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Effects of landscape, climate and hunting on the occurrence of White-browed Guan *Penelope jacucaca* in central-north Caatinga, Brazil

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ORNITHOLOGICAL SCIENCE

Abstract The White-browed Guan *Penelope jacucaca* is an endangered member of the family Cracidae endemic to the Caatinga region of northeast Brazil. Hunting and habitat loss are the presumed major threats to the species, however, their impacts on its occurrence have been insufficiently tested. We used field observations and information on hunting activity to assess whether hunting, landscape and/or climate affect the occurrence of the White-browed Guan in the Caatinga. We sampled 23 localities within the Caatinga and recorded the species' occurrence and hunting encounters. For each locality, we extracted three landscape metrics (vegetation cover, patch aggregation, and patch richness); two climate variables (temperature seasonality and mean precipitation of the wettest month); and one topographic variable (mean slope). We then used generalized linear models based on proportion to determine if the species' occurrence was related to these environmental factors. We found a greater likelihood of detecting the species in localities with greater slope, greater heterogeneity of habitats and more stable temperatures, whereas hunting activity presented a trend of negative impact on occurrence. Our results emphasize the relevance of using different environmental metrics to implement conservation programs for this threatened species.

Key words Cracidae, Ecology, Game birds, Habitat heterogeneity, Neotropical region

The White-browed Guan *Penelope jacucaca* is a member of the family Cracidae. Its distribution is restricted to the Caatinga, a semiarid region of northeast Brazil, that represents the largest area of dry forest in the Neotropics (Pennington et al. 2000). The species is considered Vulnerable both nationally and globally (Ministério do Meio Ambiente 2014; International Union of Conservation of Nature and Natural Resources 2021), on the presumed basis of hunting and habitat loss (Silveira & Straube 2008). Although there have been several studies of its biology, such as that of Valtuille (2017), most of them have been descriptive with observations on its occurrence (Albano & Girão 2008), behavior (Olmos 1993) and reproduction (Snethlage 1928). Employing a more analytical perspective to determine how the species interacts with its environment has the potential to advance our understanding of its ecology, which could be very important in the development of tools for its conservation.

Birds of the family Cracidae have traditionally been the targets of several human hunting cultures (Brooks 1999), and hunting is the major threat to

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populations of several species (Begazo & Bodmer 1998; Barros et al. 2011). The White-browed Guan is commonly hunted in the Caatinga as a source of protein and for cultural reasons (Albuquerque & Andrade 2002). Declines in populations of the species' due to hunting have been scientifically demonstrated at local scales (Bezerra et al. 2019), and tales of it having vanished have become common amongst its hunters (Valtuille 2017). In this sense, the occurrence of the species is also expected to be affected by hunting, but there is no information on such effects on its occurrence in most parts of the Caatinga, especially outside protected areas (Bezerra et al. 2019). Therefore, to improve the effectiveness of conservation strategies for the White-browed Guan, it is crucial to understand the association between hunting and its occurrence at localities with direct human activities.

Climate change and land conversion are two of the leading causes of biodiversity loss throughout the world (Cardinale et al. 2000), and species with restricted distributions are especially threatened by these factors (Powers & Jetz 2019). Thus, the occurrence of the White-browed Guan may also be determined by climate and habitat loss, since its distribution is strictly limited to a single domain (Delacour & Amadon 2004; Araujo & Silva 2017). The species tends to use habitats that occur exclusively within the Caatinga biome, and climate is also a relevant determinant of its distribution (Bezerra et al. 2019). In addition, it is known that climate and native vegetation cover constrain the avian diversity of the Caatinga (Correia et al. 2020), reinforcing the importance of predicting the occurrence of this cracid based on variables representing climate gradients and landscape structure. In this context, advances in spatial analysis have provided relevant tools for detecting the effects of human disturbances on biodiversity (McGarigal et al. 2012) and have facilitated inferring landscape patterns that are associated with a given biological process (Uuemaa et al. 2009). Hence, uncovering the effects of different landscape metrics on the occurrence of the White-browed Guan could bring new insights into the role of the environment from different perspectives and show whether vegetation loss, fragmentation and/or habitat heterogeneity are related to its occurrence.

Thus, our aim was to determine which factors underlie the occurrence of the White-browed Guan in the central-north Caatinga. This region has areas of high conservation priority (Tabarelli & Silva 2003; Fonseca et al. 2017), yet they have been rarely sampled (Kaminski et al. 2016). We specifically tested whether climate (temperature seasonality and maximum precipitation), vegetation area, vegetation aggregation, habitat heterogeneity, and hunting activity affect the occurrence of the species in this region. Together, our analyses help assess the contribution of local anthropogenic disturbances and climate to the presence of this threatened bird.

MATERIALS AND METHODS

1) An overview of the Caatinga environments of the study area

The central-north Caatinga presents typical semi-arid caatinga-type landscapes, with shallow soils, low annual precipitation (500–1,000 mm) and mainly caatinga shrub vegetation (Velloso et al. 2001) with arboreal caatinga formations on mountain slopes (both formations are considered caatinga *stricto sensu*). Forests relicts (e.g., dry forests) survive in the northern portion of the study area, whereas localities in the southwestern portion include open caatinga or grassland (Andrade-Lima 1981; Prado 2003). The region is extensively used as pasture for goats, which local farmers rear in natural environments (Medeiros et al. 2000).

2) Field sampling

We sampled 23 localities across the central-north Caatinga (Fig. 1) between 2012 and 2015, as part of an environmental licensing study (Fig. 1). All of the localities were located outside protected areas and goats were present. The localities were sampled on at least two occasions (Appendix S1), with ten ornithologist-days per occasion. A study area with a 2−km radius was established at each locality and three traditional bird inventory methods (point counts, linear transects, and unsystematic observations) were performed along existing trails and roads to sample most of the area within each study area. These methods were carried out daily, during the morning (four hours of effort after sunrise) and afternoon (four hours of effort before sunset), for a total of 80 h of sampling effort on each occasion. We considered 80 h of effort to be satisfactory to assume the absence of the White-browed Guan when the species was not recorded. We also assumed the same probability of species encounter regardless of the observer, since all observers participated in training prior to sampling. In this study, all records of the White-browed Guan, regardless of the methodology, were pooled. Due to

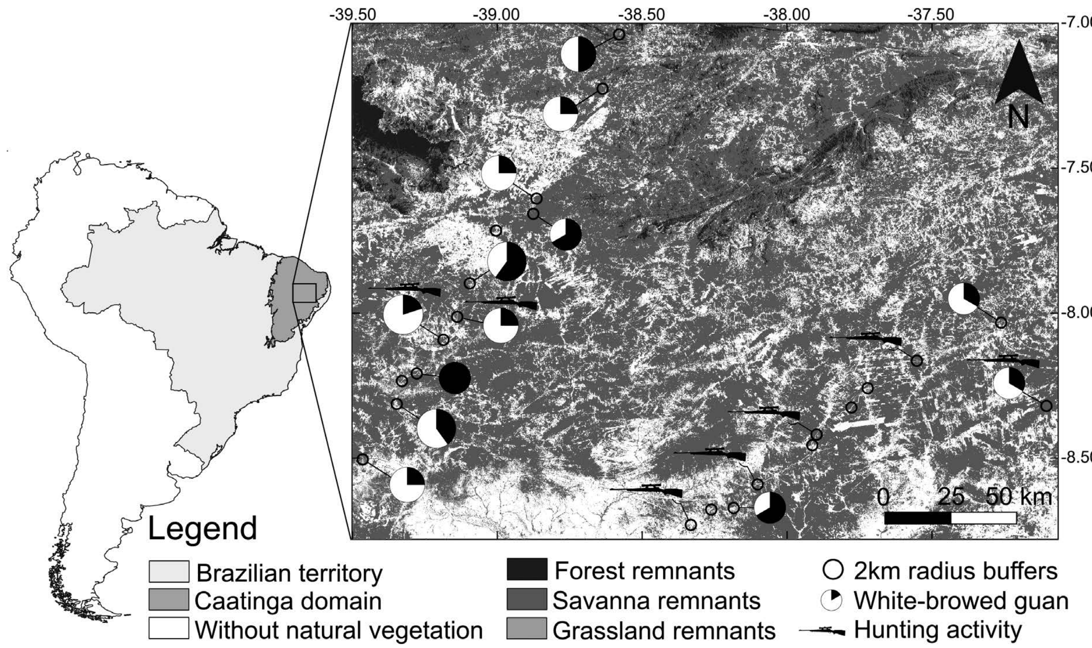

Fig. 1. Map of South America (left), highlighting Brazil and the Caatinga domain and; (right) the 23 sampling localities in the central-north Caatinga (black circles) and the land vegetation cover. Pie charts size refer to the number of the sampling occasion (three to five occasions), black portions indicate White-browed Guan occurrence and rifle silhouettes represent the presence of hunting activity at each locality. Sampling localities without White-browed Guan and hunting records are shown without symbols (for sampling effort see Appendix S1, Table S1).

differences in detectability among methods, a presence/absence record was generated for each sampling occasion without considering the number of individuals observed by each methodology (see Appendix S1 for detailed information on sampling).

3) Hunting, landscape and climate data

At each site, we considered active hunting and hunting blind sites as hunting activities and interviewed people who lived nearby to confirm whether hunting was a constant activity in the area. Based on these interviews, we established that hunting tends to be constant throughout the year, which corroborates the cultural aspects and importance of the focal species to the local people (Valtuille 2017). Thus, we considered hunting to be present at a sampling locality regardless of when it was recorded (Appendix S1).

We characterized the climate for each site based on two bioclimatic variables from WorldClim 2017 (https://worldclim.org/data/bioclim.html), at 1’ arc-minute scale (approximately 2 km^2): temperature seasonality (BIO4) and precipitation of wettest month (BIO13). The first describes differences in annual temperature, with lower values representing more stable temperatures throughout the year. The second variable refers to the total precipitation of the rainiest month of the year. We chose these variables because they have previously been demonstrated as important factors in the distribution of the White-browed Guan in caatinga (Bezerra et al. 2019).

For landscape structure we used three vegetation variables to establish if habitat loss, fragmentation and/or heterogeneity affect White-browed Guan occurrence. We downloaded landcover satellite images from MapBiomas (https://mapbiomas.org/colecoes-mapbiomas-1?cama_set_language=pt-BR, 30 m resolution, satellite image from 2014) and extracted three landscape metrics representing caatinga vegetation within each 2−km radius study area: percentage of vegetation area, which is related to habitat cover; vegetation aggregation index, a fragmentation metric that calculates the percentage of aggregation of a given landscape class, with low values representing dispersed patches and higher values being related to a continuous distribution (McGarigal et al. 2012); and patch richness, which corresponds to natural habitat heterogeneity (Hesselbarth et al. 2019). We considered caatinga *stricto sensu* vegetation in the first two metrics, while the last metric was a count of native vegetation types (forest, caatinga *stricto sensu* and grassland) found within a given study area (1–3 for one to three vegetation types).

The currently available landcover satellite images were not able to distinguish different formations within caatinga *stricto sensu*. However, White-browed Guan presence is usually associated with arboreal caatinga, a vegetation formation found within caatinga *stricto sensu* (Silveira & Straube 2008; Bezerra et al. 2019). This formation is strictly related to regional geomorphology, occurring exclusively on mountain slopes (Prado 2003). Furthermore, the best preserved areas within a given region are generally located on mountain slopes (e.g., "Serra do Mar" region within Atlantic Forest: Ribeiro et al. 2009), where the topography makes land use and land conversion difficult (Elsen et al. 2020). In this context, such slopes may act as refuges for various species that are sensitive to anthropogenic disturbance (Ferreti & Pomarico 2013; Sylvester et al. 2014), such as mammals (e.g., Cougar *Puma concolor*, Dickson & Beier 2007; and Mountain Sheep *Ovis canadensis* Bleich et al. 1994) and snakes (e.g., Lataste's Viper *Vipera latastei*, Santos et al. 2006), and may also benefit White-browed Guan occurrence. Based on these assumptions, we included the mean slope within each study area (2−km radius) as a landscape variable, with low values of slope representing areas of low potential for arboreal caatinga and/or White-browed Guan occurrence. To do this, we downloaded a digital elevation database with 90 m of resolution from SRTM (https://srtm.csi.cgiar.org; Jarvis et al. 2008), computed the terrain slope based on Horn (1981) and calculated the mean slope within each study area. Geographical coordinates and variable values for each sampling locality are provided in Appendix S1.

4) Statistical analysis

We used a generalized linear model (GLM) based on proportional data (binomial error distribution) and considered the number of sampling localities as the sample size. We used the occurrence of the White-browed Guan in each sampling locality (count of presences, count of absences) as the response variable and hunting activity (presence/absence), temperature, seasonality, precipitation in the wettest month, vegetation area, vegetation aggregation, patch richness, and slope, as predictors. Prior to running the model, we centred and scaled continuous and discrete variables (mean=0, SD=1) for a better fit, and validated the global model based on residual distribution, leverage and Cook-distance (Zuur et al. 2009). We also used the Moran I test to assess the spatial dependence of our global model using the 'spdep' package (Bivand et al. 2013) and tested the effect of season on the occurrence of the species using a generalized linear model (binomial distribution). Based on the two latter analyses we found White-browed Guan occurrence to be spatial and temporally independent (space: Moran I statistic standard deviate=1.0737, P=0.141, N=23; season: χ^2=1.112, df=3, P=0.774, N=88).

As landscape and climate variables are usually correlated (Appendix S2), we generated a set of model combinations based on subsets of the global model considering only the subsets without collinear variables as the resulting models. We measured collinearity between variables using Spearman's product moment correlation coefficient (r), adopting a threshold of r <0.5 to keep that variable combination in the models. We also computed a null model in which the response variable was regressed against 1. For each model, we calculated its corrected Akaike's Information Criteria (AICc) and its weight (w). To select the most parsimonious yet informative model, we used a multi-model inference based on Information-Theory (Burnham et al. 2011). We considered corrected Akaike Information delta values less than four (ΔAICc <4) as our condition, and then conducted model averaging to determine the relative importance of each variable across the conditional subset of models in which the focal variable was present. Based on the conditional model averaging, we calculated the estimate (β) and 95% confidence interval (CI) for each variable, considering alpha values lower than 0.05 as significant. This multi-model analysis avoids spurious results commonly observed when selecting the "best" model (Burnham et al. 2011). This analysis was performed in R 3.5.1 (R Development Core Team 2018) and used the MuMIn package (Barton 2018).

RESULTS

1) Overall patterns of White-browed Guan occurrence

We recorded White-browed Guan on 21 of the 88 total sampling occasions (23.86%; Appendix S1). The records were distributed among 13 of the 23 sampling localities (Fig. 1). The highest occurrence proportion (three occasions; 100%) was observed at only one locality, whereas the species was not detected at ten localities (Fig. 1). We also found hunting activity at seven of the sampling localities (Fig. 1).

2) Determinants of White-browed Guan occurrence in the Caatinga

Our averaged resulting models were consistent, with an AICc cumulative weight of approximately 95%, while the null model had an ΔAICc higher than five, which did not meet our condition (ΔAICc <4) (Table 1). Model averaging showed that the occurrence frequency was positively associated with patch richness (β=1.183, CI=0.130 – 2.236, P=0.028, N=23) and slope (β=0.597, CI=0.058 – 1.134, P=0.029, N=23), but negatively related to temperature seasonality (β=−0.629, CI=−1.26 – −0.001, P=0.049, N=23). We found no statistical relationships for the other variables (Fig. 2, Appendix S3); however, it is worth noting a negative tendency for occurrence at localities with hunting activity (β=−1.131, CI=−2.653 – 0.392, P=0.145, N=23). Precipitation in the wettest month was also marginally significant (β=0.496, CI=−0.043 – 1.041, P=0.071, N=23).

DISCUSSION

Our study revealed that the occurrence of the White-browed Guan in the central-north Caatinga is particularly related to patch richness and slope, with both variables having the potential to positively influence occurrence. In addition, temperature seasonality was also related, negatively, to species occurrence. Based on our results and despite the long history of hunting activity targeting this species, we found

Table 1. The best parsimonious resulting models (based on ΔAICc lower than 4.0) used to calculate the effect of climate, landscape and hunting activity on White-browed Guan occurrence. We present the corrected Akaike Information Criteria (AICc), the respective distances form the best model (Δ_i), the AICc weight (w_i) and the cumulative weight. bio4: temperature seasonality; bio13: precipitation in the wettest month; Hunting: hunting activity; PatchRic: patch richness; Slope: mean slope; VegAgg: Caatinga vegetation aggregation index, and; VegArea: percentage of caatinga vegetation area.

Model	AICc	AICc (Δ_i)	AICc weight (w_i)	Cumulative (w_i)
~Hunting+Slope	57.096	0	0.096	0.096
~PatchRic	57.181	0.085	0.092	0.19
~Slope	57.788	0.691	0.068	0.26
~PatchRic+VegAgg	57.935	0.839	0.063	0.32
~Hunting+PatchRic	57.990	0.894	0.061	0.38
~PatchRic+VegArea	58.052	0.955	0.060	0.44
~bio4	58.190	1.093	0.060	0.50
~Hunting+PatchRic+VegAgg	58.272	1.176	0.053	0.55
~Hunting+Slope+VegAgg	58.501	1.405	0.048	0.60
~Hunting+PatchRic+VegArea	58.795	1.698	0.041	0.64
~Hunting+Slope+VegArea	59.284	2.188	0.032	0.67
~bio4+VegAgg	59.319	2.223	0.032	0.70
~bio4+Hunting	59.434	2.338	0.030	0.73
~Slope+VegAgg	59.483	2.387	0.029	0.76
~bio4+VegArea	59.587	2.491	0.028	0.79
~Hunting+VegAgg	59.807	2.711	0.025	0.81
~Slope+VegArea	59.937	2.841	0.023	0.84
~bio4+Hunting+VegAgg	60.038	2.941	0.022	0.86
~bio13	60.158	3.062	0.021	0.88
~bio13+Hunting	60.415	3.318	0.018	0.90
~Hunting+VegArea	60.469	3.372	0.018	0.92
~bio4+Hunting+VegArea	60.530	3.433	0.017	0.93
~Hunting	60.581	3.485	0.017	0.95
~1	63.011	5.914	0.005	NA

hunting only to have a tendency for a negative influence on White-browed Guan occurrence, and without sufficient statistical strength to infer that it is one of the main factors associated with species' occurrence in the sampled region.

The White-browed Guan tends to occupy localities in mountainous areas with more heterogenous vegetation types. Caatinga environments are usually considered homogeneous, although there is wide variation regarding its vegetation (Andrade-Lima 1981). Central-north Caatinga contains dense shrub caatinga formations with mountain slopes covered with arboreal caatinga (Andrade-Lima 1981; Prado 2003). However, there were also grasslands (open caatinga) and forests (seasonally dry forests) in some of our sampling localities (Fig. 2), enhancing habitat heterogeneity. Considering that White-browed Guan occupancy is commonly related to the arboreal caatinga formation (Delacour & Amadon 2004; Roos & Antas 2006), and that heterogeneous landscapes increase resource availability (Oliver et al. 2010), localities with higher patch richness and the presence of hills (higher slope values) may provide more suitable habitats for White-browed Guan. In addition, the species is considered to have a low adaptive capacity, being found only in undisturbed or almost undisturbed ecosystems (Araujo & Silva 2017). Thus, mountain slopes can become refugea for the species, enhancing the relevance of this variable for its occurrence.

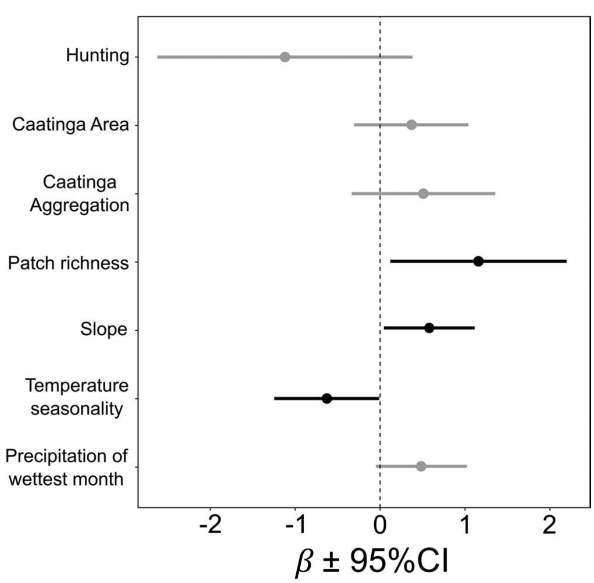

Fig. 2. β estimates and the 95% confidence intervals of the predictor variables for White-browed Guan occurrence. The black bars indicate significant values.

White-browed Guan occurrence was not affected by vegetation cover or vegetation aggregation. The study region harbours large remnants of caatinga *stricto sensu* (Castelletti et al. 2003; Silva & Barbosa 2017) and all but one of the sampled localities had at least 45% native vegetation cover, the exception being one with 27% and where the species was not recorded (Fig. 1; Appendix S1). The lack of a relationship between occurrence and vegetation cover or vegetation aggregation may, therefore, be explained by the high proportion of native vegetation in the sampling localities.

We found the probability of White-browed Guan occurrence in central-north Caatinga to be higher for localities with more stable temperatures throughout the year. Despite the congruence between this climate effect and the predicted distribution of the species (Bezerra et al. 2019), landcover variables tend to be more relevant than climate at finer spatial scales (Tellería 1992) and underlying patterns associated with climate may also be acting on these results. For instance, caatinga vegetation is mainly shaped by climate (Oliveira et al. 2019) with temperature seasonality being one of the major drivers of the distributions of specialist tree species in this biome (Rodrigues et al. 2015). Arboreal caatinga formations largely comprise specialist tree species (e.g., angical: formation dominated by *Anadenanthera macrocarpa*), and are usually associated with the occurrence of the White-browed Guan (Delacour & Amadon 2004). In this context, it is a climatic variable that drives the distribution of caatinga specialist tree species and also affects White-browed Guan occurrence.

The caatinga possesses a semiarid climate with long periods of drought (Andrade-Lima 1981), during which animals of these semiarid environments tend to depend on water holes (Vaughan & Weis 1999), including White-browed Guan (Redies 2013). Here, we found a positive trend between precipitation in the wettest month and White-browed Guan occurrence, indicating that precipitation has some effect on the occurrence of the species in central-north Caatinga. It is important to note that our sampling design did not allow us to relate the occurrence of the species with intermittent water sources nor with riparian vegetation. However, this weak association may be due to the low variability of this climatic variable among the sampled localities, ranging from just 119 mm to 211 mm. Despite precipitation having a positive effect on the presence of water holes (Maltchik & Bianchini 2006), water availability also depends on other variables, such as topography (Rodhe & Seibert 1999). Considering that the sampling localities vary little in precipitation and that slope also affects the presence of water, the occurrence of White-browed Guan in the sampled region may depend upon the ability of a locality to retain water with less precipitation than the amount during the wet season.

We found a weak association between hunting activity and White-browed Guan occurrence in central-north Caatinga. However, this result needs to be interpreted with caution as this human activity presented a negative estimate coefficient with the response variable (Fig. 2). Furthermore, hunting may be found to be a determinant of White-browed Guan occurrence in studies using other spatial scales (e.g., local or even regional), methods (e.g., quantitative methods with hunting records and individual birds) or sample sizes. Human activities are certainly known to be among the greatest threats to cracid birds (Brooks et al. 2006), and with an estimated yearly loss of approximately 109,000 White-browed Guan in the caatinga as a result of poaching (Bezerra et al. 2019), it is certainly likely that this human activity has a negative effect on the species' persistence (Olmos 1993).

The weak association between White-browed Guan occurrence and hunting might, however, be due to other biological reasons, such as the social behaviour and local movements of the species. For example, this guan usually lives in groups, with individuals foraging and resting together (Redies 2013). It is also known to undertake local movements during the dry season to find food and water (Snethlage 1928). Once a group finds resources, its individuals are likely to occupy the area until the late dry season or early wet season (Redies 2013). Hunters may benefit from this behaviour, since individuals need to remain at the same locality because of resource scarcity (Fernandes-Ferreira et al. 2012). In this context, some individuals of a group may be taken by hunters at a given locality, but the group may survive there, albeit with a reduced number of individuals, as we presumably observed during field sampling. In September 2015 (Long: −39.187; Lat: −8.091), we observed three White-browed Guan feeding on seeds of *Anadenanthera macrocarpa* on the ground. On the same occasion, we also encountered a hunter in a blind just a few meters from where the birds were observed, a few minutes after which we heard a gunshot. The following day we recorded only two individuals at the locality. Although we cannot confirm that the hunter took an individual, the presence of only two individuals one day after the shot suggests so, while the other two individuals remained at the locality. Therefore, hunting may have a negative impact on population density in spite of it not being a good predictor of the occurrence of the species in the sampled region.

Central-north Caatinga proved to be a relevant region for the conservation of the White-browed Guan, given that the species was recorded in 56% of the sampling localities. The high proportion of caatinga *stricto sensu* vegetation in the region, combined with its habitat heterogeneity, may meet the biological requirements of the species, thus favouring its occurrence. Climatic factors are determinants of the occurrence of the species, emphasizing the importance of climate in the establishment of conservation areas in the Caatinga (Correia et al. 2020). Furthermore, the presence of hunting is not indicative of the presence or absence of the White-browed Guan at a given locality. Therefore, our results reinforce the importance of establishing protected areas dedicated to safeguarding heterogeneous caatinga remnants with mountain slopes and that account for climate, and thus be fully suitable for White-browed Guan conservation. These results are particularly useful, given the actual present climate change scenario, for implementing efficient conservation efforts for this vulnerable species.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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