002, Alarcón-Nieto and Palacios 2008). We found that for the Yungas Guan, the riparian forests represent a critical forest type, at least in the dry season, although this pattern needs to be confirmed for the rainy season. If the species relies on resources in riparian forests, then the conservation of this forest type should be a priority.

We did not find a significant relationship between the probability of Yungas Guan occurrence and human influence; this result is in contrast to previous findings (Malzof *et al.* 2012, Zalazar *et al.* 2018) reporting both positive and negative associations. For example, the influence of human settlements was reported in the Brazilian Atlantic Forest, where guans suffer high hunting pressure by both the locals and people from urban centres, with drastic reductions in their populations (Pereira-Ribeiro *et al.* 2018). However, in the Southern Yungas, hunting pressure on this species is apparently low (S. Tejerina pers. obs.). It has been suggested that hunting could be an important mortality factor for the Yungas Guan in the Southern Yungas (Ministerio de

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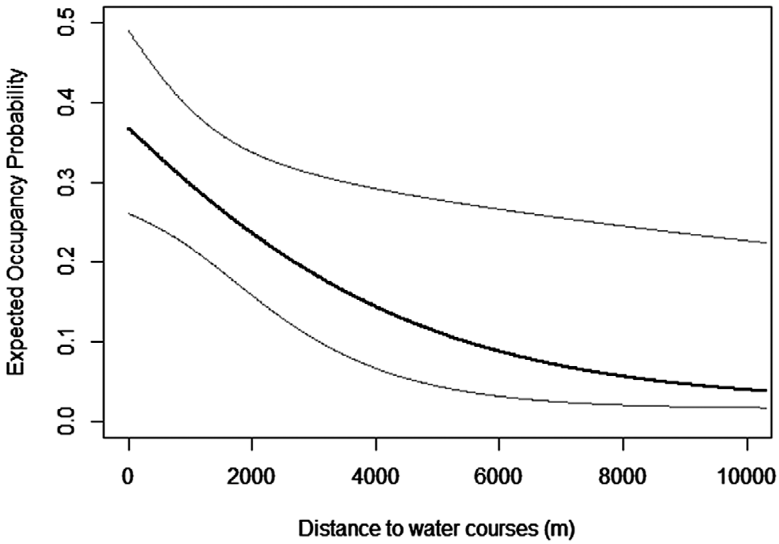

Figure 3. Probability of expected habitat use (bracketed by 95% CI in grey) of Yungas Guan in the Southern Yungas as a function of distance to rivers. This variable explained 44% of the variation in probability of habitat use.

Ambiente y Desarrollo Sustentable and Aves Argentinas 2017); however, we found no published quantitative information about this topic.

Our estimated occupancy value was lower than that reported for other cracid species. For *P. superciliaris* in the Atlantic Forest of Brazil, the probability of occupancy (Ψ) was 0.64, with an increase in occupancy as the distance to roads increased (Pereira-Ribeiro *et al.* 2018). The occupancy value (Ψ) for *Crax fasciolata* throughout the gallery forests of the humid Chaco rivers of Argentina was 0.47, and distance to rivers was less important than distance to human settlements, probably due to high hunting pressure and selective logging of woody species near human settlements (Zalazar *et al.* 2018).

The probability of detection obtained in our work would make feasible to monitor this species with camera traps. Beaudrot *et al.* (2019) suggested that changes of up to 15% in the probability of occupancy within a period of up to three years and using 90 camera traps could be detected. Our work shows the usefulness of camera traps as a sampling tool to study the Yungas Guan. Previous works found this technique to be useful for studying habitat use, occupancy, potential distribution, and behavioural aspects, among other types of data relevant to the study and management of cracid species (O'Brien and Kinnaird 2008, Srbek-Araujo *et al.* 2012, Blake *et al.* 2013, 2017, Michalski *et al.* 2015, Pérez-Irineo and Santos-Moreno 2017).

The global population size of Yungas Guan has not been quantified. However, in a previous assessment of the former Dusky-legged Guan that included Yungas Guan and two other subspecies (*P. o. obscura* and *P. o. bronzine*) (Del Hoyo and Kirwan 2013), the species was described as "frequent" (Stotz *et al.* 1996) in its range. In addition, at the time of the assessment, Dusky-legged Guan was considered far from the thresholds for the IUCN Red List population reduction criteria. For these reasons, the Dusky-legged Guan was categorized as Least Concern (BirdLife International 2021). However, the recognition of Yungas Guan as a separate species implies it is endemic and more vulnerable to different threat factors, since species with restricted distribution are

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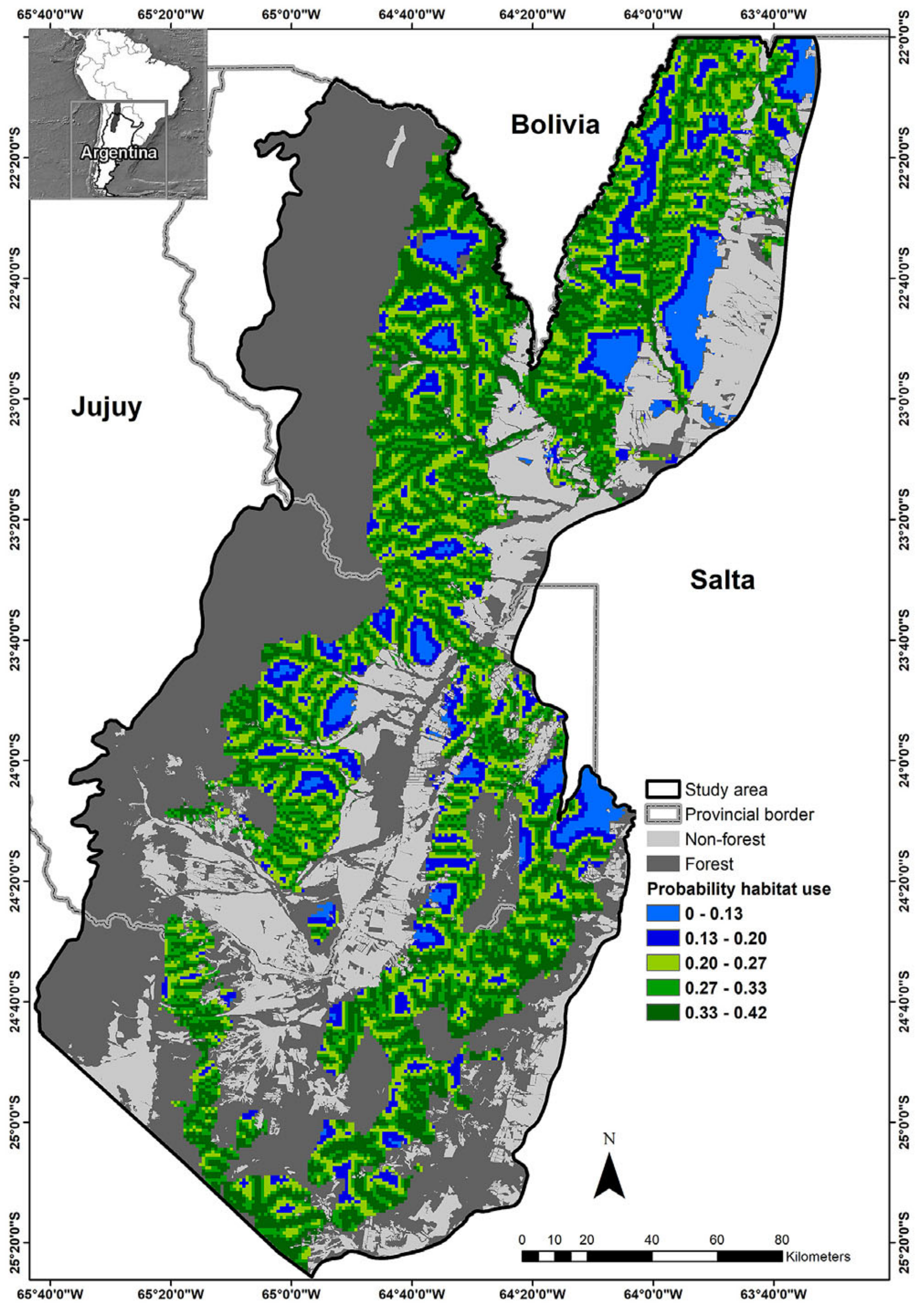

Figure 4. Distribution of the potential habitat and probability of habitat use of the Yungas Guan in the Southern Yungas of Argentina.

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generally habitat specialists or depend on some resource that limits them spatially (Brown 1984, Gaston *et al.* 1997). Additionally, we show that its potential habitat has been reduced by 9% mainly due to land conversion, and that the species has a relatively low probability of habitat use. Therefore, a first assessment of the Yungas Guan's conservation status is urgently needed.

Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270921000563

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