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Thomas Denis, Bruno Hérault, Gaëlle Jaouen, Olivier Brunaux, Stéphane Guitet, et al.. Black Curassow habitat relationships in terra firme forests of the GuianaShield: A multiscale approach. *Condor*, 2016, 118 (2), pp.253-273. 10.1650/CONDOR-15-28.1 . hal-01455653

HAL Id: hal-01455653

<https://hal.science/hal-01455653v1>

Submitted on 3 Feb 2017

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RESEARCH ARTICLE

Black Curassow habitat relationships in *terra firme* forests of the Guiana Shield: A multiscale approach

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Submitted February 24, 2015; Accepted December 21, 2015; Published March 2, 2016

ABSTRACT

The Black Curassow (*Crax alector*) is a large game bird with Vulnerable conservation status found in north-central South America. We examined its distributional pattern across French Guiana using a large number of environmental descriptors at 3 scales of analysis: landscape, forest type, and microhabitat. We used a hierarchical model with temporary emigration and imperfect detection for data collected by standard distance sampling methods at 35 study sites. At the landscape scale, Black Curassow density decreased with hunting pressure and increased with steeper slopes in both hunted and unhunted areas. Topography appeared to be a good proxy for Black Curassow ecological requirements and probably reflected habitat quality. At the forest scale, population density was negatively correlated with the abundance of palms and Mimosoideae and positively correlated with the abundance of Lauraceae. Botanical families did not directly influence Black Curassow distribution, but rather determined spatial patterns by being markers of a particular forest type. At the microhabitat scale, Black Curassows used hilltops more frequently than other parts of the local topographical gradient. Our multiscale analysis shows that this species' distribution can be explained by biotic or abiotic conditions, regardless of the scale. For conservation, we recommend maintaining connectivity between Black Curassow populations separated by hunted areas. Our predicted densities could be used to adapt hunting quotas across French Guiana's forests. We show that combining field and remote sensing data helps to understand the ecological processes responsible for Black Curassow habitat relationships.

Keywords: Cracidae, *Crax alector*, hunting, multiscale analysis, species–habitat relationships, *terra firme* forests

Relaciones del *Crax alector* con su hábitat en el bosque de *terra firme* del Escudo guayanés: una aproximación multiescala

RESUMEN

El *Crax alector* es una especie cinegética de ave de gran tamaño, con un estado de conservación vulnerable. Se ha estudiado su patrón de distribución en la Guayana Francesa a partir de numerosas variables ambientales, a tres escalas de análisis: paisaje, tipo de bosque, y microhabitat. Se ha aplicado un modelo jerárquico, con emigración temporal y probabilidad de detección imperfecta, sobre datos obtenidos aplicando un protocolo estandarizado de distance sampling en 35 localidades. A la escala del paisaje, se muestra que la densidad del *Crax alector* disminuyó bajo la presión de caza, y que aumentó en zonas de fuerte pendiente, tanto en áreas con como sin actividad de caza. La topografía parece ser un buen descriptor de los requisitos ecológicos del *Crax alector*, y probablemente informa sobre la calidad del hábitat. A la escala del bosque, la densidad del *Crax alector* está negativamente correlacionada con la abundancia de palmeras y de plantas de la familia Mimosoideae, y positivamente correlacionada con la familia Lauraceae. Las familias de plantas no influyen directamente en la distribución de la especie, pero influyen en el patrón espacial como un indicador de un tipo de bosque particular. A la escala de microhabitat, el *Crax alector* prefiere las cumbres de las colinas que otras partes del gradiente topográfico. El análisis multiescala muestra que la distribución de esta especie puede explicarse por factores bióticos o abióticos según la escala de estudio. Como medidas de conservación se propone mantener la conectividad entre poblaciones, ya que la áreas con caza dividen las poblaciones, así como utilizar las densidades predichas por el modelo para establecer cuotas de caza en la

Guayana Francesa. Se demuestra también que la combinación de teledetección con datos de campo facilita la comprensión los procesos ecológicos que explican los vínculos del *Crax alector* y su hábitat.

Palabras clave: análisis multiescala, bosque de tierra firme, caza, Cracidae, *Crax alector*, relación especie-habitat

INTRODUCTION

Species–habitat relationships occur in geographic and ecological spaces where environmental heterogeneity is expressed at different spatial scales. At each scale, a given population, group, or individual is associated with specific environmental features. We define habitat as the resources and environmental conditions (abiotic and biotic) present in an area that determine the presence, survival, and reproduction of a population, which implies that habitat is species-specific (Hall et al. 1997, Gaillard et al. 2010). The hierarchical approach developed by Johnson (1980) to characterize habitat selection can help to determine the conceptual framework of habitat models by examining species–habitat relationships from the scale of distribution (the broadest scale of species–habitat relationships) to specific requirements, e.g., nest, shelter, and food (the finest scale of species–habitat relationships). The challenge is to identify the scale of analysis (i.e. the spatial extent and spatial resolution of measurement; Rahbek and Graves 2000, Kie et al. 2002, Betts et al. 2006) that will maximize the likelihood of detecting a potential effect of an environmental feature on an animal. Today, remote sensing combined with statistical techniques and GIS has become an extremely useful approach to describe environmental characteristics over large spatial extents (Kerr and Ostrovsky 2003, Peres et al. 2006, Chambers et al. 2007) and is potentially a major methodological step forward for our knowledge of the broadest scales of species–habitat relationships. However, field observation remains the method that provides the most useful data to investigate the finest scales of species–habitat relationships.

Across the Amazon forest basin, landscape heterogeneity (i.e. *terra firme* vs. floodplain forests) is of primary importance for determining primate and bird assemblages (Haugaasen and Peres 2009, Palminteri et al. 2011). Most forested areas in the Guiana Shield do not flood and are classified as *terra firme*. However, recent studies have demonstrated that forest structure and plant community composition (Tuomisto et al. 2003, Gond et al. 2011, Figueiredo et al. 2014, Guitet et al. 2015) are heterogeneous even in *terra firme* forests. Five landscape types have been identified in French Guiana based on geomorphological features (Guitet et al. 2013). Strong subregional patterns (mostly geomorphological) within these landscapes shape alpha and beta tree diversities and beta diversity of medium- to large-bodied vertebrates (Guitet et al. 2014, Richard-Hansen et al. 2015). At smaller spatial

extents, forest structure and dynamics are strongly influenced by topography and soil hydromorphy (Robert and Moravie 2003, Koponen et al. 2004, Ferry and Morneau 2010). Given that the apparent homogeneity of *terra firme* forests throughout the Guiana Shield masks their inherent heterogeneity when observed at a finer scale, we wondered how these multiscale spatial patterns might drive species–habitat relationships.

The Black Curassow (*Crax alector*; Figure 1) is a large game bird found in north-central South America. Across its distributional range (Figure 2), the Black Curassow is threatened by deforestation (e.g., across the Amazon basin), hunting, and trapping (IUCN 2014). In the Guiana Shield, deforestation rates are very low and the inaccessibility of the southern and central forests limits human impacts on Black Curassows (de Thoisy et al. 2010). However, human disturbances such as hunting and forest clearing in the wake of timber harvesting may cause local risks of extinction, and these risks may increase in the coming decades due to human population dynamics in these areas (Wright 2005, INSEE 2014, IUCN 2014). Black Curassows are typically associated with old-growth forests and are considered highly sensitive to disturbance. They are thus considered bioindicators of forest integrity (Brooks 2006, de Thoisy et al. 2010). In French Guiana the Black Curassow occurs only in undisturbed forests, but elsewhere it sometimes occurs in secondary forests that have regrown after clear-cutting often followed by burning (Zent 1997, Borges 1999). In terms of habitat use within their home ranges, the availability of fallen fruit may be particularly important. Black Curassows may supplement their diet with nitrogen-rich leaves and invertebrates as sources of protein (Jimenez et al. 2001, Parra et al. 2001, Erard et al. 2007).

Apart from studies of their diet, little research exists on relationships between Black Curassows and their habitat based on resources and environmental conditions (Kattan et al. 2016). We examined how environmental features shape Black Curassow distribution in French Guiana, in particular in the absence of hunting pressure. We used a multiscale approach inspired by the selection order of Johnson (1980): (1) relationships between Black Curassow populations and French Guiana's forest landscapes (large spatial extent of $\sim 85,000$ km² and coarse-resolution remote-sensing descriptors), referred to as the 'landscape scale'; (2) relationships between Black Curassow populations and French Guiana's forest types (same spatial extent, but with fine-resolution descriptors computed from field-based measurements), referred to as the 'forest scale'; and



FIGURE 1. Black Curassow (*Crax alector*), Nouragues Research Station (CNRS), Nouragues National Nature Reserve (co-managed by the GEPOG and the ONF), Regina, French Guiana, France. Photo credit: Antoine Baglan

(3) relationships of individual Black Curassows with forest microhabitats (small spatial extent of $\sim 50 \text{ km}^2$ and same fine-resolution descriptors), referred to as the ‘microhabitat scale.’ We used both remote sensing and field data to reveal landscape-scale effects (topographic and hydromorphic conditions and forest structure) and forest-scale effects (physical conditions, forest structure, and botanical composition).

METHODS

Study Area

French Guiana (4°N , 53°W) covers $\sim 85,000 \text{ km}^2$ in the eastern part of the Guiana Shield between Suriname and the Brazilian state of Amapá. Elevation ranges between 0 and 200 m a.s.l. (mean = 140 m), with a few peaks above 800 m. The climate is equatorial. Annual rainfall ranges between 3,600 mm in the northeast and 2,000 mm in the south and west. Mean annual temperature is $\sim 26^\circ\text{C}$. The number of consecutive months with $< 100 \text{ mm}$ of

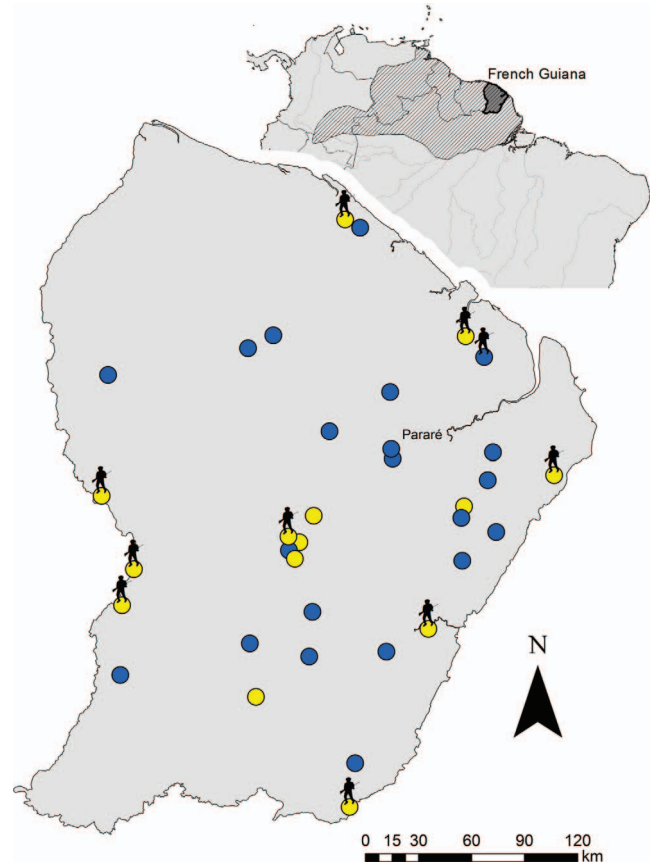


FIGURE 2. The study area in French Guiana, northern South America, covering 35 survey sites for Black Curassows. Yellow circles = sites described by remote sensing data only; blue circles = sites described by remote sensing and field data; hunter on top of circle = sites subject to hunting pressure. The study area is compared with the Black Curassow distributional range (hatched area) in the map to the top (IUCN 2014).

precipitation (dry season) varies from 2 in the north to 3 in the south, with high interannual variation (Sombroek 2001, Wagner et al. 2011). The geological background is a 2.2–1.9-Gyr-old crystalline basement, which makes up the oldest and most homogeneous part of the Guiana Shield (Delor et al. 2003). Savannas and mangroves occur, but exclusively in the coastal sedimentary plain. Evergreen rainforest covers more than 90% of the country (FAO 2010). In 2014, 88% of the population (250,400 people) lived in the coastal strip in human-modified areas (artificial, agricultural, and disturbed areas) covering $\sim 1,000 \text{ km}^2$ (ONF 2011). Outside this area, the average population density is $0.04 \text{ people km}^{-2}$ (INSEE 2014).

This study is based on data from 35 study sites distributed across French Guiana (Figure 2). Among these sites, 10 were close to villages or towns, and thus were easily accessible and regularly hunted. The other 25 sites were located either within territory under strict protection

laws, or far enough (at least 6 km on foot) from human activities to be considered free from hunting pressure, including that from indigenous communities.

Line Transect Censuses

We used standard distance sampling methods to count Black Curassow individuals along line transects (Peres 1999, Jimenez et al. 2003). One design was used for all sampling sites, and consisted of 2–4 individual 3-km transects radiating from a central point. Transects were walked at a speed of $<1 \text{ km hr}^{-1}$ twice daily, once in the morning (07:00–11:00) and once in the afternoon (14:30–18:00) by one observer per transect (C. Richard-Hansen, T. Denis, and others). Observers alternated transects on consecutive days to avoid observer bias. Encounters with Black Curassows (groups or individuals) and their locations along the transect were recorded. The perpendicular distance from the transect to the animal (or group centroid) was measured with a laser range finder to the nearest meter. Surveys were conducted during the dry season (between July 1 and December 31), except for 1 survey in January and 1 in June. Only adult-sized animals were observed during the surveys, likely because hatching takes place after the end of the dry season (Delacour and Amadon 2004, C. Richard-Hansen personal observation) and because birds reach adult size $<1 \text{ yr}$ after hatching (C. Richard-Hansen personal observation). Each site was surveyed once during an 8-day field session. Surveys were conducted between 2000 and 2013, with more than two-thirds (23 of 35) conducted from 2007 onward.

Only one site, Pararé, was surveyed more than once. Sampling surveys were conducted at the Pararé site twice a year (once in the rainy season and once in the dry season) for a period of 6 yr (from 2007 to 2013), representing 11 sampling surveys and a total of 154 half-day replicates. The extended sampling effort ($\sim 920 \text{ km}$ along 2 transects comprising 60 units each) at this site helped to highlight Black Curassow habitat relationships at the microhabitat scale. The Pararé site data were analyzed separately.

Ecological Descriptors

All study sites were located in *terra firme* forests where no long-term flooding occurs. The sites were selected to ensure the most accurate representation of different landscape types in *terra firme* forests (Guitet et al. 2015): coastal plain ($n = 3$ sites); plateau ($n = 9$ sites); mountain ($n = 15$ sites); multiconvex, e.g., dome form ($n = 4$ sites); and multiconcave, e.g., basin form ($n = 4$ sites). Environmental descriptors taken from field data and remote sensing were used for the 3 different scales of analysis.

At the landscape scale ($n = 35$ sites), we used 11 coarse-resolution descriptors extracted from remote sensing data

within a 4-km radius around the centroid of each site. We used a recent geomorphological landform map (Guitet et al. 2013) generated from full-resolution Shuttle Radar Topography Mission (SRTM; 1 arc sec $\sim 30 \text{ m}$) data to obtain mean topographical parameters (slope, elevational range, and elevation). The proportion of hydromorphic areas and dominant geomorphological types (mesoforms, at a resolution of $\sim 10 \text{ km}^2$) was extracted. At 1 km^2 resolution, forest types were taken from remote sensing landscape classes (RSLC) based on the analysis of a 1-yr daily dataset (from January 1 to December 31, 2000) from the VEGETATION sensor of the SPOT-4 satellite (Gond et al. 2011; Appendix Table 3A).

Acquisition of field descriptors was based on the standardized sampling protocol of the HABITAT program, which aims to describe all *terra firme* forests by analyzing the faunal and floral composition (Guitet et al. 2015, Richard-Hansen et al. 2015). Each sampling transect used for animal censuses was divided into 30 0.2-ha units ($100 \times 20 \text{ m}$) described in the field with fine-resolution descriptors as follows: (1) 9 physical condition descriptors (mean slope, mean maximum slope, mean elevational range, elevation, abundance of rocky outcrops, and 4 plant abundances [Rapataceae, *Euterpe* spp., Bromeliaceae, and *Carex* spp.]) as indicators of hydromorphic soil conditions; (2) 15 forest structure descriptors (ordinal variables for understory density, canopy openings [importance of canopy gaps], and liana density, and continuous variables for canopy height, understory palm density, total palm density, total tree density, tree [20–30 cm DBH] density, tree [55–75 cm DBH] density, total tree basal area, tree [20–30 cm DBH] basal area, tree [55–75 cm DBH] basal area, mean number of tree-fall gaps, mean size of tree-fall gaps, and total area of tree-fall gaps); and (3) botanical composition: Density of tree species (trees ha^{-1}) equal to or larger than 20 cm DBH₁₃₀ (diameter at breast height measured 130 cm above the forest floor) using rapid forestry surveys (completed by S. Guitet, O. Brunaux, G. Jaouen, and others) that proved to be sufficiently effective to distinguish 50 botanical families (Guitet et al. 2014). All descriptors were collected over a period of 1 mo before conducting Black Curassow counts.

At the forest scale (subset of 20 sites described in the field and chosen explicitly for the absence of hunting), we used the averaged or summed value for continuous variables (e.g., canopy height or total basal area) to extrapolate from the fine-resolution forest descriptors at the level of transects to the site level (larger scale of analysis). For ordinal variables (abundance of rocky outcrops; Rapataceae, *Euterpe* spp., Bromeliaceae, and *Carex* spp. abundances; understory density; canopy openings; and liana density), we created an index for each site ranging from 0 to 1 using the following linear transformation:

$$Index_i = \sum_{j=1}^k \frac{l_j}{L} \times \frac{j-1}{k-1},$$

where l_j is the number of transect units ordered by category $j = 1, 2, \dots, k$, and L is the total number of transect units at site i . For example, if we consider the ordinal variable V with 3 categories, where $V_1 < V_2 < V_3$ in site A: If $l_1 = 5$, $l_2 = 105$, and $l_3 = 10$ ($L = 120$), then $Index_A = \frac{5}{120} \times \frac{1-1}{3-1} + \frac{105}{120} \times \frac{2-1}{3-1} + \frac{10}{120} \times \frac{3-1}{3-1} = 0.00 + 0.44 + 0.08 = 0.52$; and for $l_1 = 120$, $l_2 = 0$, and $l_3 = 0$, $Index_A = 0$; and for $l_1 = 0$, $l_2 = 60$, and $l_3 = 60$, $Index_A = 0.75$ (see Appendix Table 3B for a complete list, with the transformation type specified in square brackets).

The dataset resulting from the 6-yr survey at Pararé research station was used to examine Black Curassow habitat relationships at the microhabitat scale. We used the same field descriptors for the microhabitat scale as those used at the forest scale, except when the descriptor captured no variability (identical values) across transect units (Appendix Table 3C).

Data Analysis

Environmental features analysis. Explanatory variables are often correlated, and strong collinearity may affect the ability to correctly estimate model parameters and interpret the results of models. Thus, we first ran a principal components analysis (PCA) on the entire set of variables (Rao 1964) at the landscape scale. Secondly, we used the Kaiser (1960) rule, which recommends that only the axes with an eigenvalue at least equal to 1 are kept. Above this threshold, the amount of variance of the component is greater than that contributed by 1 variable. Finally, we kept the explanatory variable most correlated with each selected PCA axis using factorial plans and absolute and relative contributions.

At the forest and microhabitat scales, we first ran a PCA on each of the 2 distinct sets of covariates, i.e. physical condition and forest structure descriptors. For each scale of analysis, we implemented the same methodological framework as above to select the explanatory covariates. We then applied a correspondence analysis (CA) to the 3rd dataset on tree abundance (botanical composition) to show the distributional patterns of families (Hill 1974). The selection of the number of axes was guided by the break in the ranked eigenvalues plot. If no break was observed, we selected the 1st axes that contributed to 80% of the total inertia. Botanical families were chosen based on their absolute and relative contribution and their biological significance.

Modeling Black Curassow habitat relationships. Environmental features can cause major biases due to different sources of measurement error. Among the

landscape types distinguishable from their landform types and forest structure, visibility for observers may be variable, which may affect the detection of animals. Furthermore, the Black Curassow is a large and mobile species with a home range size of at least 80 ha (de Coster 2011), which is close to that of similar cracid species such as the Salvin's Curassow (*Mitu salvini*) and Yellow-knobbed Curassow (*Crax daubentoni*; Parra et al. 2001, Bertsch and Barreto 2008). Temporary emigration (individuals entering and leaving the sampled strip during the survey period) can also bias density estimates because the assumption of a closed population no longer holds. Consequently, we used the generalized distance sampling model of Chandler et al. (2011), which is an extension of the N -mixture models for repeated count data. Compared with other distance sampling methods (Marques and Buckland 2003), the Chandler et al. (2011) model determines the probability of detecting an animal given its presence (p) and the probability of its being present during the survey period (ϕ), thus allowing studies with an open population. This hierarchical model allows inferences to be drawn about the superpopulation size (M) (i.e. the total number of individuals likely to use the sampled strip during the survey period). The superpopulation size is an outcome of a discrete probability distribution (Poisson or negative binomial) with mean (λ). Black Curassow abundance (N , computed as the product of the superpopulation size and ϕ) can be estimated while incorporating multiple covariates in order to: (1) explain variations in density due to environmental features; (2) minimize or eliminate biases due to temporary emigration (the probability that individuals may be out of the sampling area during the survey period = $1 - \phi$); and (3) minimize detection bias when objects are easier to see in some conditions than in others. Akaike's Information Criterion (AIC) was used to compare models.

At each scale of analysis, the abundance of Black Curassows was modeled as a random effect with a negative binomial (landscape and forest scales) or a Poisson (microhabitat scale) distribution (Kéry et al. 2005) using the number of Black Curassows observed per experimental unit and per replicate. All continuous covariates were scaled to avoid convergence problems. We assumed that temporary emigration was constant across experimental units. We applied the half-normal function to the pooled data from all sites at the forest and landscape scales and from all transect units at the microhabitat scale to estimate the detection probability parameters. At the landscape and forest scales, the 2–4 individual 3-km transects were considered as a single line transect (experimental unit). Ten and 13 replicates were carried out during the repeat survey at the landscape and forest scales, respectively. The sampling effort across sites varied from 58 to 174 km (mean 116.3 ± 18.9 SD km) at the landscape scale and from 75 to 226 km (151.2 ± 25.8 km) at the forest scale.

At the microhabitat scale (estimates from the Pararé site), we considered each transect unit (20×100 m) of the 2 3-km transects as an experimental unit. Given the small number of Black Curassows observed (85 individuals) during the 6-yr survey, we cumulated the 154 half-day replicates by 14 half-days to obtain 11 new replicates in order to facilitate model convergence. The sampling effort per transect unit was 15.3 km. We used the Chandler et al. (2011) model to estimate the local distribution of Black Curassows according to the characteristics of microhabitats.

Model selection and model averaging. We ran N -mixture models following Chandler et al. (2011) using Akaike's Information Criterion (AIC) to rank models and to calculate Akaike weights (w_i). Akaike weights may be interpreted as the probability that the model is the 'best' among all of the candidate models. The combined weight (relative importance) of each covariate can be compared by summing the Akaike weights of all models that contain each respective covariate (Burnham and Anderson 2002). A set of all candidate models corresponded to all of the combinations of additive models, and each covariate (and parameter) thus appeared an equal number of times within the candidate model set. At the 3 scales of analysis, the combined weight (relative variable importance) of an environmental covariate can thus be examined to explain Black Curassow habitat relationships. Akaike weights were also used to calculate model-averaged coefficients, such as the environmental covariate parameters and their standard errors. We calculated predictions by model-averaging the density estimates (using function `modavgPred` in R package `AICcmodavg`; Mazerolle 2015) of all candidate models with a Δ AIC lower than 2 units. The model-averaged coefficients of each explanatory covariate were calculated as the sum of the product of the Akaike weights and the estimated coefficients of all the candidate models over the combined weight of the covariate. Cade (2015) stressed that averaging model parameters makes no sense because the scaling of units in the denominators of the regression coefficients changes when there is multicollinearity among predictors. Cade (2015) proposed solutions for multiple linear regression models and generalized linear models. We think that these methods should not apply for the model of Chandler et al. (2011) because their methods have not been validated for this hierarchical model type. Thus, the values of model-averaged parameters are used here to illustrate covariate effects, but not to predict density. In addition, the effects of the most important covariates on Black Curassow density are shown by fixing the values of the other covariates when displaying results in graph form. We did not include the first-order interactions of covariates in the global model because of their large number.

At the landscape scale, we added latitude and longitude to the explanatory remote sensing covariates when building the global model in order to account for a possible regional linear gradient effect. In this way, we tried to avoid a potential unimodal or multimodal pattern within the Black Curassow distributional range caused by climatic or other biophysical conditions (Morrison et al. 2006). Hunting pressure was also included through a presence-absence predictor, because hunting is known to have a strong influence on the density of game species such as the Black Curassow (Peres and Dolman 2000, Bodmer and Robinson 2004, de Thoisy et al. 2009). A site was considered to be hunted when it was easily accessible from roads, trails, or rivers and when there were indications that the area was hunted (e.g., presence of hunters, shotgun cartridges, and other clues, and forest tracks). Given that *terra firme* forests differ in structure and physical characteristics (e.g., topographical differences), we used landscape types as detection covariates in the global model to correct any bias caused by potential differences in visibility among sites at the landscape scale.

At the forest scale, we selected models using 2 stages because the number of sampled sites was still low compared with the number of potential predictor covariates, even though the 3 sets of covariates were reduced by PCA and CA. We first built 3 global submodels, each with a reduced set of field covariates: descriptors of physical conditions, with mean maximum slope, *Carex* spp., and abundance of rocky outcrops; descriptors of forest structure, with tree density [55–75 cm DBH], mean size of tree-fall gaps (ground-surface disturbance), and total tree, total palm, and understory densities; and botanical composition, with *Arecaceae*, *Burseraceae*, *Lauraceae*, *Leguminosae*–*Mimosoideae*, and *Sapotaceae* abundances. Second, we built a final global model including covariates from the previous model selection stage when their combined weight was greater than 0.60. We included latitude and longitude as regional predictors for the same reasons given for the landscape scale. Mean maximum slope and understory density are probably important environmental features affecting observations of this terrestrial species, which is why we tested their effects as detection covariates in the global model. We assumed that the steepest reliefs and densest forests could reduce observer capacity to detect Black Curassows.

At the microhabitat scale, we built the global model with the explanatory covariates retained by PCA and CA for each set of environmental descriptors: descriptors of physical conditions, with mean maximum slope; descriptors of forest structure, with tree [55–75 cm DBH] basal area, tree [20–30 cm DBH] density, canopy height, area of tree-fall gaps, and liana density; and botanical composition, with *Caesalpinioideae* subfamily (*Leguminosae* family). We

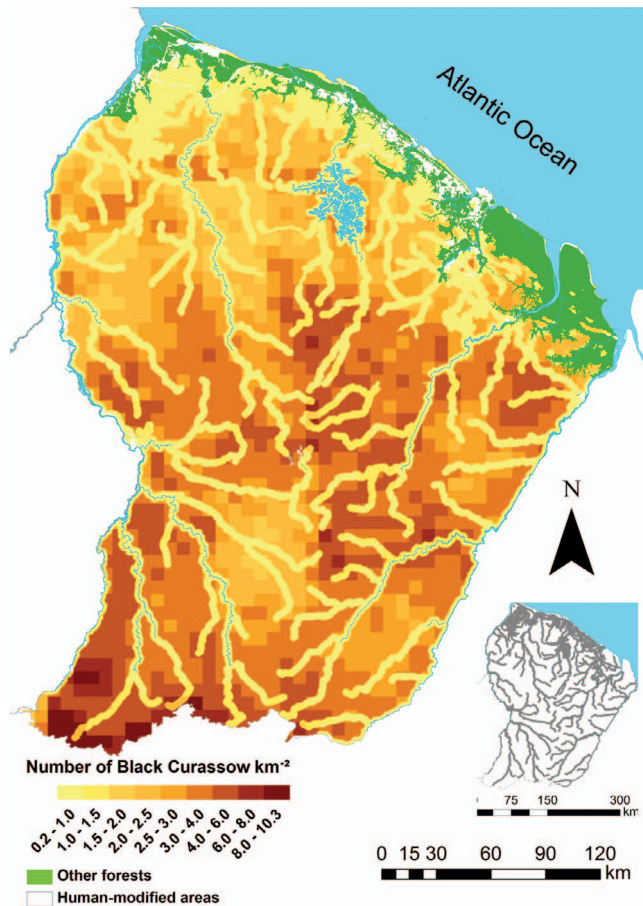


FIGURE 3. Predictive map of the distribution of adult-sized Black Curassow (individuals km^{-2}) in French Guiana according to the landscape-scale model. Black Curassow densities were not estimated outside *terra firme* forests. Forests other than *terra firme* forests (e.g., white-sand forests, seasonally flooded forests such as mangroves, swamp forests) that were not considered in this study are shown in green. Human-modified areas (savannas and artificial, agricultural, and disturbed areas) are represented in white: 90% of the population lives in the coastal strip and western border (expertise foncière du littoral et des territoires isolés de Guyane 2005–2008–2011, from Office National des Forêts [ONF], updated in 2014, <http://www.geoguyane.fr/catalogue/>). Areas of water (main rivers, the reservoir of the Petit Saut hydroelectric dam, and the Atlantic Ocean) are drawn in blue. The areas in gray on the map to the bottom right (2.5-km-wide buffer along the main rivers and roads and around human settlements) were considered to be hunted.

included mean maximum slope and understory density as detection covariates in the global model.

Predictive mapping. Remote sensing data made it possible to extrapolate predictions from the landscape model to all of French Guiana. We calculated the predicted density of Black Curassow individuals (i.e. the predicted number of adult-sized Black Curassows per km^2). Predictions of Black Curassow density on the map are shown at

the same resolution as the descriptors extracted from GIS (i.e. a 50.4-km^2 pixel) an area similar to the 4-km sampling radius around each study site. We estimated that hunting was likely to occur in a 2.5-km-wide buffer zone on each side of the main rivers and roads and around human settlements, excluding strictly protected areas (de Thoisy et al. 2010; see map to the bottom right in Figure 3).

All analyses were performed using R 3.0.3 with the `ade4`, `unmarked`, `AICcmodavg`, and `ggplot2` packages (R Development Core Team 2014).

RESULTS

Landscape Scale

No single landscape-scale model stood out as the best among the top-ranked models (those with the lowest ΔAIC) because all 9 top models differed by <2.0 AIC units (Appendix Table 4A). AIC weights were low, but the large number of candidate models must be taken into consideration. The combined weight of the landscape type covariate was 58%, which lends similar support to the hypotheses that landscape types affect or do not affect detection probabilities. However, the lowest effect on detection probability was found for coastal plain landscapes, while the effect was highest for all-slope topography landscapes (Table 1A). A number of common abundance covariates clearly featured among the top-ranked models. Mean slope and hunting were the most important covariates, with combined weights (relative variable importance) of 96% and 99%, respectively (Table 2A). The number of adult-sized individuals increased as the mean slope became steeper in both hunted and unhunted sites (Figure 4). Although latitude was included in the 2 top-ranked models, the influence of this factor on Black Curassow distribution was uncertain, with a combined weight of 58%. We note, however, that Black Curassow density was correlated negatively with latitude (Table 2A). Estimated Black Curassow density ranged from 0.37 to 1.08 individuals km^{-2} (median: 0.64; 90% range: 0.43–1.06) across the 10 hunted sites, and from 1.47 to 5.31 individuals km^{-2} (median: 2.96; 90% range: 1.99–4.26; $\phi = 0.15$) across the 25 unhunted sites. When we checked for overlap in the confidence intervals for this species–habitat relationship, Black Curassow density differed significantly (based on upper and lower 95% confidence intervals) between hunted and unhunted sites where the mean slope was $>2^\circ$ (Figure 4). Predicted density was calculated for the center of French Guiana (3.755°N , 53.181°W) and using the median values of the other covariates (simple smaller landforms [SSL] = 31.5%, and high forest with regular canopy, mostly *terra firme* forest [RSLC19] = 52.1%).

TABLE 1. Summary of detection covariates in Black Curassow habitat models at multiple scales in the *terra firme* forests of French Guiana. Detection probability is denoted by p . The combined weight (relative importance) of each explanatory covariate was calculated as the sum of the Akaike weights (w_i) across all of the models in which the parameter of interest appeared. The model-averaged coefficients (parameters and standard errors) of each covariate were calculated as the sum of the product of the Akaike weights and the estimated coefficients of all of the candidate models over the combined weight of the covariate. The model-averaged 95% confidence limits (95% CL) were calculated using model-averaged standard errors. For the landscape types (LandS), SLO = all-slope topography landscapes, PLA = more or less dissected plateaus, MCX = typical multiconvex landscapes, PLN = coastal plain landscapes, and MCV = multiconcave and joint-valley landscapes (see landscape classification by Guitet et al. [2013]). For the forest and microhabitat scales, MMS = mean maximum slope, and USD = understory density (see Appendix Table 3).

| | SLO | PLA | MCX | PLN | MCV |
|--------------------------------|-------------|-------------|------------|------------|------------|
| (A) Landscape scale | | | | | |
| Combined weight | | | 0.58 | | |
| Model-averaged parameters, p | 2.84 | 2.68 | 2.73 | 2.25 | 2.79 |
| Model-averaged 95% CL, p | 2.71, 2.97 | 2.55, 2.82 | 2.56, 2.90 | 1.98, 2.51 | 2.15, 3.42 |
| | MMS | USD | | | |
| (B) Forest scale | | | | | |
| Combined weight | | 0.94 | | | |
| Model-averaged parameters, p | -0.06 | 0.08 | | | |
| Model-averaged 95% CL, p | -0.13, 0.01 | -0.08, 0.24 | | | |
| (C) Microhabitat scale | | | | | |
| Combined weight | | 0.13 | | | |
| Model-averaged parameters, p | -0.01 | 0.01 | | | |
| Model-averaged 95% CL, p | -0.28, 0.26 | -0.01, 0.03 | | | |

Forest Scale

The 5 top models (out of 128 candidate models) for the forest scale were very similar, and represented 56% of the cumulative weight of the set of all candidate models (Appendix Table 4B). Mean maximum slope (MMS) and

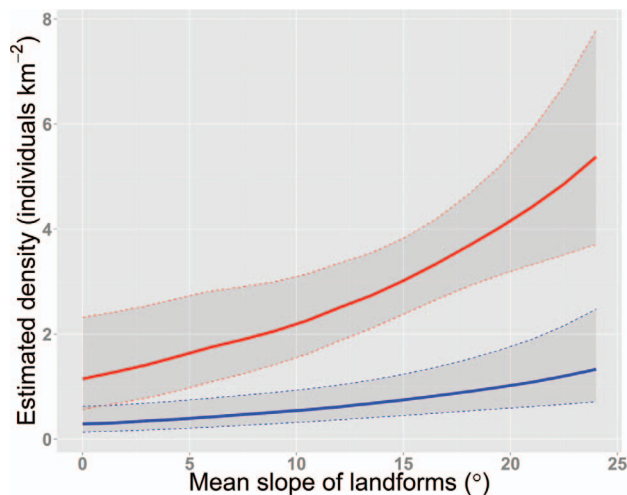


FIGURE 4. Landscape-scale predictions (thick lines) of the estimated density (N) of adult-sized Black Curassow (individuals km^{-2}) in French Guiana in response to the presence (blue line) or absence (red line) of hunting and mean landform slope. Dashed lines represent upper and lower 95% confidence intervals. Density estimates were calculated for the center of French Guiana (3.755°N , 53.181°W) and using the median values of the other covariates (SSL [simple smaller landforms] = 31.5%, and RSLC19 [high forest with regular canopy, mostly *terra firme* forest] = 52.1%).

understory density (USD) had negative and positive effects, respectively, on the probability of detection of Black Curassows (Table 1B), which was consistent with our expectations. The combined weight for $p(\text{MMS} + \text{USD})$ was 94% (Table 1B), which supports the hypothesis that these 2 covariates influence the detection of Black Curassow individuals. With regard to abundance covariates, the combined weights of the Arecaceae, Lauraceae, and Mimosoideae families were 94%, 80%, and 79%, respectively. The effects of Arecaceae and Mimosaceae on abundance were negative, while the effect of Lauraceae was positive (Table 2B, Figure 5). Out of the 51 botanical families, these 3 botanical families were the only ones that were likely to influence Black Curassow distribution. None of the physical descriptors (topography, hydromorphy, and so on) helped to explain Black Curassow distribution at the forest scale. Black Curassow densities ranged from 1.52 to 5.48 individuals km^{-2} (median: 3.01; 90% range: 1.66–4.60; $\phi = 0.13$) across the subset of 20 unhunted sites in which these data were collected.

Microhabitat Scale

The 8 top models, out of 256 candidate models for the microhabitat scale, all had a $\Delta\text{AIC} < 2$ units. No candidate model stood out clearly among these top 8 models (Appendix Table 4C). At this scale, the combined weight of the mean maximum slope and understory density was only 13%, indicating that Black Curassow detection was unlikely to have been affected by these 2 environmental features (Table 1C). These covariates appeared for the first

TABLE 2. Summary of abundance covariates in Black Curassow habitat models at multiple scales in the *terra firme* forests of French Guiana. Population abundance is denoted by λ . The combined weight (relative importance) of each explanatory covariate was calculated as the sum of the Akaike weights (w_i) across all of the models in which the parameter of interest appeared. The model-averaged coefficients (parameters and standard errors) of each covariate were calculated as the sum of the product of the Akaike weights and the estimated coefficients of all of the candidate models over the combined weight of the covariate. The model-averaged 95% confidence limits (95% CL) were calculated using model-averaged standard errors. Covariate abbreviations: MS = remote sensing mean slope; Hunt = hunting pressure; (pres) = presence of hunting pressure; Lat = latitude; Lon = longitude; RSLC19 = high forest with regular canopy (mostly *terra firme* forest); SSL = simple smaller landforms; USD = understory density; TTD = total tree density; Mimo = Mimosoideae abundance; Are = Arecaceae abundance; Lau = Lauraceae abundance; MMS = mean maximum slope; [20–30]BA = tree (20–30 cm DBH) basal area; [55–75]TD = tree (55–75 cm DBH) density; CanH = Canopy height; LD = liana density; TFG = size of tree-fall gaps; and Caes = Caesalpinioideae abundance.

| | Combined weight | Model-averaged parameters, λ | Model-averaged 95% CL, λ |
|---|-----------------|--------------------------------------|----------------------------------|
| (A) Landscape scale: Large spatial extent, coarse resolution (remote sensing data) | | | |
| Hunt | 0.99 | −1.40 (pres) | −1.92, −0.89 |
| MS | 0.96 | 0.28 | 0.10, 0.47 |
| Lat | 0.58 | −0.18 | −0.39, 0.04 |
| RSLC19 | 0.33 | −0.06 | −0.28, 0.16 |
| SSL | 0.31 | −0.05 | −0.23, 0.13 |
| Lon | 0.27 | 0.00 | −0.20, 0.20 |
| (B) Forest scale: Large spatial extent, fine resolution (field data) | | | |
| Are | 0.94 | −0.33 | −0.56, −0.11 |
| Lau | 0.80 | 0.27 | 0.04, 0.49 |
| Mimo | 0.79 | −0.31 | −0.58, −0.03 |
| Lat | 0.48 | −0.12 | −0.29, 0.06 |
| USD | 0.39 | −0.12 | −0.37, 0.13 |
| Lon | 0.30 | 0.01 | −0.20, 0.21 |
| (C) Microhabitat scale: Small spatial extent, fine resolution (field data) | | | |
| CanH | 0.93 | 0.41 | 0.09, 0.73 |
| MMS | 0.74 | −0.36 | −0.68, −0.04 |
| [20–30]BA | 0.55 | 0.17 | −0.04, 0.38 |
| LD | 0.53 | 0.22 | −0.06, 0.49 |
| [55–75]TD | 0.34 | 0.10 | −0.17, 0.39 |
| Caes | 0.31 | −0.07 | −0.41, 0.27 |
| TFG | 0.28 | 0.02 | −0.19, 0.24 |

time in the 25th-ranked model, which had a Δ AIC of 3.99. However, our results showed that canopy height and mean maximum slope stood out among the covariates that influenced abundance, with combined weights of 93% and 74%, respectively. Black Curassow abundance increased with increasing canopy height and decreasing mean maximum slope (Table 2C, Figure 6). Local density ranged from 0.11 to 0.57 individuals per transect unit (median: 0.26; 90% range: 0.15–0.49; $\phi = 0.016$).

Predictive Mapping

From the landscape model, we estimated Black Curassow density (adult-sized individuals km^{−2}) for the whole of French Guiana (Figure 3). The lowest predicted density of Black Curassows was on the coastal plain (low relief and inhabited areas), along the main rivers where there was potential hunting pressure, and in 2 southern parts of the territory corresponding to particular geomorphological landscapes (i.e. multiconcave reliefs; see Guitet et al. 2013). In contrast, predicted Black Curassow density was highest in mountainous forested areas (i.e. areas with steeper

slopes), in the southwestern and central eastern parts of French Guiana.

DISCUSSION

Landscape Scale

Landscape effects. The population distribution of Black Curassows was strongly influenced by topography. Between sampling sites with little topographic variability and more mountainous sites, the predicted densities of Black Curassows varied by a factor of ~ 3 for hunted areas and ~ 4 for unhunted areas. We hypothesize that the relationship between the mean slope of landforms and the population density of Black Curassows is due to the fact that areas with higher mean slopes are those that best meet the ecological requirements of the species.

Topography is an indirect but effective predictor (i.e. good proxy; see Austin and Smith 1990, Guisan and Zimmermann 2000) that integrates information about historical ecological trajectories leading to divergences in *terra firme* forests (Guitet et al. 2015). The mean slope of

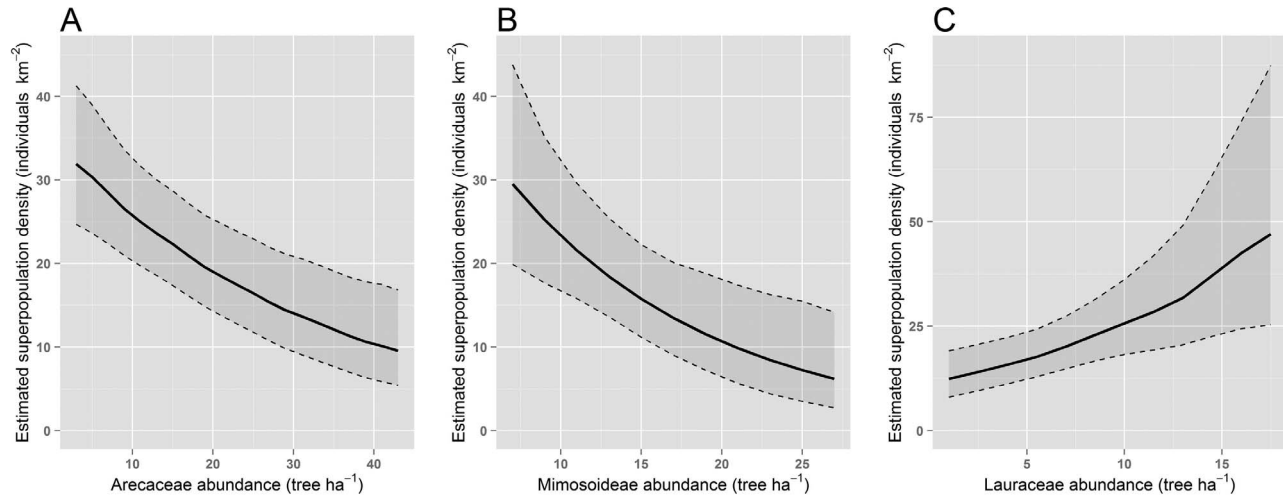


FIGURE 5. Forest-scale predictions (thick lines) of the estimated superpopulation density (M) of adult-sized Black Curassow (individuals km^{-2}) in French Guiana in response to botanical composition: **(A)** Arecaceae, **(B)** Mimosoideae, and **(C)** Lauraceae. Dashed lines represent upper and lower 95% confidence intervals. Density estimates were calculated for the center of French Guiana (3.755°N , 53.181°W) and using the median values of the other covariates: Understorey density (index) = 0.38, Arecaceae = 10 trees ha^{-1} , and/or Mimosoideae = 14.5 trees ha^{-1} , and/or Lauraceae = 4.5 trees ha^{-1} .

landforms was strongly negatively correlated with soil hydromorphy in our dataset ($r^2 = 0.66$, P -value = 1.5×10^{-9}), and in French Guiana reflects a generally varied landscape relief. Together, relief, topography, and soil hydromorphy drive vegetation characteristics such as forest structure and the botanical composition of tropical forests (Vormisto et al. 2004, de Castilho et al. 2006, Ferry and Morneau 2010).

Sites with high curassow density were generally steeper (e.g., plateau and all-slope landscapes). High densities of Black Curassows may be due to decreases in the size of home ranges or to overlap between home ranges. The latter may be important for this species, with an overlap of 45% and 75% (95% kernel method) for 2 home ranges (de Coster 2011). Qualitatively and/or quantitatively, the steepest sites appear to offer better resources and/or environmental conditions for this species.

Another hypothesis to explain the relationship between Black Curassows and mean slope is the influence of long-term human occupation. The main rivers and coastal strip of French Guiana have been inhabited for several thousand years. Hunting impacts may decrease from the inhabited areas and access paths to the steepest areas because the increase in relief may restrict hunters' penetration into the forest. However, in most cases, hunters do not move for more than half a day from their base camp (along rivers) or from access paths, during which time they may walk several kilometers of tropical forest trails, making long-term human disturbance an unlikely explanation for the relationship between Black Curassow population density and mean slope. Furthermore, while human occupation over time may have shaped the distribution of Black Curassows close to the coastal strip, it is unlikely to have

done so in the central and southern parts of French Guiana where human population density is very low (0.04 people km^{-2}) and the human population (27,404 inhabitants) is concentrated in a dozen villages (INSEE 2014).

Hunting in the area as a whole. Our landscape model confirms the vulnerability of the Black Curassow to hunting pressure, a result already found for other Cracidae (Begazo and Bodmer 1998, Brooks et al. 2001, Barrio 2011, Kattan et al. 2016). Hunting is the most important factor explaining the distribution of Black Curassows across French Guiana. Even when optimum resources and conditions are available (steep mean slopes), the population drops to a very low density in sites affected by hunting. Like other Cracidae across the Amazon basin, the Black Curassow is a popular game bird. Its meat is sought after, and its large body size and behavior make it easy to find and hunt when the population density is high (Brooks et al. 2001). During a 15-yr hunting survey carried out in French Guiana, of 8,069 prey animals, Black Curassows represented $\sim 5\%$ of prey animals recorded and 40% of the bird biomass (C. Richard-Hansen personal observation). A preliminary study has already suggested that the Black Curassow is unsustainably hunted across French Guiana (Niel et al. 2008). The high vulnerability of the species to hunting makes it a good candidate to be an indicator of hunting pressure on a broad scale, as highlighted by some authors (Brooks 2006, de Thoisy et al. 2010). However, our results show that the influence of slope on densities also has to be taken into account in the assessment of the potential impact of hunting: in steep areas, a low density of Black Curassows in hunting surveys would probably be an indication of highly unsustainable hunting, whereas in

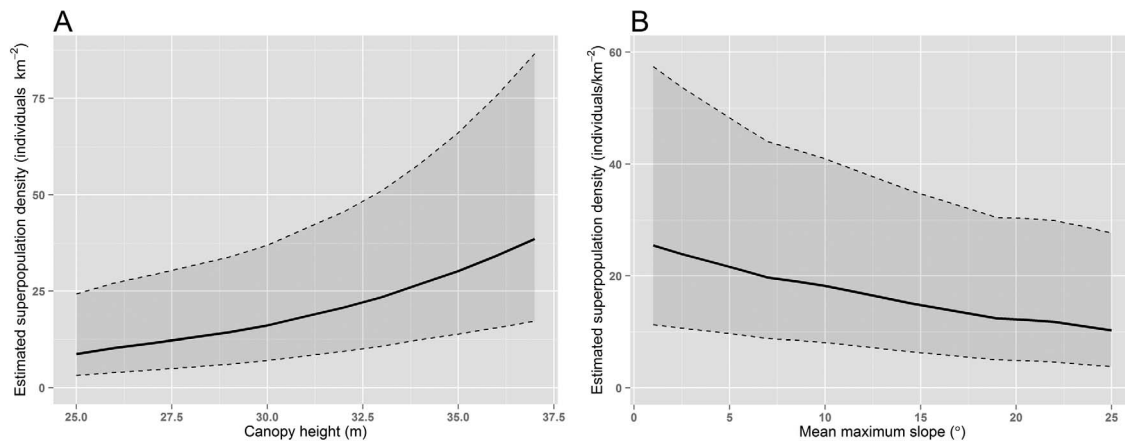


FIGURE 6. Microhabitat-scale predictions (thick lines) of the estimated superpopulation density (M) of adult-sized Black Curassow (individuals km^{-2}) in French Guiana in response to **(A)** canopy height and **(B)** mean maximum slope. Dashed lines represent upper and lower 95% confidence intervals. Density estimates were calculated using the median values of the other covariates: Understorey density (index) = 2.0, mean tree (55–75 cm DBH) density = 23.1 trees ha^{-1} , mean tree (20–30 cm DBH) density = 112.6 trees ha^{-1} , Caesalpinoideae abundance = 40.0 trees ha^{-1} , Liana density (index) = 1, size of tree-fall gaps = 0 m^2 , and mean maximum slope = 12.5° or canopy height = 30 m.

areas with no steep slopes, low densities would mainly be a result of poor habitat quality.

Forest Scale

The forest types associated with the largest Black Curassow populations were characterized by the lowest abundances of Arecaceae (palms) and Mimosoideae and the highest abundance of Lauraceae. A major latitudinal gradient and significant subregional patterns in tree composition have been highlighted in French Guianan forests, which can be explained by the geomorphological features that incorporate current and past environmental filters and historical biogeographical processes (Guitet et al. 2015).

The latitudinal gradient is partly related to the increase in Mimosoideae abundance from north to south. Mimosoideae are also found in high abundance in both the peneplains of the south and on steeply sloping reliefs in forests. Lauraceae abundance is particularly high in the steepest areas (Guitet et al. 2015). Lauraceae is one of the 6 most important plant families in cracid diets (Muñoz and Kattan 2007). However, diets are broad and plastic in Cracidae. Thus, diet is unlikely to explain variation in population density (Muñoz and Kattan 2007, Kattan et al. 2016). Furthermore, in the case of the Pararé site, Lauraceae represents only a low proportion ($\sim 5\%$) of the diet of Black Curassows (Erard et al. 2007), but the population density estimate is high (4.55 individuals km^{-2}) based on the forest model. Complementary information is needed to relate Lauraceae abundance to its dietary role in Black Curassow distribution. In our dataset, the palm taxa were made up of 52% *Oenocarpus* spp. and 33% *Astrocaryum sciophilum*. Guitet et al. (2015) did not note

any patterns in palm distribution across French Guiana. We did not find any concrete interpretation for the effects of botanical families on Black Curassow densities.

At this modeling scale, it is risky to link the effect of a botanical family with a particular type of animal behavior (foraging, nesting, shelter, etc.) because species–habitat relationships occur at the population level and there is therefore no direct tree abundance effect on the behavior of an individual or a group. We do not think that botanical families directly influence Black Curassow distribution, but rather suggest that they determine patterns of favorable or unfavorable habitat distribution associated with particular forest types. Our results at the forest scale were not always consistent with those at the landscape scale, even though our analyses were implemented at the same spatial extent. We focused on ecological processes occurring on a smaller scale than that of the landscape by using fine-resolution descriptors.

Microhabitat Scale

In addition to identifying landscape and forest types favorable for Black Curassow populations, we also tried to identify Black Curassow habitat relationships at the microhabitat scale. Black Curassows were considerably more common in areas with the highest trees and the flattest topography (i.e. on hilltops). These microhabitats were visited 5 times more often than others. Our data showed that the average canopy height of bottomlands (28 m) was shorter than that of slopes (32.5 m) and hilltops (31.1 m). Considering that the Black Curassow diet comprises a high proportion of fruits (Erard et al. 1991, 2007, Muñoz and Kattan 2007), mainly from tall trees, hilltops may be important for foraging. Black Curassows

also consume a significant proportion of fruits from shrubs and smaller trees (Erard et al. 2007) that can be found in other microhabitats. However, bottomlands such as riversides and *Euterpe*-dominated forests situated mainly along the southern transects and slopes along the northern transects were used less frequently than hilltops.

The Black Curassow is a mobile species that uses the center of its stable home range more frequently than the edges (de Coster 2011). This biological characteristic may produce spatial autocorrelation, e.g., locations close to each other may display more similar values than those farther apart (Dormann et al. 2007). Black Curassow distribution in core home ranges may therefore be spatially dependent. Black Curassows may be found in unfavorable or 'neutral' areas simply because they are close to other favorable areas within the core home range.

We did not include spatial autocorrelation in this study. The model of Chandler et al. (2011) makes the use of most methods impossible by reducing spatial autocorrelation in model residuals. Not having found any satisfactory methods that would have allowed us to take spatial autocorrelation into account, coefficient estimates may consequently be biased (Dormann et al. 2007). Given that our microhabitat-scale analysis was conducted at only one site (Pararé), we must be cautious in extrapolating Black Curassow habitat relationships to the rest of French Guiana. Available resources and environmental conditions differ, thereby affecting microhabitat choices (Gaillard et al. 2010). Moreover, species–habitat relationships are generally density dependent (Gadenne et al. 2014).

Predictive Mapping

Predictive mapping based on mean slope and hunting pressure revealed significant heterogeneity in the distribution of Black Curassow populations (Figure 3). It is generally believed that population abundance is a reliable way of measuring the habitat quality of a species on a broad scale (Bock and Jones 2004, Johnson 2007), but this is not necessarily the case at the local scale (Van Horne 1983). The predictive map of Black Curassow distribution shows that low densities may occur even in remote areas because of poor habitat quality, which, combined with hunting pressure and considering other recent studies on threats to this species (de Thoisy et al. 2010, Clément et al. 2014), should be taken into account in defining the conservation status of the Black Curassow.

Predictive maps have a number of direct and indirect management applications as decision-support tools for the development of conservation policies. From our predictive map of Black Curassow distribution, we recommend, as the best course of action, maintaining connectivity between Black Curassow populations across French Guiana's forests by (1) partly restricting hunting along rivers, roads, and trails, particularly in the north,

and (2) planning protected areas to optimize reserve functions and corridors (Saunders et al. 1991) according to the habitat quality of this sensitive species. Mountainous areas where Black Curassows are most abundant are also those with a high rate of endemism and rare species, thus providing more diverse and singular environmental conditions (e.g., plateaus on lateritic crust, deep valleys, cliffs, and granitic outcrops; see de Granville et al. [1993] and Sarthou et al. [2003] for vascular plants). Therefore, optimum Black Curassow habitat is potentially of high conservation value.

However, with almost 30% of French Guiana already under high protection status, it is unlikely that many new protected areas will be created in the future. A second, and perhaps more realistic, course of action would be to introduce direct restrictions on the hunting of Black Curassows, either through species protection measures or by setting hunting quotas, as was recently done in French Guiana (see Order of the Prefect no. 583, Guiana Environment, Planning and Housing Directorate, April 12th, 2011, which sets hunting quotas for various species including the Black Curassow). The variation in density estimates for Black Curassows across the whole of French Guiana, which is related to habitat characteristics, should be taken into account when establishing hunting quotas. However, sustainable quotas for this species would need to be low as our results lead us to believe that, whatever the intensity of hunting pressure, Black Curassow density is always close to zero in hunted areas.

How far human disturbance affects the distribution of the species is difficult to estimate spatially because it depends on many complex factors. The exact locations and sizes of areas affected by hunting strongly depend on ease of access, distance to a populated area, and hunting practices (Peres and Lake 2003, Kumara and Singh 2004, Willcox and Nambu 2007, Parry et al. 2009). The hunted area estimate (map to the bottom right in Figure 3) should be refined, especially in areas that are more remote from the coastal strip and from inhabited areas. Even when rivers are large enough to reach these areas, the distance from a village could reduce the area actually hunted, particularly in the sparsely populated south of French Guiana, because access to more remote areas is costly and time consuming. Another required refinement is to adjust for high mean slope values, found in the extreme southwest of French Guiana due to the number of rocky outcrops (inselbergs), and thus overestimation of Black Curassow densities. The species does not often use the tops of these granitic outcrops, but can be found in high forests at their feet. There is a threshold value at which the effect of mean slope on Black Curassow density decreases. Furthermore, because of the lack of data on the steepest sites, there is significant uncertainty as regards Black Curassow density where the mean slope is $>20^\circ$ (Figure 4).

Our predictive map closely resembles the map based on the geomorphological landscape classification of Guitet et al. (2013; Appendix Table 5, Appendix Figure 7). This confirms a landscape approach as a promising management and conservation tool for French Guiana (Richard-Hansen et al. 2015).

Conclusions

We showed that abiotic conditions (topographic descriptors) determined the spatial distribution of the Black Curassow at the landscape and microhabitat scales, while biotic conditions (botanical composition and canopy height) were important at the forest and microhabitat scales. Our results for the different scales studied show that the distribution of this species may be explained by both biotic and abiotic conditions, but that neither type is more closely associated with one scale or another.

Combining field and remote sensing data in a multiscale approach to species–habitat relationships helps our understanding of the underlying biological processes of these relationships and our interpretation of which habitat components are chosen by a species. Several studies have implemented this kind of strategy to identify how a species perceives and responds to resources or environmental gradients (Kie et al. 2002, Betts et al. 2006), underlining the importance of taking spatial extent and measurement resolution into account (Guisan and Zimmermann 2000, Morrison et al. 2006). For our study, the mean slope measured by remote sensing over large areas was a relevant predictor of distribution, whereas the mean slope measured along linear transects during field sampling was not, which shows that ecological significance may differ depending on spatial resolution. Remote sensing data made it possible to extrapolate density predictions and to build density distribution maps. Data from remote sensing or other GIS layers reflect not only biophysical conditions (Kerr and Ostrovsky 2003), but also anthropic disturbances (Peres et al. 2006). Greater availability of such data, together with new modeling techniques and GIS tools, should make it easier to map species distributions, not only over large spatial extents but also at smaller spatial scales, and to work at finer resolutions, e.g., to examine species–habitat relationships within the home range (Palminteri et al. 2012, Nagendra et al. 2013).

ACKNOWLEDGMENTS

We are very grateful to all participants in the line transect surveys, including those from the ONCFS (Office National de la Chasse et de la Faune Sauvage) and PAG (Parc Amazonien de Guyane) institutions and some hard-working and passionate volunteers. Special thanks to Stéphane Traissac, Marie-Pierre Etienne, Héctor Rodríguez-Pérez, and Hervé Lormée for their assistance, corrections, and constructive comments

on how to improve the manuscript. The authors are grateful to 2 anonymous reviewers and the Associate Editor, Amy Davis, for helpful comments on previous versions of the manuscript.

Funding statement: Funding was provided over many years by ONCFS and various external sources: the EU *HABITAT* and *CHASSE* programs, the French Ministry for Overseas Territories, the French Ministry of the Environment (ECO-TROP program), the Parc Amazonien de Guyane (PAG), Office National des Forêts, and the CNRS (Centre national de la recherche scientifique) Nouragues program. T.D. and B.H. were supported by a grant from the Investing for the Future program (Investissements d'Avenir) managed by the French National Research Agency (Agence nationale de la recherche, CEBA, ref. ANR-10-LABX-0025). None of the funders had any input into the content of the manuscript, nor required their approval of the manuscript before submission or publication.

Ethics statement: The animals were not treated badly nor captured. Data were collected respecting the lives and the habitats of the animals.

Author contributions: T.D., B.H., G.J., S.G., O.B., and C.R.-H. conceived the idea, design, or experiment (supervised research, formulated question or hypothesis); T.D., G.J., S.G., O.B., and C.R.-H. performed the experiments (collected data, conducted the research); T.D., B. H., G.J., S.G., and C.R.-H. wrote the paper (or substantially edited the paper); T.D., B. H., S.G., and C.R.-H. developed or designed the methods; and T.D. analyzed the data.

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APPENDIX TABLE 3. Summary of explanatory covariates in Black Curassow habitat models at multiple scales in the *terra firme* forests of French Guiana. VFL = very flat landforms; SSL = simple smaller landforms; LCL = large complex landforms; HL = high landforms (Guitet et al. 2013); RSLC18 = low dense forest, including savanna on poorly drained soils; RSLC19 = high forest with regular canopy (mostly *terra firme* forest); RSLC20 = high forest with disrupted canopy; RSLC21 = mixed high open forest; and RSLC22 = open forest and *Euterpe* spp. palm forest (Gond et al. 2011). Terms in square brackets represent the transformation type used to change the scale from transect units (fine-resolution field descriptors) to sites (larger scale of analysis).

| | Median (90% range) | Units | Ecological significance |
|---|---------------------|----------------------------------|-----------------------------------|
| (A) Landscape scale: Large spatial extent, coarse resolution (remote sensing data) | | | |
| Hydromorphic area rate | | | |
| Mean elevation | 0.29 (0.20–0.48) | — | Physical conditions (hydromorphy) |
| Mean slope of landforms | 131.5 (48.3–348.5) | m | Physical conditions (topography) |
| Mean elevational range of landforms | 13.6 (7.8–21.3) | degrees | Physical conditions (topography) |
| Proportion of VFL | 57.8 (26.7–114.7) | m | Physical conditions (topography) |
| Proportion of SSL | 0.01 (0.00–52.00) | % | Physical conditions (topography) |
| Proportion of LCL | 28.8 (2.7–76.7) | % | Physical conditions (topography) |
| Proportion of HL | 23.1 (0.1–76.7) | % | Physical conditions (topography) |
| Proportion of RSLC18 | 13.8 (0.0–79.1) | % | Physical conditions (topography) |
| Proportion of RSLC19 | 0.0 (0.0–23.5) | % | Forest structure |
| Proportion of RSLC20 | 45.1 (0.0–93.4) | % | Forest structure |
| Proportion of RSLC21 | 2.1 (0.0–37.7) | % | Forest structure |
| Proportion of RSLC22 | 20.4 (0.0–80.2) | % | Forest structure |
| (B) Forest scale: Large spatial extent, fine resolution (field data) | | | |
| Mean slope [mean] | 9.0 (4.6–16.0) | degrees | Physical conditions (topography) |
| Mean maximum slope [mean] | 20.2 (10.6–36.4) | degrees | Physical conditions (topography) |
| Mean elevation [mean] | 130.6 (48.6–333.6) | m | Physical conditions (topography) |
| Mean elevational range [mean] | 8.8 (4.6–15.2) | m | Physical conditions (topography) |
| Rocky outcrops abundance [index] | 0.01 (0.00–0.38) | — | Physical conditions (pedology) |
| Rapateaceae abundance [index] | 0.02 (0.00–0.12) | — | Physical conditions (hydromorphy) |
| <i>Euterpe</i> spp. abundance [index] | 0.03 (0.00–0.15) | — | Physical conditions (hydromorphy) |
| Bromeliaceae abundance [index] | 0.00 (0.00–0.06) | — | Physical conditions (hydromorphy) |
| <i>Carex</i> spp. abundance [index] | 0.00 (0.00–0.06) | — | Physical conditions (hydromorphy) |
| Understorey density [index] | 0.68 (0.51–0.83) | — | Forest structure |
| Canopy opening [index] | 0.66 (0.54–0.82) | — | Forest structure |
| Canopy height [mean] | 33.6 (28.7–41.9) | m | Forest structure |
| Liana density [index] | 0.35 (0.13–0.43) | — | Forest structure |
| Understorey palm density [mean] | 201.3 (105.4–387.7) | palms ha ⁻¹ | Forest structure |
| Total palm density [mean] | 254.8 (139.7–433.8) | palms ha ⁻¹ | Forest structure |
| Total tree density [mean] | 194.0 (161.6–217.8) | trees ha ⁻¹ | Forest structure |
| Total basal area [mean] | 24.5 (20.1–26.6) | m ² ha ⁻¹ | Forest structure |
| Tree (20–30 cm DBH) density [mean] | 112.6 (76.9–133.6) | trees ha ⁻¹ | Forest structure |
| Tree (55–75 cm DBH) density [mean] | 23.1 (17.1–27.5) | trees ha ⁻¹ | Forest structure |
| Tree (20–30 cm DBH) basal area [mean] | 5.2 (2.7–6.2) | m ² ha ⁻¹ | Forest structure |
| Tree (55–75 cm DBH) basal area [mean] | 7.2 (5.2–8.6) | m ² ha ⁻¹ | Forest structure |
| Mean number of tree-fall gaps [mean] | 0.55 (0.21–1.20) | gaps transect unit ⁻¹ | Forest structure |
| Mean size of tree-fall gaps [mean] | 166.7 (80.4–311.7) | m ² | Forest structure |
| Total area of tree-fall gaps [sum] | 2.0 (0.8–3.6) | ha | Forest structure |
| 51 botanical subfamilies or families of trees [mean] | | trees ha ⁻¹ | Botanical composition |

APPENDIX TABLE 3. Continued.

| | Median (90% range) | Units | Ecological significance |
|---|---------------------|----------------------------------|-----------------------------------|
| (C) Microhabitat scale: Small spatial extent, fine resolution (field data) | | | |
| Mean slope | 6.1 (0.9–22.2) | degrees | Physical conditions (topography) |
| Mean maximum slope | 12.5 (2.5–30.1) | degrees | Physical conditions (topography) |
| Mean elevation | 70.2 (57.2–109.6) | m | Physical conditions (topography) |
| Mean elevational range | 5.5 (1.0–21.3) | m | Physical conditions (topography) |
| Rocky outcrops abundance | 0 (0–0) | — | Physical conditions (pedology) |
| <i>Euterpe</i> spp. abundance | 0 (0–1) | — | Physical conditions (hydromorphy) |
| Understory density | 2 (1–3) | — | Forest structure |
| Canopy opening | 2 (1–2) | — | Forest structure |
| Canopy height | 30 (25–35) | m | Forest structure |
| Liana density | 1 (1–2) | — | Forest structure |
| Understory palm density | 136.1 (39.5–298.4) | palms ha ⁻¹ | Forest structure |
| Total palm density | 153.0 (60.4–397.3) | palms ha ⁻¹ | Forest structure |
| Total tree density | 161.3 (103.0–260.4) | trees ha ⁻¹ | Forest structure |
| Total basal area | 24.3 (13.1–32.1) | m ² ha ⁻¹ | Forest structure |
| Tree (20–30 cm DBH) density | 80.3 (41.1–154.9) | trees ha ⁻¹ | Forest structure |
| Tree (55–75 cm DBH) density | 24.9 (20.1–73.8) | trees ha ⁻¹ | Forest structure |
| Tree (20–30 cm DBH) basal area | 3.5 (2.0–6.4) | m ² ha ⁻¹ | Forest structure |
| Tree (55–75 cm DBH) basal area | 7.2 (5.7–46.0) | m ² ha ⁻¹ | Forest structure |
| Number of tree-fall gaps | 0 (0–1) | gaps transect unit ⁻¹ | Forest structure |
| Size of tree-fall gaps | 0 (0–148) | m ² | Forest structure |
| 51 botanical subfamilies or families of trees | | trees ha ⁻¹ | Botanical composition |

APPENDIX TABLE 4. Summary of the modeling results for Black Curassow habitat relationships at multiple scales in the *terra firme* forests of French Guiana. For each model, Δ AIC is the difference between the model's Akaike's Information Criterion (AIC) value and the minimum AIC of the set of all candidate models (landscape = 128 candidate models, forest = 128, microhabitat = 256), and w_i is the Akaike weight for a model, representing the probability that a given model is the best model in the set of candidate models. For each model description, Cum.w = cumulative Akaike weight; K = the number of estimated parameters; and $-2l$ = the negative log-likelihood. Models are ranked in ascending order of Δ AIC, and only the top 9 models are shown for each scale. Detection probability is denoted by p , and λ represents population abundance. LandS = landscape types (Guitet et al. 2013), MS = mean slope determined by remote sensing, Hunt = presence or absence of hunting pressure, Lat = latitude, Lon = longitude, RSLC19 = high forest with regular canopy (mostly *terra firme* forest), SSL = simple smaller landforms, USD = understory density, TTD = total tree density, Mimo = Mimosoideae abundance, Are = Arecaceae abundance, Lau = Lauraceae abundance, MMS = mean maximum slope, [20–35]BA = tree (20–35 cm DBH) basal area, [55–75]BA = tree (55–75cm DBH) basal area, CanH = canopy height, LD = liana density, TFG = size of tree-fall gaps, and Caes = Caesalpinioideae abundance.

| Model description | Δ AIC | w_i | Cum.w | K | $-2l$ |
|--|--------------|-------|-------|-----|--------|
| (A) Landscape scale: Large spatial extent, coarse resolution (remote sensing data) | | | | | |
| $p(\text{LandS}) \lambda(\text{MS} + \text{Hunt} + \text{Lat})^a$ | 0.00 | 10% | 10% | 11 | 2012.4 |
| $p(.) \lambda(\text{MS} + \text{Hunt} + \text{Lat})$ | 0.04 | 10% | 20% | 7 | 2020.5 |
| $p(.) \lambda(\text{MS} + \text{Hunt})$ | 0.29 | 9% | 29% | 10 | 2014.7 |
| $p(\text{LandS}) \lambda(\text{MS} + \text{Hunt} + \text{RSLC19})$ | 1.34 | 5% | 34% | 11 | 2013.8 |
| $p(.) \lambda(\text{MS} + \text{SSL} + \text{Hunt} + \text{Lat})$ | 1.38 | 5% | 39% | 8 | 2019.8 |
| $p(\text{LandS}) \lambda(\text{MS} + \text{SSL} + \text{Hunt} + \text{Lat})$ | 1.72 | 4% | 43% | 12 | 2012.1 |
| $p(.) \lambda(\text{MS} + \text{RSLC19} + \text{Hunt} + \text{Lat})$ | 1.93 | 4% | 47% | 8 | 2020.4 |
| $p(\text{LandS}) \lambda(\text{MS} + \text{RSLC19} + \text{Hunt} + \text{Lat})$ | 1.97 | 4% | 51% | 12 | 2012.4 |
| $p(\text{LandS}) \lambda(\text{MS} + \text{Hunt} + \text{Lon} + \text{Lat})$ | 1.99 | 4% | 55% | 12 | 2012.4 |
| (B) Forest scale: Large spatial extent, fine resolution (field data) | | | | | |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Lau} + \text{Are} + \text{Lat} + \text{Mimo})^b$ | 0.00 | 18% | 18% | 10 | 1733.5 |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Lau} + \text{Are} + \text{Mimo})$ | 0.27 | 16% | 34% | 9 | 1735.8 |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Lau} + \text{Are} + \text{Lat} + \text{Mimo} + \text{USD})$ | 1.63 | 8% | 42% | 11 | 1733.2 |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Lau} + \text{Are} + \text{Lat} + \text{Mimo} + \text{Lon})$ | 1.78 | 7% | 49% | 11 | 1733.3 |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Lau} + \text{Are} + \text{Mimo} + \text{USD})$ | 1.95 | 7% | 56% | 10 | 1735.5 |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Lau} + \text{Are} + \text{Mimo} + \text{Lon})$ | 2.12 | 6% | 62% | 10 | 1735.7 |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Lau} + \text{Are} + \text{Lat} + \text{Mimo} + \text{USD} + \text{Lon})$ | 3.5 | 3% | 65% | 12 | 1733.0 |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Are} + \text{USD})$ | 3.82 | 3% | 68% | 8 | 1741.4 |
| $p(\text{MMS} + \text{USD}) \lambda(\text{Lau} + \text{Are} + \text{Mimo} + \text{USD} + \text{Lon})$ | 3.87 | 3% | 71% | 11 | 1735.4 |
| (C) Microhabitat scale: Small spatial extent, fine resolution (field data) | | | | | |
| $p(.) \lambda(\text{MMS} + [55-75]\text{BA} + \text{CanH} + \text{LD})^c$ | 0.00 | 7% | 7% | 7 | 723.1 |
| $p(.) \lambda(\text{MMS} + \text{CanH} + \text{LD})$ | 0.07 | 7% | 14% | 6 | 725.2 |
| $p(.) \lambda(\text{MMS} + [55-75]\text{BA} + \text{CanH})$ | 0.72 | 5% | 19% | 6 | 725.8 |
| $p(.) \lambda(\text{MMS} + \text{CanH})$ | 0.93 | 5% | 24% | 5 | 728.1 |
| $p(.) \lambda(\text{MMS} + [20-35]\text{BA} + [55-75]\text{BA} + \text{CanH} + \text{LD})$ | 1.27 | 4% | 28% | 8 | 722.4 |
| $p(.) \lambda(\text{MMS} + [20-35]\text{BA} + \text{CanH} + \text{LD})$ | 1.47 | 4% | 32% | 7 | 724.6 |
| $p(.) \lambda(\text{MMS} + [55-75]\text{BA} + \text{CanH} + \text{LD} + \text{Caes})$ | 1.97 | 3% | 35% | 8 | 723.1 |
| $p(.) \lambda(\text{MMS} + [55-75]\text{BA} + \text{CanH} + \text{TFG} + \text{LD})$ | 1.99 | 3% | 38% | 8 | 723.1 |
| $p(.) \lambda(\text{MMS} + \text{CanH} + \text{LD} + \text{Caes})$ | 2.04 | 3% | 41% | 7 | 725.2 |

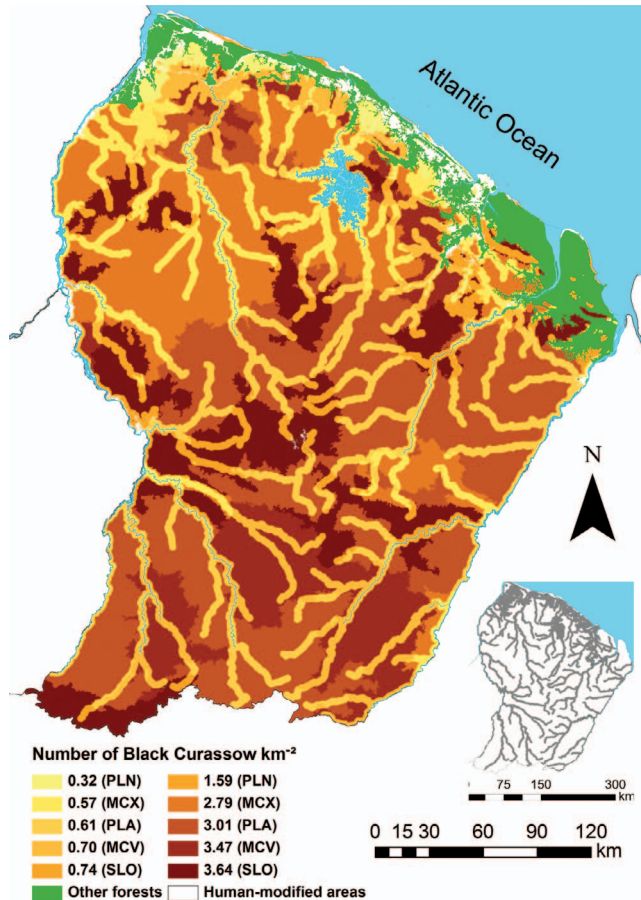
^aThe AIC value of the top model = 2034.4.

^bThe AIC value of the top model = 1753.5.

^cThe AIC value of the top model = 737.1.

APPENDIX TABLE 5. Modeling Black Curassow distribution using landscapes as abundance covariates. We tested the predictive power of the landscape classification (LandS) of Guitet et al. (2013) against that of remotely sensed mean slope (MS). We used the generalized distance sampling model of Chandler et al. (2011), which is a hierarchical model that allows inference about the density of unmarked populations subject to temporary emigration and imperfect detection. We compared the LandS model, i.e. $p(\text{LandS}) \lambda(\text{LandS} + \text{Hunt} + \text{Lat})$ with the MS top-ranked model, i.e. $p(\text{MS}) \lambda(\text{MS} + \text{Hunt} + \text{Lat})$ using Akaike's Information Criterion (AIC). The landscape classification proved to be appropriate to predict large-scale variations in Black Curassow densities with the highest values in mountainous landscapes (SLO). The coastal plain (PLN) landscape held the lowest densities. Although density prediction based on landscape classification (Appendix Figure 7) was obviously less accurate (AIC = 2044.42) than direct mapping (Figure 3) from the landscape model (AIC = 2034.42), this classification nevertheless captured the major patterns of variation in density. This is important because the work done here with Black Curassows will be difficult to pursue for all species of large animal in Guiana's forests. Whether or not the predictive power of this map is confirmed for other species or key groups (Richard-Hansen et al. 2015), the classification by Guitet et al. (2013) is a good operational tool for the management of forests and game resources. For the landscape types (LandS), PLN = coastal plain landscapes, MCX = typical multiconvex landscapes, MCV = multiconcave and joint-valley landscapes, PLA = more or less dissected plateaus, and SLO = all-slope topography landscapes. Hunt = hunting pressure; (pres) = presence of hunting pressure.

| | SLO | PLA | MCX | PLN | MCV | |
|--------------------------------------|---------------------------|-------------|------|-------|-------|-------|
| Coefficients of detection covariates | | | | | | |
| Parameters, p | 2.84 | 2.70 | 2.71 | 2.31 | 2.76 | |
| Standard errors, p | 0.11 | 0.12 | 0.15 | 0.26 | 0.10 | |
| | Intercept (Nonhunted MCV) | Hunt | SLO | PLA | MCX | PLN |
| Coefficients of abundance covariates | | | | | | |
| Parameters, λ | 3.76 | -1.59(pres) | 0.05 | -0.14 | -0.21 | -0.45 |
| Standard errors, λ | 0.27 | 0.27 | 0.05 | 0.31 | 0.39 | 0.56 |



APPENDIX FIGURE 7. Predictive map of the distribution of adult-sized Black Curassow (individuals km⁻²) in French Guiana from the landscape classification by Guitet et al. (2013): PLN = coastal plain landscapes; MCX = typical multiconvex landscapes; MCV = multiconcave and joint-valley landscapes; PLA = more or less dissected plateaus; and SLO = all-slope topography landscapes. Black Curassow densities were not estimated outside *terra firme* forests. Forests other than *terra firme* forests (white-sand forests, seasonally flooded forests such as mangroves, swamp forests, etc.) that were not considered in this study are shown in green. Human-modified areas (savannas and artificial, agricultural, and disturbed areas) are represented in white: 90% of the population lives in the coastal strip and western border (expertise foncière du littoral et des territoires isolés de Guyane 2005–2008–2011, from Office National des Forêts [ONF], updated in 2014, <http://www.geoguyane.fr/catalogue/>). Areas of water (main rivers, the reservoir of the Petit Saut hydroelectric dam, and the Atlantic Ocean) are drawn in blue. The areas in gray on the map to the bottom right (2.5-km-wide buffer along the main rivers and roads and around human settlements) were considered to be hunted.