Seasonal Variation in the Home Ranges of Black Curassow, Crax alector, in French Guiana

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Seasonal Variation in the Home Ranges of Black Curassow, *Crax alector*, in French Guiana

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Abstract

Cracidae is the most threatened avian family in the Neotropics, mainly because of habitat destruction, heavy hunting pressure and poaching. In French Guiana, Black Curassows are heavily hunted, although basic knowledge of the ecological and demographical traits of the species remains limited. Such a gap prevents any attempt to assess the impact of hunting and to help stakeholders to develop proposals ensuring hunting sustainability. The spatial relationship between animals and their habitat is important for conservation management, being related to population densities through complex patterns. Here, we report on a radio-tracking study of Black Curassows in tropical primary rainforest, in Nouragues National Reserve, French Guiana. The aims of the study were to estimate home range size and its variation across seasons, and to quantify movement patterns of the birds. We captured and fitted VHF tags to four adults, and tracked them for 10 to 21.5 months. Daily movements were recorded, and home ranges estimated using the Kernel Density method, for two consecutive wet seasons and one dry season. Using 95% and 50% Kernel densities, the average annual home range and core area were 96.3 ± 32.6 ha (SE) and 22.8 ± 2.8 ha respectively. Home ranges appeared spatially stable over the two years, and overlapped between neighbouring groups. During the dry season, Black Curassows did not migrate but tended to enlarge their home range, with greater daily movements and higher home range overlap. Although additional data are still needed, our results can help to improve the knowledge and management of this poorly studied species.

Keywords

spatial ecology, Cracids, tracking, Kernel method, Home range, movement pattern

Introduction

Cracids (curassows, guans, and chachalacas) comprise a group of large, forest-dwelling frugivorous birds and represent the most threatened avian family in the Neotropics (Brooks, 2006a; del Hoyo et al., 1994; Kattan et al., 2016; Strahl et al., 1997b), 50% of the species within this family being listed as "Vulnerable" or at higher risk of extinction (IUCN, 2018). Due to decreasing population trends, the Black Curassow *Crax alector* was uplisted in 2012 from "Least Concern" to "Vulnerable" in the IUCN red list (Birdlife International, 2016; A3c). It is considered to be one of the first species to disappear from areas subjected to heavy hunting pressure, having almost vanished from forests near the coast, around settled areas and villages, along large rivers, and wherever hunting pressure is high (Delacour & Amadon, 2004; Denis et al., 2016). In French Guiana, Niel et al. (2008) highlighted the risk of

local overharvesting on this species, using the demographic invariant method (Niel & Lebreton, 2005), while Denis et al. (2016) further showed a negative correlation

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between hunting pressure and Black Curassow densities. Accordingly, in order to reduce the hunting pressure on this population, the trade of Black Curassows (mainly hunted for meat) was officially banned in 2007, and hunting was slightly constrained in 2012 by setting a bag limit of two Black Curassows harvested per hunter and hunting trip (with no limitation on the number of hunting trips). No stronger regulation could be set at that time given the absence of hunting licence and general hunting management laws in French Guiana. However, despite this critical situation, basic knowledge of the ecological and demographic traits of Black Curassows remain scarce.

Among those biological traits, spatial patterns as home range size and habitat use are of main interest. Home ranges reveal the relationships between animals and their habitat, and are closely related to population densities through complex relationships (Efford, 2014; Efford et al., 2015). Understanding ranging behaviour is a prerequisite for wildlife management and conservation, and basic spatial parameters are frequently needed to model abundance (Rowcliffe et al., 2008; Royle et al., 2016) and movement ecology. Moreover, knowledge of spatial patterns of habitat use is necessary in the assessment of hunting sustainability (Constantino, 2015; Levi et al., 2011; Shaffer et al., 2018). The previous sustainability assessment made on Black Curassow in French Guiana used home ranges size estimates extrapolated from other countries or cracid species, because the information was unavailable at that time (Niel et al., 2008).

To fill this knowledge gap, we therefore initiated a study to estimate home range used by Black Curassows in 2010 in French Guiana (De Coster, 2011; Rocheteau, 2010). This local scale study was complementary to a larger scale approach undertaken over the whole territory, aiming at understanding the abundance and density of the species in relation to habitat type and hunting pressure (Denis et al., 2016; Richard-Hansen et al., 2015). The main goal of the present study was to increase our knowledge on Black Curassow behaviour and spatial ecology and for the first time to estimate home range size and its seasonal variation. The study was undertaken in the protected area of Nouragues National Reserve, where hunting and forest disturbance are currently absent, to get baseline data. The accurate evaluation of these parameters could highly improve the assessment of local hunting impact and help environmental managers and stakeholders to implement the best management decisions for hunting sustainability.

Methods

Study Site

We conducted fieldwork totalling 336 days of tracking, from March 2010 to August 2013 (Table 1) in the Nouragues National Reserve and Nouragues Ecological Research Stations, French Guiana (4°05'15" N, 52°40'46" W). The Nouragues reserve is located ca.95 km inland and covers ca.2500 ha, and consists entirely of tropical primary rainforest of the Guiana Shield. The Research Station is located in the Nouragues creek watershed, a tributary of the Arataye River. Elevation varies between 100 m and 411 m asl, the height of the inselberg (granitic rocky mountain). The vegetation is dominated by *terra firme* forest, with canopy height between 30 and 50 m, with patches of palm-swamp, liana or bamboo forests (Bongers et al., 2001). Habitat and landscape type were classified as all-slope in the recent forest typology of *terra firme* French Guianan forests (Guitet et al., 2015), Caesalpiniaceae, Lecythidaceae, Sapotaceae and Burseraceae being among the most common tree families (Poncy et al., 2001). Two distinct study sites, ca.5 km apart, were used: the Pararé site was located along the Arataye river in the lower part of the area (25m – 170 m asl), and the Inselberg site was located at a higher elevation, with steeper slopes, and situated just beneath the ca.410 m inselberg.

In French Guiana, a dry season occurs from August to November, and a long rainy season from December to July, with a small decrease in rainfall around March. Mean monthly maximum temperatures rise from 29°C (January) to 34°C (October), while mean minimal ones stay around 22°C all year round. Average annual rainfall is 2990 mm, monthly rainfall being above 100 mm in September-October and up to 500 mm at the peak of rainy season (May; Bongers et al., 2001). Tree fruiting peaks in March-May and is minimal in August-September (Norden et al., 2007, Sabatier & Puig, 1985). Among 48 trees and liana species, 54% showed an annual fruiting pattern, 23% a masting fruiting pattern (mainly animal-dispersed trees), and 23% an irregular fruiting pattern (Norden et al., 2007).

Capture

Capture, tagging and tracking of Black Curassow were made in compliance with legal requirement (Décret n° 95-1299 portant création de la réserve naturelle des Nouragues (Guyane)). Capture was really challenging, and we needed various attempts using several methods, of which only two were successful. We first identified the tracks routinely used by family groups of curassows near the field research stations, and then we used two different types of traps: hoop net and leg laces. The hoop net was made of two converging 20 to 30 meters long walls of mist-net, deployed in a "V" shape on each side of the track. The last ten meters of the hoop "head" were covered by nets to prevent the bird to flush. When a bird entered the hoop net, we gently pushed it towards the

head of the hoop and caught it when it was trapped in the net. Alternatively, we also positioned leg laces on the birds' tracks, the laces being attached to a 1.5 m long rubber extensible spring to prevent the bird being injured. As soon as the bird was captured, its head was covered with a black sock to reduce stress. We weighed birds to the nearest 10 g with a 5000-g Walter® spring balance.

Tracking

We tracked Black Curassows fitted with TW3 twin cells Biotrack pip tags (weight 70g) using a Biotrack Sika receiver and two types of handheld directional antennas (3-element Yagi from Biotrack and RA-23K "H" antenna from Telonics). Captured birds' body mass ranged from 2.7 to 3.3 kg, thus the mass ratio between bird and transmitter ranged from 2 to 2.6%. The transmitters were fastened onto the birds' back using a double loop harness made with tubular Teflon ribbon (diameter 0.33 inch), passing over each wing. We previously tested transmitter design and mounting for several days on captive Black Curassows from the Zoo of Cayenne. As also found in a test study on captive and reintroduced neighbouring species (Bernardo et al., 2011a), the backpack and antennas were not conspicuous, being covered by feathers, and did not modify the behavior of the birds held captive in the zoo. Processing of the birds took on average 30 minutes. The tracking period began one day after release and lasted until the battery of the transmitter failed. Transmitters had an expected battery life of 2 years and a theoretical ground-to-ground detection range of 3 to 6 km.

We determined the sex of birds mainly by behavioural observations: only males perform territorial vocalizations (booming) (Delacour & Amadon, 2004) and whistle or clucking calls differ between sexes (fieldworker observations during this study). Moreover, the colour of eyes is dark for males and brownish for females (Todd et al., 1992). As all birds within a family group stay always very close to each other, the location of the tagged bird generally corresponded to the location of the whole group.

Locations were determined by moving in the direction of a radio signal until we saw the bird. We then noted its behaviour and, after the bird moved, we recorded the location's coordinates via a Garmin 60 CSX GPS unit. The location error was estimated as 9.79 ± 0.29 m (SE). When the thick vegetation prevented us to see the bird, even at short distance (less than 50 m between the observer and the bird), we estimated a most likely location. If the bird moved in response to our approach, the location of the bird prior to moving was recorded. We tracked birds 3 to 4 times each day. The delay between successive locations was at least 3 to 4 hours, in order to satisfy the biological independence of locations, as curassows can easily travel through their whole home range in less

than 3 hours. We chose the tracking hours randomly every day for each bird, aiming to obtain, over the whole study period, a roughly equivalent number of locations for every hour from dawn (06:00) to dusk (18:00). We considered locations obtained at dawn and dusk as representative of roosting sites.

Additionally, some days were dedicated to a continuous tracking of birds. After some weeks, Male A and Male B groups were very accustomed to human presence, and did not modify their behaviour as long as the observer stayed at a minimum distance. We then tracked animals by foot during the diurnal period, keeping visual contact, as long as possible, while a GPS recorded the track and a fix every minute. The GPS human track was considered to match that of the birds, and the behaviour was also noted every minute. We recorded different behaviours (travelling, feeding, resting, grooming and territorial behaviours), however in the present study we only used travelling (hereafter "movement") data.

Home Range Estimation

We estimated home range size using both Minimum Convex Polygon (MCP; (White & Garrot, 1990) and Kernel methods, with the href smoothing method (Seaman & Powell, 1996). The MCP method encompasses all locations, and includes exploratory movements, while the Kernel density estimator produces an unbiased density estimate of presence probability directly from data and is not influenced by grid size or placement (Silverman, 1986). The fixes recorded during the continuous tracking days were not included in this analysis, because they were strongly autocorrelated. Data were analysed using the software R (version 3.0.1; R Core Team, 2014) and the packages 'ade4' (Chessel et al., 2004), 'adehabitat' (Calenge, 2006) and 'maps' (Becker et al., 2007). We used the extension Hawth's Analysis Tools 3.27 on the GIS application ArcMap 9.2 to estimate MCP.

To standardize and compare the various estimates of home-range size using the Kernel method within seasons (wet, dry) or over the whole annual cycle (wet + dry seasons), we first estimated 50% and 95% Kernel home ranges using a smoothing parameter *h ref* (Seaman & Powell, 1996) for each individual separately. Then we calculated a mean *h ref* within each time period (wet season, dry season, annual cycle) and used this value to run again the estimation of 50% and 95% kernel home ranges.

Movement Patterns

We modelled the distance travelled by the birds (m) in relation to time-period (hourly from 06:00 to 18:00 as a

Table 1. Tracking Periods for Each Tagged Black Curassow.

	2010		2011		2012		2013		
	rainy	dry	rainy	dry	rainy	dry	rainy	fixes	tracking days
	M A M J J A S O N D		J F M A M J J A S O N D		J F M A M J J A S O N D		J F M A		
Male A	■■■■■■ ■■■■		■■■■■■■					555	252
Male B + family	■ ■■■ ■		■■■■■■■					345	252
Female D (with A)	■■■ ■							53	45
Female D alone	■■■■		■■■ ■					42	32
Female C					■ ■■■■■■		■	263	84

Black cells indicate months when tracking was performed.

categorical factor) and season (dry and wet), and included two-way interaction effects. For this purpose, we used a generalized linear mixed model (GLMM, function glmer (MASS package 7.3-45, (Venables & Ripley, 2002) with a negative binomial error structure to estimate distance travelled. We included individual birds (or female/male group), and the repetition of tracking hours as random effects. Finally, Wald tests were implemented to test fixed effects from season and time-period (and their interactions), discarding effects that do not differ significantly from zero (Bolker et al., 2009).

Results

Four Black Curassows, two males (A, B) and two females (C, D), were captured and tracked, three of them in the inselberg station, and one (C) in the Pararé station. The whole tracking period lasted a minimum of 10 months (female C) to a maximum of 21.5 months (male A) and the number of locations for each tagged bird ranged from 95 to 608 (see Table 1). Female D was initially paired with male A, but the pair split several times, and no home range could be estimated for the female D because she dispersed too far to be regularly located. Male A stayed in the same area and was observed paired with another female for the rest of the study.

The Male B group initially included an adult female and a fully feathered juvenile. From the 18 February 2011, we could see this group with two downy chicks; the juvenile was still there and, together with adults, was providing care to the chicks. One of the chicks disappeared in early May 2011. We did not see the juvenile after April 2012, presumably because it left the family group. At the end of the tracking study, the surviving chick was still with the adults and was in full-grown juvenile plumage.

Female C was initially paired with a male, and two chicks were observed in March 2013. However, we often observed female C joining another neighbouring group, without the initial male, which stayed in the same area.

Home Range

For groups A and B, we were able to estimate home ranges for two consecutive wet seasons and one dry season, and for female C, over one full annual cycle. On the basis of 95% and 50% Kernel estimates, the average annual home range and core area were 96.3 ± 32.6 ha (SE) and 22.8 ± 2.8 ha (Table 2; Figure 1A to C). Using MCP, this annual home range was 107.8 ± 32.6 ha (Table 2). Home ranges sizes of Male A and Female C were relatively similar but the home range and core area of Male B was much larger, twice the size when using MCP.

During the wet season, the average home range area was markedly lower than during the dry season (95% Kernel: 79 ± 4.4 ha versus 100.8 ± 18.6; MCP: 55.2 ± 4.3 ha versus 90.7 ± 36.9; Table 3; Figure 2A to C), particularly for Male B's home range. Female C's 95% Kernel home range was however slightly larger in wet season than in the dry season. Contrarily, the core area showed very little variation between seasons (wet season: 21.2 ± 1.1 ha, dry season 19.8 ± 2.5 ha; Table 3). The extended home range during the dry season was not associated with any dramatic changes in the area foraged by birds, since for groups A and B, the home range during the dry season (using 95% Kernel home range) overlapped respectively 70.5% and 80% of home ranges covered during the wet season.

The two family groups tracked in the Inselberg site showed an important overlap in their home ranges, reaching up to 63% of the group A annual home range (using 95% Kernel) and even 11.6% of the core area. This overlap was more pronounced during the dry season, reaching a maximum value of 60.1% of group A's home range (30.9% for core area) versus 46.4% during the wet season (and no overlap for core area).

Movement Patterns

We recorded continuous tracking data on 35 diurnal sessions (18 during the wet season, 17 during the dry season), for a total of 232 hours (120 hours during the wet season, 112 hours during the dry season). The majority of the data was collected on males A and B

Table 2. Annual Home Ranges Used by Black Curassows Tracked in French Guiana Estimated Through MCP and Kernel Methods.

Bird	Locations (N)	h	MCP	Kernel 50%	Kernel 75%	Kernel 95%
A	313	89	76.9	21.1	42.6	83.7
B	341		173	28.3	56.9	117.3
C	286		73.4	18.9	40.7	83.9

h refers to the smoothing parameter used to calculate area through Kernel method.
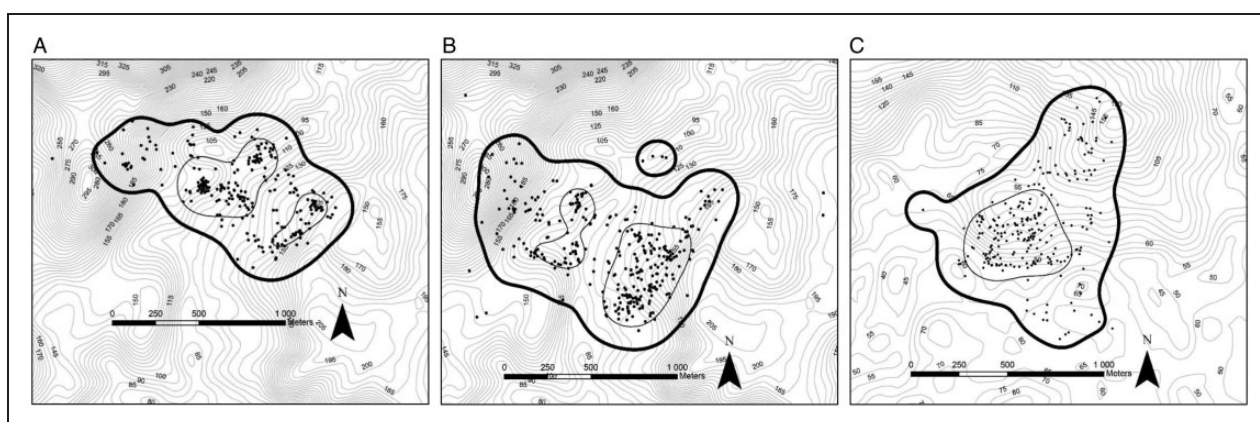
Figure 1. Location and 1-Year Home Range (95% and 50% href Kernel) for A and B and C Black Curassow Groups (Respectively A, B, C); Bold Lines = 95% Kernel, Thin Lines = 50% Kernel, Grey Lines: Elevation.

Table 3. Seasonal Home Ranges Used by Black Curassows Tracked in French Guiana Estimated Through MCP and Kernel Methods;

Bird	Season (year)	Locations (N)	h	MCP	Kernel 50%	Kernel 75%	Kernel 95%
A	Wet (2010)	230	100	51	19.7	37.5	70.4
	Dry (2010)	83		53.8	23	45.7	90.1
B	Dry (2010)	95		164.5	21.7	55.9	136.9
	Wet (2011)	247		63.8	20.7	43.8	84.9
C	Dry (2012)	142		53.8	14.8	33.3	75.3
	Wet (2013)	144		50.9	23.3	42.4	81.6

h refers to the smoothing parameter used to calculate area through Kernel method.

(190 hours). The mean duration of the tracking sessions was 4h: 57 min ± 36 min (SE; min: 1h: 00, max: 12h: 00). All time-periods from 06:00 to 19:00 were sampled, and the mean hourly distance travelled by birds could be compared. The median number of tracking sessions per hour was 18 (range 5–25). The movement activity differed during the daytime (P<0.001, $\chi^2 = 707.2$, df = 11), and according to the season (P < 0.001, $\chi^2 = 22.7$, df = 1; interaction P<0.001, $\chi^2 = 247.4$, df = 11). On average, birds travelled 189 ± 32 m/hour (SE; overall 2455 m/day) in the wet season and 372 ± 57 m/hour (overall 4843 m/day) in the dry season. Animals travelled longer distances per minute during the dry season than during the wet season (Dry season 11.8 m/minute ± 0.21 (SE), Wet season 7.7 ± 0.19 (SE),

difference: + 4.1 m in dry season, $P < 0.001$). We observed maximum movement earlier in the morning (6:00–7:00) and later in the evening (17:00–18:00) in the dry season than in the wet season (7:00–8:00 and 16:00–18:00). Minimum movement activity occurred at mid-day (11:00–12:00) for both seasons (Figure 3).

Discussion

This study presents the first estimation of *Crax alector* home range based on tracking data on more than one bird or pair, and over a full annual cycle or more. Literature on the ecology and spatial behaviour of Cracids relies upon a limited number of tracking data across their distribution range. To our knowledge, the
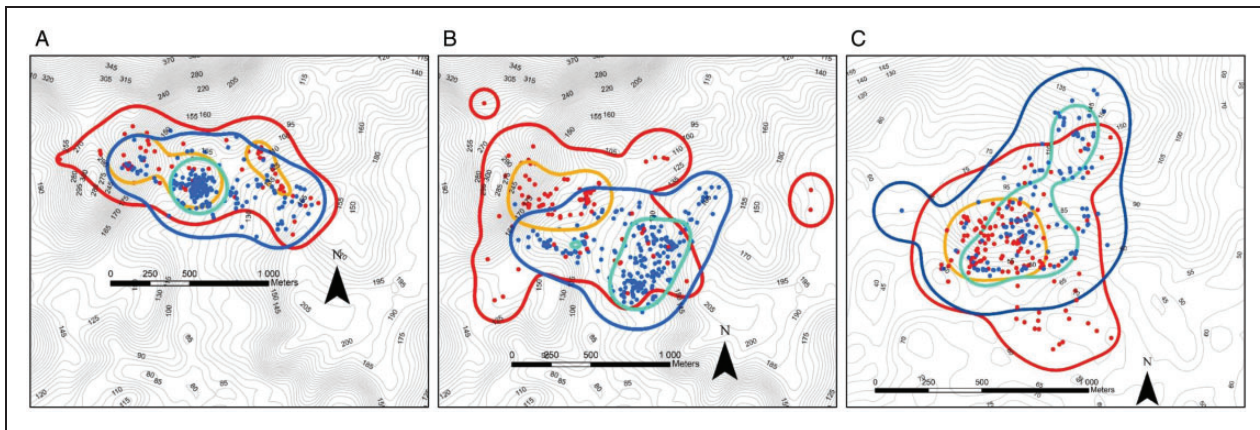
Figure 2. Location and Seasonal Home Ranges (95% and 50% href Kernel) for A and B and C Black Curassow Groups (Respectively A, B, C); Wet Season Home Ranges Are Figured With Dark Blue (95% Kernel) and Light Blue Lines (50% Kernel), and Dry Season Home Ranges Are Figured With Red (95% Kernel) and Orange Lines (50% Kernel), Grey Lines: Elevation.
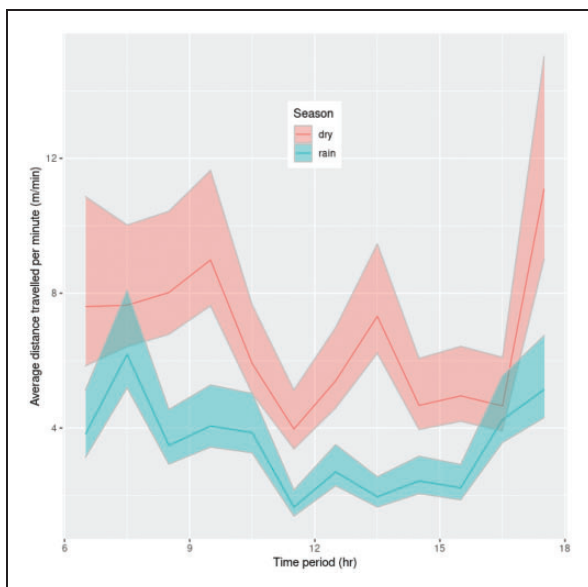

Figure 3. Average Distance Travelled (M) per Minute in Each Hour of the Day for Black Curassow, by Season. Upper and lower 95% confidence intervals are figured by pink and blue areas.

determination of annual home range size has been considered for a very limited number of cracid species (*Crax alector* (Bernal & Mejía, 1995; Erard & Sabatier, 1989); *Crax daubentoni* (Bertsch & Barreto, 2008a); *Crax blumenbachi* (reintroduced population; Bernardo et al., 2011b); *Crax globulosa* (Leite et al., 2018); *M. salvini*: (Parra et al., 2001; Santamaria & Franco, 2000; Yumoto, 1999). In many of those cases, it relies upon the monitoring of only one familial group. Moreover, the methodological tools used to estimate home range greatly differ between studies (MCP, Kernel, empirical estimation on the field…), which hampers eventual

comparisons between studies. We summarize these different estimates in Table 4. Overall, our own estimate (95% kernel: 96 ha, MCP: 108 ha) tends to be smaller than results obtained by the other tracking studies available on *Crax* species (*C. daubentoni* 149 to 197 ha; *C. blumenbachii* 125 ha), and particularly *C. globulosa* in western amazon (468 ha or 804 ha with respectively 95% Kernel and 95% MCP). Bernal and Mejía (1995) in Leite (2017) estimated 185 ha for *C. alector*'s home range size in Bolivia. All these home ranges (our study included) were estimated in protected areas where no hunting occurs. Former values for *C. alector* home range sizes available in French Guiana were empirically estimated from the field without radio-tracking nor definite method (Erard & Sabatier, 1989) or from the literature for modelling purposes (Niel et al., 2008: 19.63 ha) and clearly underestimated the annual home range in comparison with our results. Our study also suggests that, at least for the two males, home ranges tend to remain stable from one year to the next. Detailed spatial data as daily movements also provides useful parameters for ecological functional approaches and modelling, as dispersal ability of juveniles (Bowman, 2003) or seed dispersal distance (Donoso et al., 2020), although Crax' strong gizzard probably crushes larger seeds (Erard et al., 1991).

Temporal variation in habitat-use has been mentioned for various large Cracid species (*Crax rubra griscomi* (Martinez-Morales, 1999), *Crax daubentoni*: (Bertsch & Barreto, 2008b, Strahl et al., 1997a), *Crax blumenbachii* (Srbek-Araujo et al., 2012); *Crax globulosa* (Leite et al., 2018; Luna-Maira et al., 2013); *Crax alector* (Bernal & Mejía, 1995) and *Mitu salvini* (Parra et al., 2001; Santamaria & Franco, 2000; Yumoto, 1999). Parra et al. (2001) followed a pair of *M. salvini* over 6 months, including the wet and part of the dry season, and pointed

Table 4. Data Available in Scientific Literature on Annual or Seasonal Home Ranges in Cracid Species.

Species	Country	Period/season	Method	Home range (ha)	Reference
Crax daubentoni	*Venezuela*	*3 months (dry)*	*Fixed Kernel 95%*	*149 ± 125*	*a*
Crax daubentoni	*Venezuela*	*3 months (dry)*	*Adaptive Kernel 95%*	*197 ± 178*	*a*
Crax alector	*Colombia*	*Year*	*?*	*185 (1gp)*	*b*
Crax alector	*Colombia*	*Wet*	*?*	*34 (1gp)*	*b*
Crax alector	*Colombia*	*Dry*	*?*	*127 (1gp)*	*b*
Crax alector	*French Guiana*	*?*	*empirical*	*19.63*	*c*
Crax alector	*French Guiana*	*year*	*H ref Kernel 95%*	*96.3 ± 32.6 (SE)*	*d*
Crax alector	*French Guiana*	*Dry*	*H ref Kernel 95%*	*100.8 ± 18.6 (SE)*	*d*
Crax alector	*French Guiana*	*Wet*	*H ref Kernel 95%*	*79 ± 4.4 (SE)*	*d*
Crax alector	*French Guiana*	*Late dry – early wet season*	*empirical*	*10–15*	*e*
Crax blumenbachii	*Brazil*	*25 months*	*Neighbour linkage 95%*	*125.8 ± 12.3 (SE)*	*f*
Mitu salvini	*Colombia*	*Year*	*MCP 100%*	*150 (1gp)*	*g*
Mitu salvini	*Colombia*	*Dry season*	*MCP 100%*	*34.4 (1gp)*	*h*
Mitu salvini	*Colombia*	*Dry/wet seasons*	*MCP 100%*	*72 (1 gp)*	*i*
Mitu salvini	*Colombia*	*?*	*MCP 100%*	*150 (1 gp)*	*i*
Crax globulosa	*Brazil*	*Dry season*	*MCP 95% H fixed Kernel 95%*	*537 ± 349 (SD; 3 gp.)* *364 ± 143 (SD; 3 gp.)*	*j*
Crax globulosa	*Brazil*	*Wet season*	*MCP 95% H fixed Kernel 95%*	*482 ± 223 (SD; 3 gp.)* *478 ± 421 (SD;3 gp.)*	*j*
Crax globulosa	*Brazil*	*Year*	*MCP 95% H fixed Kernel 95%*	*804 ± 556 (SD; 3 gp)* *468 ± 369 (SD; 3 gp)*	*j*

(a) Bertsch & Barreto 2008a (10.1b) Bernal & Mejia, 1995 in Delacour & Amadon, 2004, (c) Niel et al., 2007, (d) this study, (e) Erard & Sabatier, 1989, (f) Bernardo et al., 2011b, (g) Santamaria & Franco, 2000, (h) Yumoto, 1999, (i) Parra et al., 2001, (j) Leite et al., 2018. "gp" = "number of family groups studied".

out marked changes in habitat use over time. In contrast, Leite et al. (2018) noted for *Crax globulosa* the consistency in home range size across dry and wet seasons, the species locations being highly restricted to rivers and floodplains. A family group of Black Curassows followed for 7 months in Colombia had a smaller home range during the wet season (39 ha in September) than during the dry season (127 ha in December: Bernal & Mejía, 1995). The seasonal home ranges estimated in our study were similar to those estimated by Bernal and Mejía (1995) in both seasons, larger than those estimated for *M. salvini* during the dry season but apparently similar during the wet season. On the other hand, whatever the season, they were four to six times smaller than those estimated for *C. globulosa* (see Table 4). During the dry season, our tracked birds increased their home range but did not move significantly to other parts of the forest since home range overlap between the two seasons always exceeded 70%. This indicates that, as the dry season progressed, Black Curassows did not make migration-like movements towards other parts of the forest but rather extended the boundaries of their home range. For one female, however, the Kernel estimation of home range was not higher in the dry season, although the MCP estimation was.

As suggested in other studies on curassow species, seasonal differences in home range may reflect changes in habitat use in relation to variation in resource abundance throughout the year (Bertsch & Barreto, 2008b; Luna-Maira et al., 2013; Muñoz & Kattan, 2007; Parra et al., 2001; Santamaria & Franco, 2000; Srbek-Araujo et al., 2012). According to the study and species, movements may be reduced during fruit or water scarcity (Santamaria & Franco, 2000 for *Mitu salvini* and Leite et al., 2018 for *Crax globulosa*), or expanded (Parra et al., 2001, for *Mitu salvini*). More generally, movement ecology predicts that when resources become scarce, straighter and faster movements become more efficient than tortuous ones, as they result in high net displacement, thereby minimizing the chance of revisiting an already visited resource, increasing the chance of finding new resources, and giving time for stock to replenish (de Knegt et al., 2007; Viswanathan et al., 2008). This pattern would correspond to our results, showing an increase of travelled distances and home range size during the dry season, while the fructification peak is occurring during the wet season (February to May: Sabatier, 1985). Few tree species fruit during the dry season (Sabatier, 1985), and that may influence the ranging behaviour of frugivorous animals. For example, the Lauraceae *Ocotea cf. cinerea*, and the Moraceae *Naucleopsis guianensis* fruiting period occurred during the dry season only, and were heavily consumed at this time by the Black Curassows we tracked. These key resources were scattered, and located at the periphery of the home ranges in

our study area, probably contributing to the extension of the home range in dry season, (in the western part for group B, and in the southern part for animal C). During these months, birds were often observed walking straight for longer time towards these remote fruiting trees, and spending more time feeding on the same place, before going back to the core area for the night, while in the wet/fruiting season, feeding bouts were shorter and more regularly distributed during the day. Water availability may not greatly influence birds' movement in our study area, as most streams flowed permanently, even during the dry season. Studies on *Crax alector* in French Guiana (Erard et al., 1991) and eastern Colombia (Jiménez et al., 2001) have shown little variation in diet composition among seasons. Consumption of seeds and seedlings increased during the rainy season in the Colombian study, while in French Guiana, the amount and diversity of fruits in the diet remained stable between seasons, but the specific composition was not studied (Erard et al., 1991).

Our results also revealed a high degree of home range overlap between family groups, also affecting the core area, and increasing during the dry season. Home range overlapping had already been mentioned in two *Crax* species (Delacour & Amadon, 2004) but not quantified, while home range of adult males in a reintroduced Red-billed Curassow population did not overlap and were often separated by distances of up to 3 km (Bernardo et al., 2011b).

We conducted our study in an area where hunting is absent and within a mountainous habitat: in French Guiana, mountainous-forested habitats have been shown to be favourable for this species and associated with the highest curassow densities measured (Denis et al., 2016). The locally high density of Black Curassows in our study area might therefore result in a high degree of overlapping in home ranges.

Implications for Conservation

This study allowed to improve our knowledge on the movement behavior of Black Curassows, which is crucial for the management and conservation of such key species (Allen & Singh, 2016). Overall, our estimates of both annual and seasonal home ranges sizes were markedly larger than previous empirical estimates in French Guiana (Erard et al., 1991; Niel et al., 2008) but smaller than some estimates for the species from Colombia, at least for annual and wet season home ranges (Bernal & Mejia, 1995). The home range radius was included by Niel et al. (2008) as a parameter in the hunting sustainability index (SI), with a larger value increasing SI estimates by decreasing the Harvest rate (Harvest rate H = Offtake/Area; Niel & Lebreton, 2005; Slade et al., 1998). The impact of hunting is particularly sensitive to

parameters such as the size of the hunted area, harvest rate and density, which need detailed ecological studies to be improved (Niel et al., 2008). Previous studies on hunting sustainability underlined the major role of source/sink processes (Richard-Hansen et al., 2019), in which the dispersal ability of species, related to their spatial behavior, has strong implications for population recovering. Moreover, the seasonal variation in home range area and overlap can potentially affect local densities throughout the year, and should be taken into account. Habitat also influences curassow densities (Denis et al., 2016), and resource abundance and distribution are likely to shape the birds movements and home range size. More data on resource needs, habitat use and spatial ecology in various areas will help to improve the management of this sensitive species in French Guiana.

Declaration of Conflicting Interests

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References

Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, *3*, 155.

Becker, R. A., Wilks, A. R., Brownrigg, R., & Minka, T. P. (2007). *Original S code by Richard R. Becker & Allan R. Wilks R version by Ray Brownrigg. Enhancements by Thomas P. Minka 2007. Draw Geographical Maps* (R package version 2.0-39).

Bernal, X., & Mejía, C. A. (1995). Uso del espacio por un grupo de *Crax alector*. In A, M. C (Ed.), *Informe preliminar de un estudio de paujíles del Parque Nacional Natural Tinigua* (pp. 24–36). Centro de Investigaciones Ecológicas Macarena.

Bernardo, C. S. S., Cresswell, B. B., Lloyd, H., Azeredo, T., & Simpson, J. (2011a). Selection of radio transmitter and attachment method for post-release monitoring of captive-bred reintroduced Red-billed Curassow *Crax blumenbachii*, Brazil. *European Journal of Wildlife Research*, 57, 689–694.

Bernardo, C. S. S., Lloyd, H., Olmos, F., Cancian, L. F., & Galetti, M. (2011b). Using post-release monitoring data to optimize avian reintroduction programs: A 2-year case study from the Brazilian Atlantic Rainforest. *Animal Conservation*, 14, 676–686.

Bertsch, C., & Barreto, G. R. (2008a). Abundancia y area de accion del Pauji de copete (*Crax daubentoni*) en los llanos centrales de venezuela. *Ornitologia Neotropical*, 19, 1–7.

Bertsch, C., & Barreto, G. R. (2008b). Diet of the Yellow-knobbed Curassow in the Central Venezuelan Llanos. *The Wilson Journal of Ornithology*, 120, 767–777.

BirdLife International. (2016). *Crax alector. The IUCN red list of threatened species* 2016: e.T22678534A92777326. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22678534A92777326.en

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., & Stevens, M. H. H. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24, 127–135.

Bongers, F., Charles-Dominique, C., Forget, P. M., & Théry, M. (2001). *Nouragues dynamics and plant-animal interactions in a neotropical rainforest*. Kluwer Academic Publishers.

Bowman, J. (2003). Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology*, 81(2), 195–202.

Brooks, D. (2006a). Conserving Cracids: *The most Threatened Family of Birds in the Americas*. Miscellaneous Publications of The Houston Museum of Natural Science, Number 6.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519.

Chessel, D., Dufour, A. B., & Thioulouse, J. (2004). The ade4 package - I: One-table methods. *R News*, 4, 5–10.

Constantino, P. A. L. (2015). Dynamics of hunting territories and prey distribution in Amazonian Indigenous Lands. *Applied Geography*, 56, 222–231.

De Coster, F. (2011). *Ecology of the Hocco in French Guiana: an approach of space occupation* (Master 2 report). Université de Corse.

de Knegt, H. J., Hengeveld, G. M., van Langevelde, F., de Boer, W. F., & Kirkman, K. P. (2007). Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioural Ecology*, 18(6), 1065–1072

Delacour, J., & Amadon, D. (2004). *Curassows and related birds*, Lynx Edicions and the National Museum of Natural History.

del Hoyo, J., Elliot, A., & Sartagal, J. (1994). *Handbook of the birds of the World, Vol. 2*. Lynx Edicions.

Denis, T., Hérault, B., Jaouen, G., Brunaux, O., Guitet, S., & Richard-Hansen, C. (2016). Black Curassow habitat relationships in terra firme forests of the Guiana Shield: A multiscale approach. *The Condor*, 118, 253–273.

Donoso, I., Sorensen, M. C., Blendinger, P. G., Kissling, W. D., Neuschulz, E. L., Mueller, T., & Schleuning, M. (2020). Downsizing of animal communities triggers stronger functional than structural decay in seed-dispersal networks. *Nature Communications*, 11(1), 1–8.

Efford, M. G. (2014). Bias from heterogeneous usage of space in spatially explicit capture–recapture analyses. *Methods in Ecology and Evolution*, 5, 599–602.

Efford, M. G., Dawson, D. K., Jhala, Y. V., & Qureshi, Q. (2015). Density-dependent home-range size revealed by spatially explicit capture–recapture. *Ecography*, 39, 676–688.

Erard, C., & Sabatier, D. (1989). The role of terrestrial fruit-eating birds in forest dynamics in French Guiana. In H. Ouellet (Eds.), *Acta XIX Congressus Internationalis Ornithologici* (pp. 803–815). University of Ottawa Press.

Erard, C., Thery, M., & Sabatier, D. (1991). Diet of *Tinamus major* (Tinamidae), *Crax alector* (Cracidae) and *Psophia crepitans* (Psophidae) in French Guiana forest. *Gibier Faune Sauvage*, 8, 183–210.

Guitet, S., Pelissier, R., Brunaux, O., Jaouen, G., & Sabatier, D. (2015). Geomorphological landscape features explain floristic patterns in French Guiana rainforest. *Journal of Biogeography*, 24, 1215–1237.

IUCN. (2018). *The IUCN red list of threatened species* (Version 2017-3). www.iucnredlist.org

Jiménez, I., Parra, J. L., Agudelo, M., Londoño, G. A., & Molina, Y. (2001). Temporal variation in the diet of Black Curassows (*Crax alector*, Cracidae). In D. M. Brooks & F. Gonzalez-Garcia (Eds.), *Cracid ecology and conservation in the new millenium* (pp. 195–211). Miscellaneous Publications of The Houston Museum of Natural Science.

Kattan, G. H., Muñoz, M. C., & Kikuchi, D. W. (2016). Population densities of curassows, guans, and chachalacas (Cracidae): Effects of body size, habitat, season, and hunting. *The Condor*, 118, 24–32.

Leite, G. A. (2017). *Conhecer para conservar: Crax globulosa (Aves: Cracidae), da genética de populações à seleção do habitat*. Instituto Nacional de Pesquisas da Amazônia-INPA.

Leite, G. A., Farias, I. P., Gonçalves, A. L. S., Hawes, J. E., & Peres C. A. (2018). Coarse- and fine-scale patterns of distribution and habitat selection places an Amazonian floodplain curassow in double jeopardy. *Peer J*, 6, e4617. https://doi.org/10.7717/peerj.4617

Levi, T., Shepard, G. H., Ohl-Schacherer, J., Wilmers, C. C., Peres, C. A., & Yu, D. W. (2011). Spatial tools for modeling the sustainability of subsistence hunting in tropical forests. *Ecological Applications*, 21(5), 1802–1818.

Luna-Maira, L., Alarcon-Nieto, G., Haugaasen, T., & D. M. Brooks. (2013). Habitat use and ecology of Wattled Curassows on islands in the lower Caquet'a River, Colombia. *Journal of Field Ornithology*, *84*, 23–31.

Martinez-Morales, M. A. (1999). Conservation status and habitat preferences of the Cozumel curassow. *The Condor*, *101*, 14–20.

Muñoz, M. C., & Kattan, G. H. (2007). Diets of Cracids: How much do we know? *Ornitologia Neotropical*, *18*, 21–36.

Niel, C., & Lebreton, J. D. (2005). Using demographic invariants to detect overharvested bird populations from incomplete data. *Conservation Biology*, *19*, 826–835.

Niel, C., Richard-Hansen, C., & Debeir, L. (2008). *Uncertainty in estimating the sustainability of hunting: the case of the Black Curassow in French Guiana*. 2007 ONCFS Scientific report, pp. 27–31.

Norden, N., Chave, J., Belbenoit, P., Caubère, A., Châtelet, P., Forget, P-M., & Thébaud, C. (2007). Mast fruiting is a frequent strategy in woody species of Eastern South America. *PLoS One*, *2*(10), e1079. https://doi.org/10.1371/journal.pone.0001079

Parra, J. L., Aguledo, M., Molina, Y., & Londoño, G. (2001). Use of space by a pair of Salvin's Curassows (*Mitu salvini*) in northwestern columbian Amazon. *Ornitologia Neotropical*, *12*, 189–204.

Poncy, O., Sabatier, D., Prévost, M.-F., & Hardy, I. (2001). The lowland high rainforest: Structure and tree species diversity. In F. Bongers, P. Charles-Dominique, P.-M. Forget, & M. Théry (Eds.), *Nouragues: Dynamics and plant-animal interactions in a neotropical rainforest* (pp. 31–46). Kluwer Academic Publishers.

R Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Richard-Hansen, C., Davy, D., Longin, G., Gaillard L., Renoux, F., Grenand, P., Rinaldo, R. (2019). Hunting in French Guiana across time, space and livelihoods. *Frontiers in Ecology and Evolution*, *7*, 289. https://doi.org/10.3389/fevo.2019.00289

Richard-Hansen, C., Jaouen, G., Denis, T., Brunaux, O., Marcon, E., & Guitet, S. (2015). Landscape patterns influence communities of medium- to large-bodied vertebrates in undisturbed *terra firme* forests of French Guiana. *Journal of Tropical Ecology*, *31*, 423–436.

Rocheteau, V. (2010). *Ecology of Black Curassow (Crax alector) in French Guiana* (Master2 report). Université d'Angers.

Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, *45*, 1228–1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x

Royle, J. A., Fuller, K. T., & Sutherland, C. (2016). Spatial capture–recapture models allowing Markovian transience or dispersal. *Population Ecology*, *58*, 53–62.

Sabatier, D. (1985). Seasonality and determinism of peak fruiting in the French Guiana Forest. *Revue d'Ecologie (Terre Vie)*, *40*, 289–320.

Sabatier, D., & Puig, H. (1985). Phenology and seasonality of flowering and fruiting in the dense Guyanese forest. *Mémoires du Museum National d'Histoire Naturelle*, *132*, 173–184.

Santamaria, M., & Franco, A. M. (2000). Frugivory of Salvin's Curassow in a rainforest of the Columbian amazon. *Wilson Bulletin*, *112*, 473–481.

Seaman, D. E., & Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, *77*, 2075–2085.

Shaffer, C. A., Yukuma, C., Marawanaru, E., & Suse, P. (2018). Assessing the sustainability of Waiwai subsistence hunting in Guyana by comparison of static indices and spatially explicit, biodemographic models. *Animal Conservation*, *21*, 148–158.

Silverman, B. W. (1986). *Density estimation for statistics and data analysis*, Chapman and Hall.

Slade, N. A., Gomulkiewicz, R., & Alexander, H. M. (1998). Alternatives to Robinson and Redford's method of assessing overharvest from incomplete demographic data. *Conservation Biology*, *12*, 148–155.

Srbek-Araujo, A. C., Silveira, L. F., & Chiarello, A. G. (2012). The Red-billed Curassow (*Crax blumenbachii*): Social organization, and daily activity patterns. *Wilson Journal of Ornithology*, *124*, 321–327.

Strahl, S. D., Beaujon, S., Brooks, D. M., Begazo, A. J., Sedaghatkish, G., & Olmos, F. (1997b). *The Cracidae. Their biology and conservation*. Hancock House Publishers Ltd.

Strahl, S. D., Silva, J. L., & Buchholz, R. (1997a). Variación estacional en el uso del hábitat, comportamiento de grupo, y un sistema aparentemente polígamo en el Paují copete de plumas, *Crax daubentoni*. In S. D. Strahl, S. Beaujon, D. M. Brooks, A. Begazo, G. Sedaghatkish, & F. Olmos (Eds.), *The Cracidae: Their biology and conservation* (p. 79). Hancock House Publishers.

Todd, W. T., Plasse, R., & Eckart, C. (1992). Curassow husbandry: Suggested protocol. In *Houston Zoo zoological gardens* (2nd ed.). Houston, p. 16.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.

Viswanathan, G. M., Raposo, E. P., & da Luz, M. G. E. (2008). Lévy flights and superdiffusion in the context of biological encounters and random searches. *Physics of Life Reviews*, *5*, 133–150.

White, G. C., & Garrot, R. A. (1990). *Analysis of wildlife radio tracking data*. Academic Press Inc.

Yumoto, T. (1999). Seed Dispersal by Salvin's Curassow, *Mitu salvini* (Cracidae), in a tropical forest of Colombia: Direct measurements of dispersaI distance. *Biotropica*, *31*, 654–660.