Primate Communities Along a Protected Area Border: A Two-site Comparison of Abundance and Hunting Response in Bioko, Equatorial Guinea

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Abstract: Bioko Island, Equatorial Guinea is home to seven diurnal primate taxa, threatened with extinction largely due to high rates of illegal bushmeat hunting. The Gran Caldera Scientific Reserve (GCSR), one of two protected areas on Bioko, is the only remaining site where all seven taxa can be found. Historically, much of the wildlife in the GCSR has been passively protected due to its isolation, but a lack of effective law enforcement has allowed hunting to proliferate, and recent road and infrastructure development threatens more hunting in the future. Many calls have been made for the development of a comprehensive management plan to effectively protect the GCSR, but data are needed to understand the dynamics of the varying human-wildlife systems along its borders to develop well-informed and cost-effective management strategies. This study investigated the abundance and species richness of primates along the GCSR border near the village of Moka over four years (2011-2014), and compared results to those of a previous study near a similar GCSR-border village, Belebu. Although we found considerable inter-annual variation in the relative abundance of primates at Moka, the overall relative abundance there was significantly higher than at Belebu. We attribute this primarily to the higher observed hunting intensity at Belebu, differences in historical hunting patterns and accessibility, and the presence of a long-term research site and activities at Moka, which may deter hunters in the area. Further research is needed to provide greater resolution on complementary factors influencing abundance and distribution patterns. However, our results highlight the persistence of a notable primate community near Moka and emphasize the importance of understanding dynamics along protected area borders when planning for conservations. Relatively similar sites may require different approaches for effective management.

Key words: Bioko, hunting, bushmeat, surveys, protected areas

INTRODUCTION

Bushmeat, or the meat of wildlife from forests, has long been a dietary staple of people in tropical African forests (Asibey 1977; Afolayan 1980; Fa *et al.* 2002; Robinson & Bennett 2004). While wild harvest can be a sustainable and accessible proteinsource (Albrechtsen *et al.* 2007), accelerating human population growth, increased use of firearms, and greater accessibility to remote forests has led to the commercialization of the bushmeat trade (Abernethy *et al.* 2013; Albrechtsen *et al.* 2007; Fa *et al.* 2005; Ziegler *et al.* 2016). The rapid growth of the bushmeat trade now threatens many taxa with

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Figure 1. (A) A map of Bioko Island, Equatorial Guinea, including the study sites, major towns and roads, and Bioko's two protected areas: Pico Basilé National Park (PBNP), and the Gran Caldera Scientific Reserve (GCSR). Ureca, the only village within the GCSR is also shown. (B) A magnification of the Moka study area and the survey transects used to assess primate abundance and hunting pressure.

extinction (Oates et al. 2004). In central Africa, hunting is one of the leading causes of decline of most larger-bodied mammals, especially primates and ungulates (Oates et al. 2004). Diurnal primates are among the most heavily hunted taxonomic groups in the region, comprising approximately 10-20% of carcasses recorded in market studies (Fa et al. 2000, 2006; Cronin et al. 2015). Extinction or decline of primate species can lead to negative cascading ecological effects in their communities (Wright et al. 2000, 2007; Abernethy et al. 2013, Effiom et al. 2013). Many primates have a primarily frugivorous diet, and thus provide crucial ecosystem maintenance functions, such as seed dispersal (Chapman & Onderdonk 1998; Lambert 2001; Poulsen et al. 2001, 2002). Tree diversity in hunted forests is lower than in non-hunted forests, and their composition is significantly different from non-hunted forests, largely due to the absence of large-bodied frugivores (e.g., primates) (Sork 1985; Chapman & Chapman 1996; Chapman & Onderdonk 1998; Effiom et al. 2013).

Bioko Island, Equatorial Guinea (Figure 1) is home to numerous endemics, namely, six diurnal primate subspecies, and one endemic primate species (Table 1), all of which are threatened with extinction (IUCN 2016). The primary threat to these species is bushmeat hunting to supply the capital city of Malabo, where there is a large, thriving bushmeat market (Fa et al. 2000; Albrechtsen et al. 2007; Cronin et al. 2015). Over 100,000 kg of bushmeat are consumed annually on Bioko alone, according to several estimates (Fa et al. 2000; Albrechtsen et al. 2007), of which primates comprise approximately 20% of all carcasses (Cronin et al. 2015). While the causes of decline in diurnal primates on Bioko are well established, government led conservation efforts and management plans on Bioko have yet to lead to any profound successes, despite a presidential decree that bans primate hunting (Republic of Equatorial Guinea 2007). Approximately 40% of the island falls within the borders of two protected areas, giving Bioko great potential for conservation. The protected areas, however, have done little to impede hunting, as protected area borders are not well-marked, and environmental legislation is not strongly enforced (Colell et al. 1994; Cronin et al. 2010; 2016; Grande-Vega et al. 2013, 2016). Over time, the threat to primates on Bioko has continued to increase, due to an increase in hunting and demand for bushmeat (Butynski & Koster 1994; Fa 2000; Hearn et al. 2006; Cronin et al. 2010, 2015).

Vornacular nama	Rinomial name	Red List category		
vernacular hanne		Species	Subspecies	
Bioko black colobus ^a	Colobus satanas satanas	Vulnerable	Endangered	
Pennant's red colobus ^{a,b}	Procolobus pennantii pennantii	Critically Endangered	Endangered	
Bioko drillª	Mandrillus leucophaeus poensis	Endangered	Endangered	
Bioko Preuss's monkey ^{a,c}	Allochrocebus preussi insularis	Endangered	Endangered	
Bioko red-eared monkey ^a	Cercopithecus erythrotis erythrotis	Vulnerable	Vulnerable	
Crowned monkey	Cercopithecus pogonias pogonias	Least Concern	Vulnerable	
Bioko putty-nosed monkey	Cercopithecus nictitans martini	Least Concern	Vulnerable	

Table 1. Diurnal primate taxa present on Bioko Island, Equatorial Guinea and their IUCN R
List threatened category (IUCN 2016). Table adapted from Cronin et al. (2016).

^aRecognized by Grubb *et al.* (2003) as subspecies endemic to Bioko. ^bRecognized by Groves (2007) as a species (*Piliocolobus pennantii*) endemic to Bioko. ^cAllocated to the genus *Allochrocebus* following Grubb (2006).

Several previous surveys (Schaaf et al. 1990; Butynski & Koster 1994; Hearn et al. 2004; Cronin et al. 2013) focused primarily on remote areas of the island, and especially on areas within the GCSR. Primate abundance and hunting levels in areas bordering the reserve, however, have gone relatively understudied, with the exception of a brief study at Moka by Colell et al. (1994), undergraduate surveys as part of annual field courses at the Moka Wildlife Center (MWC) over the past decade, and surveys conducted by Cronin et al. (2016) at Belebu, another town bordering the GCSR. Colell et al. (1994) studied hunting in the Moka area by both surveying hunters and conducting hunter follows in 1992, finding that hunters more commonly used traps than guns, and that hunters gradually increased the length and extent of their hunting trips over the course of their study. At Belebu, Cronin et al. (2016) encountered dramatically fewer primates and more hunting signs than at other more remote sites, which was attributed to its long-term history of organized bushmeat hunting and transport and its close proximity to Luba, Bioko's second largest city.

This study makes use of student survey data from 2011-2014 at Moka, and incorporates data collected by Cronin *et al.* (2016) at Belebu to compare differences in primate abundance and hunting intensity between the two sites to inform conservation planning. We sought to: 1) describe primate abundance and species richness at Moka; 2) quantify the hunting intensity at the site, and, if possible, its impact on Moka's primate community (e.g., decreased abundance or reduced species richness); 3) compare data from Moka and Belebu to evaluate differences in primate abundance, species richness, and gun hunting between the two sites; and 4) provide recommendations to improve the efforts to conserve Bioko's primate populations.

METHODS

Study Area

Bioko Island, Equatorial Guinea (2017 km²), a volcanic, continental island, located 37 km off of the coast of Cameroon (Figure 1), is a biodiversity hotspot and a key site for the conservation of African primate diversity (Oates 1996; Myers et al. 2000; Oates et al. 2004). Bioko spans an elevational range from 0-3,011 m asl, and a north-south precipitation gradient from 2,000 mm/year in the north to over 10,000 mm/year in the south (Font Tullot 1951; de Terán 1962). Two protected areas, Pico Basilé National Park (330 km²; PBNP) and the Gran Caldera Scientific Reserve (510 km²; GCSR), encompass approximately 40% of the island's land area. The GCSR encompasses the southern 25% of the island, which has far less human development and impact than the northern end of the island. Aside from the village of Ureka (< 80 individuals), no permanent human settlements exist within the GCSR.

This study took place near the village of Moka, located along the northeastern border of the GCSR at an elevation of 1,400 m asl on the eastern slope of Pico Biao. Moka is largely surrounded by an agricultural mosaic which transitions into montane forest away from the village. Annual precipitation at Moka is estimated to be 3,700 mm/year, with approximately 131 mm falling on average each November (when the surveys were conducted) (Font Tullot 1951). Moka is a key agricultural site on Bioko, predominantly inhabited by the Bubi ethnic group, with an established history of hunting (Colell *et al.* 1994), although Bubis have restricted gun access (Butynski & Koster 1994; Grande-Vega *et al.* 2013). In recent years, agricultural activities have expanded greatly around the town (D.T. Cronin, pers. obs.), despite its location on the border of the GCSR.

Data Collection

Surveys were conducted from 2011 to 2014, between 04 November and 26 November of each year along established multi-use footpaths near the Moka Wildlife Center (MWC) (a facility operated by the Bioko Biodiversity Protection Program, an academic partnership between Drexel University and the National University of Equatorial Guinea). ("recce") walk methodology Reconnaissance (Walsh & White 1999) was used following Cronin et al. (2013, 2016) to travel more quickly, cover more ground, avoid unnecessarily cutting trails/ destroying habitat, and to increase the likelihood of primate encounters. In recce sampling, two to four researchers walk along the path of least resistance through the forest, following natural geographic features, and existing human and game trails to maintain a general compass bearing, and cutting vegetation only when necessary (Walsh & White 1999). Three recce transects were surveyed, San Joaquin, Balacha Sur, and Balacha Norte, all of which were approximately 4 km in length. Transects were measured and marked by researchers prior to beginning surveys using either a hip chain or 50 m tape measure. Surveys were conducted at a speed of approximately 1.15 km hr⁻¹, similar to the 1 km hr⁻¹ rate established by Whitesides et al. (1988), and used in previous surveys on Bioko (Butynski & Koster 1994; Cronin et al. 2013, 2016). One transect was surveyed each day, twice per day (once in each direction), from approximately 0700-1100, and 1400-1800, unless faced with an extenuating circumstance (e.g., heavy rain). We alternated transects each day, in order to walk each transect an approximately equal number of times within our study period.

All survey data were collected by students trained by DTC (including DLF) and FM, who was present for all surveys, and recorded using a customized Cybertracker (v3.248) data collection program (Steventon 2002). Primate groups were counted to estimate relative primate abundance following Schaaf *et al.* (1990) and Cronin *et al.* (2013, 2016) due to difficulties associated with

detection of hunted primates in steep terrain with dense vegetation (Whitesides *et al.* 1988). Upon each primate encounter, the following data were recorded: (1) time of observation (2) type of encounter (visual/ auditory), (3) location (GPS coordinates), (4) elevation, (5) species, (6) number of individuals, (7) sex of individuals, (8) vocalization type, (9) height in trees/canopy (Schaaf *et al.* 1990; Butynski & Koster 1994; Cronin *et al.* 2013). Any encounter within 50 m of the previous encounter was considered part of the same group (same species) or a polyspecific association, and was not recorded separately (Oates *et al.* 1990).

To quantify hunting pressure, any sign of hunting, such as shotgun shells, traps, batteries, hunting camps, carcasses, and gun shots were tallied categorically, and summed (Linder 2008; Cronin *et al.* 2013). Each individual sign was treated as a separate encounter, and no signs were collected to avoid detection, hostility from hunters, and hunter interference in data quality (picking up shotgun shells, batteries, etc.) (Linder & Oates 2011; Cronin *et al.* 2013, 2016).

Data Analysis

Sighting frequencies were calculated as the number of social groups, including solitary primates, sighted per kilometer of transect walked. We did not analyze the data to produce sighting frequencies of individuals, as estimating group size of primate groups in hunted forests is particularly unreliable (Ferrari et al. 2010), and previous primate surveys conducted on Bioko calculated group, not individual, encounter rates (Butynski & Koster 1994; Cronin et al. 2010, 2013, 2016). Sighting frequency (groups/km) is a measure of relative density, used in place of absolute density measurements (groups/ km²) due to small sample sizes of each species and inherent difficulties in detecting hunted primates in dense forest (Fashing & Cords 2000; Marshall et al. 2008). Sighting frequencies and hunting sign encounter rates were compared to surveys conducted by Cronin et al. (2016) at Belebu, to compare abundance and hunting patterns between the two sites.

Primate sighting frequencies were compared among survey sites and years using the nonparametric test (Wilcoxon–Mann–Whitney test (Linder & Oates 2011; Cronin *et al.* 2013, 2016). The alpha level was set at 0.05 for all statistical tests and adjusted using Bonferroni correction procedures. All statistical analyses were conducted using R (v3.2.2; R Core Team 2015).

RESULTS

Sighting frequency and temporal change in Moka

The three transects were surveyed a total of 57 times (San Joaquin: 24 surveys - 81.28 km; Balacha Norte: 13 surveys - 46.66 km; Balacha Sur: 20 surveys - 70.26 km), resulting in a total survey effort of 198.2 km and 151 total encounters, for an average encounter rate of 0.75 groups/km. Visual identifications were confirmed for 119 encounters, resulting in a sighting frequency of 0.56 groups/km. Five of the seven diurnal primate species occurring on Bioko were encountered in the Moka area: *Cercopithecus erythrotis, C. pogonias, C. nictitans, Allochrocebus preussi,* and *Mandrillus leucophaeus.* The two colobine species present on Bioko, *Colobus satanas* and *Procolobus pennantii* were not encountered.

Overall sighting frequencies of all primate species each year in Moka were compared to every other year using the Wilcoxon–Mann–Whitney test. Sighting frequency was significantly higher in 2013 (0.82 groups/km) and 2014 (0.72 groups/km) than in 2011 (0.45 groups/km), and significantly higher in 2013 (0.72 groups/km) than in 2012 (0.37 groups/ km) (Wilcoxon–Mann–Whitney: 2011-2013: W = 101.5, p < 0.005; 2011-2014: W = 157, p < 0.01; 2012-2013: W = 61.5, p < 0.05) (Table 2). In all four years, *C. erythrotis* was the most frequently sighted primate (Table 2). In 2011, the only other primate species sighted was *M. leucophaeus* (Table 2). In 2012, the only other sighted primate species was *A. preussi* (Table 2). In 2013, three species were sighted at relatively low frequencies (*M. leucophaeus, A. preussi, and C. nictitans*) (Table 2). In 2014, three species were sighted, again, at relatively low frequencies (*M. leucophaeus, C. nictitans*, and *C. pogonias*) (Table 2; Figure 2).

Species richness in Moka

Species richness (i.e., the number of species encountered) varied by year, and by transect. More species were observed in 2013 and 2014 (4 species) than in 2011 and 2012 (2 species), but within years, the composition of species encountered varied among transects (Figure 2). The most species were observed on Balacha Sur in 2011 (2 species), 2013 (3 species), and 2014 (3 species) (Figure 2). In 2012, the most species were sighted on San Joaquin (2 species) (Figure 2). Across all years, the fewest species were sighted on Balacha Norte, as only *C. erythrotis* was sighted on this trail (Figure 2).

Hunting in Moka

Both gun hunting and trapping signs were encountered on all trails each year, with some



Figure 2. The percentage of each species sighted per transect per year during surveys in Moka from 2011 – 2014.

						Z	loka							* 1° C	
Species ^a		2011			2012			2013			2014			peleou	
	z	S.F. (grps/km)	%	z	S.F. (grps/km)	%	z	S.F. (grps/km)	%	Z	S.F. (grps/km)	%	z	S.F. (grps/km)	%
Cer	30	0.43 (0.10)	94	16	0.31 (0.078)	76	22	0.60 (0.19)	76	29	0.57 (0.16)	78	6	0.11 (0.045)	53
Cpo	0	0	0	0	0	0	0	0	0	7	0.042 (0.012)	5	6	0.047 (0.023)	35
Cni	0	0	0	0	0	0	1	0.023 (0.007)	3.5		0.021 (0.006)	Э	0	0	0
Apr	0	0	0	4	0.085 (0.021)	19	1	0.026 (0.008)	3.5	0	0	0	П	0.007 (0.007)	Ŋ
Mle	1	0.014~(0.003)	ŝ	0	0	0	7	0.047 (0.015)			0.021 (0.006)	e	0	0	0
Csa	0	0	0	0	0	0	0	0	0	0	0	0	П	0.016 (0.016)	9
Unk	1	0.14~(0.003)	3	1	0.016 (0.004)	Ŋ	ŝ	0.085 (0.027)	10	4	0.08 (0.024)	11	0	0	0
Total	32	0.45 (.11)		21	0.39 (0.098)		29	0.82 (0.26)		37	0.72 (0.21)		17	0.18 (0.061)	

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variation by trail and year (Table 3). Hunting signs largely comprised of shotgun shells, followed by traps, batteries, and miscellaneous hunting signs (e.g., carcasses, entrails). The highest gun sign encounter rate occurred in 2013, with a considerable decrease in 2014 (Table 3). Snares were encountered an average of 4.07 times more frequently in 2011 and 2012 than in 2013 and 2014 (Table 3).

Differential species composition and sighting frequency per site

While species richness was comparable at both sites (Belebu, 4 species; Moka, 5 species), the overall primate sighting frequency was significantly higher at Moka (0.56 groups/km) than Belebu (0.18 groups/km) (Wilcoxon–Mann–Whitney: W = 534, p <0.00001) (Figure 3). All individual species sighting frequencies were higher at Moka, except for *C. satanas*, of which no sightings were made at Moka, while a single sighting occurred at Belebu resulting in a sighting frequency of 0.016 groups/km. Two species were sighted at Moka that were not sighted at Belebu (*M. leucophaeus*, 0.017 groups/km).

Differential response to gun hunting per site

Belebu (5.56 signs/km) had a higher overall hunting sign presence than Moka (1.22 signs/km), a higher gun sign encounter rate (Belebu, 2.89 signs/ km; Moka, 0.83 signs/km), and a higher trap sign encounter rate (Belebu, 2.66 signs/km; Moka, 0.40 signs/km). Overall sighting frequency of primates was higher in Moka, where fewer hunting signs were encountered.

DISCUSSION

While several other studies have documented primate abundance and hunting pressure on Bioko Island and Cronin et al. (2015) assessed the impact of gun hunting on Bioko's diurnal primate species, this is the first study to highlight and assess relative abundance of primates and hunting pressure near two semi-urbanized towns on Bioko. Prior to this study, no primary data in the Moka area on Bioko was published. Overall primate sighting frequency was higher in Moka, where fewer hunting signs were encountered; however, differences in elevation (Cronin et al. 2016), distance from roads (Cronin et al. 2017) and habitat may also play a role, and require further research. A prominent hunting presence was revealed at both of the census locations in this study (Belebu, 5.56 signs/km; Moka, 1.22 signs/km). According to Cronin et al. (2015), primates have become a key portion of the bushmeat market in Malabo, the capital of Bioko.

Of Bioko's seven diurnal primate species, our surveys revealed the presence of five species persisting at Moka, and four at Belebu (Cronin et al. 2016). While species composition and abundance in our surveys varied from year to year, the regularity with which primates were encountered at Moka suggests that five species continue to persist in the area, and the comparably sparse encounters at Belebu suggests the contrary. C. erythrotis was the most commonly sighted species at Moka and Belebu, in accordance with previous studies on Bioko (Butynski & Koster 1994; Cronin et al. 2016), while the other five species [A. preussi (Moka, Belebu), C. satanas (Belebu), C. pogonias (Moka, Belebu), C. nictitans (Moka), and M. leuocophaeus (Moka)] were encountered at a much lower frequency. P. pennantii and C. satanas were not encountered in the Moka area, implying extremely low densities, as in the case of C. satanas, or extirpation in the areas surrounding Moka, as has been suggested for P. pennantii (Cronin et al. 2013, 2016, 2017). C. satanas has recently been observed opportunistically near Moka along the rim of the Biao crater (1 individual; D. Montgomery, pers. obs. 2013), and on the northwest flank of Pico Biao (1 individual: D. Venditti, pers. obs. 2016; 2 groups: D. L. Forrest, pers. obs. 2017). Colell et al. (1994) described a single P. pennantii carcass, reported to be taken near Pico Biao in 1992; however, P. pennantii is now believed to be restricted to a single small population in the southwestern corner of Bioko (Cronin et al. 2016, 2017). Colobus monkeys are largely understood to be highly sensitive to hunting, due to their large body size, their sluggish and conspicuous manner of movement, and low level of visual alertness (Oates 1996). On Bioko, Cronin et al. (2016) found that both C. satanas and P. pennantii are the most vulnerable species to hunting. Examples with other colobine species from mainland Equatorial Guinea (Kümpel et al. 2008), Uganda (Struhsaker 1999), Tanzania (Marshall 2007), and a comprehensive analysis of all red colobus species (Struhsaker 2005) substantiate this claim. The high vulnerability to hunting of both colobine species on Bioko likely account for their absence at our study site.

Despite the higher sighting frequency at Moka, the primate communities of both Moka and Belebu are reflective of hunted forests on Bioko (Cronin *et al.* 2016) and the Congo Basin (Linder & Oates 2011; Rovero *et al.* 2012). As in other recent surveys on the island (Cronin *et al.* 2013, 2016), the majority of sightings consisted of smaller bodied primates

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Table 3. Hunting sign totals and encounter rates per km during surveys at Moka (2011 – 2014; this study) and Belebu (2011-2012; Cronin *et al.* 2016).

Hunting Sign Type		D 1 1			
	2011	2012	2013	2014	Belebu
Gun Hunting Signs					
Balacha Norte	5	16	24	9	-
Balacha Sur	22	18	19	8	-
San Joaquin	11	17	14	6	-
All Trails	38	51	57	23	354
Trap Hunting Signs					
Balacha Norte	0	24	0	5	-
Balacha Sur	18	10	3	4	-
San Joaquin	15	0	0	0	-
All Trail	33	34	3	9	284
Total Hunting Signs					
Balacha Norte	5	40	24	14	-
Balacha Sur	40	28	22	12	-
San Joaquin	26	17	14	6	-
All Trails	71	85	60	32	638
Gun Sign E. R. (km ⁻¹)					
Balacha Norte	0.69	1.13	2.36	0.45	-
Balacha Sur	1.07	1.05	1.64	0.43	-
San Joaquin	0.30	0.77	1.46	0.52	-
All Trails	0.59	0.96	1.64	0.46	2.89
Trap Sign E. R. (km ⁻¹)					
Balacha Norte	0.00	1.70	0.20	0.25	-
Balacha Sur	0.40	0.58	1.57	0.22	-
San Joaquin	0.88	0.00	0.00	0.00	-
All Trails	0.51	0.64	0.09	0.18	2.66
Overall Hunting Sign E.R. (km ⁻¹)					
Balacha Norte	0.69	2.83	2.56	0.70	-
Balacha Sur	1.95	1.64	1.64	0.65	-
San Joaquin	0.97	0.77	1.46	0.52	-
All Trails	1.25	1.60	1.72	0.64	5.56



Figure 3. Comparison of primate sighting frequencies at Belebu and Moka. Notches indicate standard deviations from the mean sighting frequency values.

(e.g., *C. erythrotis*), while larger, more conspicuous species were encountered at either low rates (e.g., *M. leucophaeus, C. satanas*), or not at all (e.g., *P. pennantii*). *C. erythrotis* is the smallest diurnal primate occurring on Bioko (Butynski *et al.* 2009), and is most resilient to hunting pressure (Cronin *et al.* 2016). In contrast, the larger-bodied species, *M. leucophaeus, C. satanas,* and *P. pennantii*, are all vulnerable to hunting pressure and, thus, are expected to be encountered at lower frequencies (Cronin *et al.* 2016). *P. pennantii* and *C. satanas*, respectively, had the highest and second-highest vulnerability indices of all of Bioko's primates (Cronin *et al.* 2016) and, accordingly, were only

opportunistically encountered or absent in our surveys. The high proportion of *C. erythrotis* encountered during our surveys relative to largerbodied primate taxa lends further support to Cronin *et al.*'s (2016) suggestion that *C. erythrotis* may compensate for the loss of other diurnal primate taxa on Bioko. Other recent studies in Cameroon (Linder & Oates 2011) and Tanzania (Rovero *et al.* 2012) have shown similar trends with respect to the primate community composition in highly-hunted versus lesser-hunted forests (fewer larger-bodied primates, chiefly colobines, and equal or greater smaller-bodied primates, chiefly cercopithecines). Both Linder & Oates (2011) and Cronin *et al.* (2016) propose that this phenomenon could be attributed to competitive release, which may also be the case in our study.

Habitat degradation is often cited as a leading cause of primate population decline in west and central Africa (Oates 1996; Rovero et al. 2012; Barelli et al. 2015) and may play an important role in primate community dynamics at both of our study sites. The abandonment of former pastureland in Moka in the early 1990s allowed secondary forest to reclaim some areas of previously lost or degraded habitat. This potentially led to increased habitat, in some areas around Moka (Butynski & Koster 1994). However, in recent years, there has been considerable habitat loss near both Moka and Belebu, concentrated along their primary access roadways (main road to Luba and Malabo, Moka; Luba-Ureka road, Belebu), due to agricultural expansion (D.T. Cronin, D.L. Forrest, pers. obs.). Net habitat gain may be insignificant or even negative, as a result, but it is also likely that hunting efforts will be, at least in the short term, concentrated in areas just beyond agricultural expansion and along roads, due to easier accessibility.

While both the towns of Moka and Belebu are positioned along the border of the GCSR, relative primate abundance and hunting sign encounter rates differed between the two, likely due to the accessibility and land-use history of these towns. Our results indicate a higher hunting presence in Belebu than in Moka, and correspondingly fewer primates in Belebu than in Moka. The forest near Belebu is more accessible to most hunters, as Belebu is only 7.5 km from Luba, Bioko's second largest town, on the Luba-Ureka Road, and, as a result, nearer to Malabo, the largest town and location of the main bushmeat market. Belebu also has a long history of plantation agriculture of both cocoa and palm, fueling both forest loss and/or conversion, and gun hunting for bushmeat and management of agricultural pests, e.g., squirrels (Butynski & Koster 1994). Small-scale commercial agriculture also occurs in Moka, but expansion has occurred more recently, and a greater amount of intact forest remains directly surrounding the town (D. T. Cronin, D. L. Forrest, pers. obs.). Elevation is often considered an important environmental predictor of primate abundance, as higher elevation are typically associated with lower densities of primates (Barelli et al. 2015). This holds true on Bioko (Cronin et al. 2016); however, our high elevation site (Moka) had a higher sighting frequency than the lowland site (Belebu). Higher sighting frequency on trails around Moka (montane forest) than Belebu

(lowland forest) indicate that hunting pressure likely has the dominant impact on primate abundance. Other environmental factors may also play a role in the species richness and abundance at each site, and further research is necessary to investigate the impact of these ecological differences.

The results from these two towns on the boundary of the GCSR support the persistence of a number of significant issues: (1) the borders of the GCSR are permeable to hunters; (2) the legal existence of protected areas on Bioko is not sufficient to deter hunting, especially of threatened primates, which are critically important to the maintenance of ecosystem processes; and (3) the development of management strategies for the GCSR needs to account for site-specific differences in accessibility, long-term history, hunting patterns, and species assemblages, such as prioritization of the location of forest patrols, and selective positioning of bushmeat checkpoints. With the understanding of the limitations in implementing a management strategy for a protected area (limited funding, personnel, equipment, etc.), it is imperative to consider key access points, hunted areas, and the current ecological state of the area. Belebu and Moka are two of only four large towns within 2 km of the GCSR, and are the most accessible of the four. By studying the primate abundance and hunting levels in key locations nearing the reserve borders, we can better understand the pathways of entry into the reserve, level of use in different portions of the reserve, and prioritize limited resources. We contend that the difference between primate abundance in Belebu and Moka is due, in large part, to the greater accessibility and history of hunting in Belebu.

With this understanding, the current expansion of agriculture at Moka, and the completion of the new road through the GCSR to Ureka, we reiterate the recommendation made in Cronin et al. (2017) that the implementation of a management plan for the GCSR is of critical importance to the preservation of its diurnal primate taxa. Included in their recommendations were the creation and implementation of 'ranger bases' at primary access points to the GCSR and 'bushmeat checkpoints' along key transit routes between protected areas. Belebu, situated 7.5 km from the entrance to the Luba-Ureka road (Figure 1), is highly accessible to hunters coming from Luba. A checkpoint directly after Belebu along the Luba-Ureka road, coupled with vehicle searches by INDEFOR-AP, the protected area management authority would limit the amount of off-take by preventing vehicle access to the reserve. There are two major roadways leading directly to Moka, and an extensive trail system surrounding the town. While this accessibility, coupled with the Moka Wildlife Center, have provided the infrastructure for ecotourism, and has already lead to some success in this area, heavy hunting pressure and subsequent decreases in primate abundance near the town threatens to reduce, if not eliminate, the ecotourism market in the town. Increasing the number of ecoguard patrols in the area, coupled with military support may decrease the hunting presence.

Both Belebu and Moka were put forth as sites in Cronin et al.'s (2017) GCSR conservation strategy, and our study highlights the importance of these two sites to primate conservation along the GCSR border, and as access points for illegal activities. Continued hunting and defaunation in towns like Belebu and Moka along the GCSR border will, in time, lead to hunters moving further into the GCSR, reaching core areas which still maintain high densities of all 7 diurnal primate species (Cronin et al. 2017). The newly constructed road from Luba to Ureka has already enabled hunters to have vehicle access to formerly remote areas of the GCSR and contributed to increased hunting activity in the southern extent of the reserve (D.T. Cronin, unpublished data, 2015-2016). Forest patrols by INDEFOR-AP should be targeted in areas of known hunting, including Moka, Belebu, and other easy-access areas of the GCSR.

Finally, long-term research sites and the associated presence of researchers and students have been shown to contribute to significantly higher primate abundance and lower hunting intensity (Campbell et al. 2011; N'Goran et al. 2012). The Moka Wildlife Center has been a site for long-term research, educational, and conservation activities since 2006, and the consistent presence of researchers and students have likely contributed to the lower levels of hunting and higher primate abundance observed at Moka relative to Belebu in our study. Furthermore, all of the surveys at Moka were carried out by students conducting research at the Moka Wildlife Center, revealing the value of student research for informing conservation in an understudied area of the island. These student surveys occur annually, and provide a consistent source of data to frequently update the status of primate populations, as well as the effects that hunting and agriculture are having on primate populations at Moka. While much of the scientific literature has focused on more remote areas of the island, our results detail the persistence of notable primate populations, and highlight the importance of understanding the dynamics of wildlife populations in more disturbed, humandominated landscapes on Bioko when planning for conservation.

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LITERATURE CITED

- Abernethy, K.A., L. Coad, G. Taylor, M.E. Lee & F. Maisels. 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368: 1-11.
- Afolayan, T. 1980. A synopsis of wildlife conservation in Nigeria. *Environmental Conservation* 7(3): 207-212.
- Albrechtsen, L., W.M.A. David, J.J. Paul, C. Ramon & J.E. Fa. 2007. Faunal loss from bushmeat hunting: empirical evidence and policy implications in Bioko island. *Environmental Science & Policy* 10(7): 654-667.
- Asibey, E. 1977. Expected effects of land-use patterns on future supplies of bushmeat in Africa South of the Sahara. *Environmental Conservation* 4(1): 43-49.
- Barelli, C., R. Mundry, A. Araldi, K. Hodges, D. Rocchini & F. Rovero. 2015. Modeling primate abundance in complex landscapes: a case study from the Udzungwa Mountains of Tanzania. *International Journal of Primatology* 39(2): 209– 226.
- Butynski, T.M., Y. A. de Jong & G.W. Hearn. 2009. Body measurements for the monkeys of Bioko Island, Equatorial Guinea. *Primate Conservation* 24(1): 99–105.
- Butynski, T.M. & S.H. Koster. 1994. Distribution and conservation status of primates in Bioko Island, Equatorial Guinea. *Biodiversity and Conservation* 3(9): 893-909.
- Campbell, G., H. Kuehl, A. Diarrassouba, P. K. N'Goran & C. Boesch. 2011. Long-term research sites as refugia for threatened and over-harvested species. *Biology Letters* 7(5): 732-726.
- Chapman, C. A., & L. J. Chapman. 1996. Frugivory

and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology* 12(4):491–504.

- Chapman, C. A. & D. A. Onderdonk. 1998. Forests without primates: primate/plant codependency. *American Journal of Primatology* 45:127-141.
- Colell, M., C. Mate & J. E. Fa. 1994. Hunting among Moka-Bubis in Bioko: dynamics of faunal exploitation at the village level. *Biodiversity and Conservation* 3(9): 939-950.
- Cronin, D. T., D. Bocuma Meñe, T. B. Butynski, J. M. E. Echube, G. W. Hearn, S. Honarvar, J. R. Owens & C. P. Bohome. 2010. Opportunities Lost: The Rapidly Deteriorating Conservation Status of the Monkeys on Bioko Island, Equatorial Guinea (2010). A report to the Government of Equatorial Guinea by the Bioko Biodiversity Protection Program, Drexel University, Philadelphia, PA.
- Cronin, D. T., C. Riaco & G. W. Hearn. 2013. Survey of threatened monkeys in the Iladyi River Valley Region, Southeastern Bioko Island, Equatorial Guinea. *African Primates* 8: 1-8.
- Cronin, D. T., C. Riaco, J. M. Linder, R. A. Bergl, M. K. Gonder, M. P. O'Connor & G. W. Hearn. 2016. Impact of gun-hunting on monkey species and implications for primate conservation on Bioko Island, Equatorial Guinea. *Biological Conservation* 197: 180-189.
- Cronin, D. T., P. R. Sesink Clee, M. W. Mitchell, D. Bocuma Meñe, D. Fernández, C. Riaco, M. Fero Meñe, J.M. Esara Echube, G. W. Hearn & M. K. Gonder. 2017. Conservation strategies for understanding and combating the primate bushmeat trade on Bioko Island, Equatorial Guinea. *American Journal of Primatology* 79:e22663. https://doi.org/10.1002/ajp.22663
- Cronin, D. T., S. Woloszynek, W. A. Morra, S. Honarvar, J. M. Linder, M. K. Gonder, M.P. O'Connor & G. W. Hearn. 2015. Long-term urban market dynamics reveal increased bushmeat carcass volume despite economic growth and proactive environmental legislation on Bioko Island, Equatorial Guinea. *PLoS ONE* 10(8): e0134464.
- Effiom, E. O., G. Nuñez-Iturri, H. G. Smith, U. Ottosson & O. Olsson. 2013. Bushmeat hunting changes regeneration of African rainforests. *Proceedings of the Royal Society B: Biological Sciences* 280(1759): 20120303.
- Fa, J. E. 2000. Hunted animals in Bioko Island, West Africa: sustainability and future. In J. G. Robinson and E. L. Bennett, eds. *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York, NY. Pp. 168-198.

- Fa, J. E., C. A. Peres & J. Meeuwig. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conservation Biology* 16(1): 232-237.
- Fa, J. E., S. F. Ryan & D. J. Bell. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. *Biological Conservation* 121(2): 167-176.
- Fa, J. E., S. Seymour, J. Dupain, R. Amin, L. Albrechtsen & D. Macdonald. 2006. Getting to grips with the magnitude of exploitation: Bushmeat in the Cross–Sanaga rivers region, Nigeria and Cameroon. *Biological Conservation* 129(4): 497-510.
- Fa, J. E., J. E. G. Yuste & R. Castelo. 2000. Bushmeat markets on Bioko Island as a measure of hunting pressure. *Conservation Biology* 14(6): 1602-1613.
- Fashing, P. J. & M. Cords. 2000. Diurnal primate densities and biomass in the Kakamega Forest: An evaluation of census methods and a comparison with other forests. *American Journal* of *Primatology* 50(2): 139-152.
- Ferrari, S.F., R.R.D. Chagas & J.P. Souza-Alves, 2010. Line transect surveying of arboreal monkeys: problems of group size and spread in a highly fragmented landscape. *American Journal of Primatology* 72(12): 1100-1107.
- Font Tullot, I. 1951. *El Clima de las Posesiones Españoles del Golfo de Guinea.* Consejo Superior de Investigaciones Científicas, Instituto de Estudios Africanos, Madrid.
- Grande-Vega, M., B. Carpinetti, J. Duarte & J. E. Fa. 2013. Contrasts in livelihoods and protein intake between commercial and subsistence bushmeat hunters in two villages on Bioko Island, Equatorial Guinea. *Conservation Biology* 27(3): 576-587.
- Grande-Vega, M., M. Á. Farfán, A. Ondo & J. E. Fa. 2016. Decline in hunter offtake of blue duikers in Bioko Island, Equatorial Guinea. *African Journal* of Ecology 54: 49-58.
- Groves, C. P. 2007. The taxonomic diversity of the Colobinae of Africa. *Journal of Anthropological Sciences* 85: 7-34.
- Grubb, P. 2006. Geospecies and superspecies in the African primate fauna. *Primate Conservation* 20: 75-78.
- Grubb, P., T. M. Butynski, J. F. Oates, S. K. Bearder, T. R. Disotell, C. P. Groves & T. T. Struhsaker. 2003. Assessment of the diversity of African primates. *International Journal of Primatology* 24(6): 1301-1357.
- Hearn, G. W., W. Morra & T. B. Butynski. 2006. Monkeys in Trouble: The Rapidly Deteriorating

Conservation Status of the Monkeys on Bioko Island, Equatorial Guinea. Bioko Biodiversity Protection Program, Arcadia University, Glenside, Pennsylvania.

- Hearn, G. W., C. Ross, J. G. Francisco, D. F. Sobrado, M. A. E. Mba, C. P. Bohome & W. A. Morra. 2004. Monkey group encounter rates (1996-2003) in the Gran Caldera de Luba, Bioko island, Equatorial Guinea. *Folia Primatologica* 75: 271-272.
- IUCN. 2016. IUCN Red List of Threatened Species. Version 2015.4. IUCN 2016: Downloaded on 27 April, 2016.
- Kümpel, N.F., E. Milner-Gulland, J. Rowcliffe & G. Cowlishaw. 2008. Impact of gun-hunting on diurnal primates in continental Equatorial Guinea. *International Journal of Primatology* 29(4): 1065–1082.
- Lambert, J. E. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and *Strychnos mitis*: Evidence for plant benefits beyond seed dispersal. *International Journal of Primatology* 22(2): 189-201.
- Linder, J.M. 2008. The Impact of Hunting on Primates in Korup National Park, Cameroon: Implications for Primate Conservation. Doctoral dissertation, Department of Anthropology. City University of New York.
- Linder, J.M. & J. F. Oates. 2011. Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biological Conservation* 144(2): 738-745.
- Marshall, A.R. 2007. *Disturbance in the Udzungwas: Responses of monkeys in trees to forest degradation*. Centre for Ecology, Law and Policy, The University of York, Heslington, York, UK.
- Marshall, A. R., J. C. Lovett & P. C. White. 2008. Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. *American Journal of Primatology* 70(5): 452-462.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca & J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403(6772): 853-858.
- N'Goran, P. K., C. Boesch, R. Mundry, E. K. N'Goran, I. Herbinger, F. A. Yapi & H. S. Kuhl. 2012. Hunting, law enforcement, and African primate conservation. *Conservation Biology* 26(3): 565-571.
- Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L. & M. Silon. 1990. Determinants of variation in tropical

forest primate biomass: new evidence from West Africa. *Ecology* 71(1): 328–343.

- Oates, J. F. 1996. *African Primates: Status Survey and Conservation Action Plan.* International Union for Conservation of Nature (IUCN). Species Survival Commission (SSC). Primate Specialist Group, Gland, Switzerland.
- Oates, J. F., R. A. Bergl & J. M. Linder. 2004. Africa's Gulf of Guinea Forests: Biodiversity Patterns and Conservation Priorities. Advances in Applied Biodiversity Science (6). Wildlife Conservation Society (WCS), New York, and Center for Applied Biodiversity Science (CABS), Conservation International, Washington, DC.
- Poulsen, J. R., C. J. Clark, E. F. Connor & T. B. Smith. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology* 83(1): 228-240.
- Poulsen, J. R., C. J. Clark & T. B. Smith. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 17(6): 787-808.
- R Core Team. 2015. R: A Language and Environment for Statistical Computing R Foundation for Statistical Computing. Vienna, Austria.
- Republic of Equatorial Guinea. 2007. Hunting and consumption of monkeys and other primates in the republic of Equatorial Guinea is prohibited. Decree num. 72/2007, Republic of Equatorial Guinea.
- Robinson, J. G. & E. L. Bennett. 2004. Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems. *Animal Conservation* 7(4): 397-408.
- Rovero, F., A. Mtui, A. Kitegile & M.R. Nielsen. 2012. Hunting or habitat degradation? Decline of primate populations in Udzungwa Mountains, Tanzania: an analysis of threats. *Biological Conservation* 146(1): 89–96.
- Schaaf, C. D., T. B. Butynski & G. W. Hearn. 1990. The Drill (Mandrillus leucophaeus) and Other Primates in the Gran Caldera Volcanica de Luba: Results of a Survey conducted March 7-22, 1990. A Report to the Government of Equatorial Guinea, Zoo Atlanta, Atlanta, GA.
- Sork, V. L. 1985. Germination response in a largeseeded Neotropical tree species, *Gustavia* superba. Biotropica 17(2): 130-136.
- Steventon, J. 2002. Cybertracker v. 3.200. Cybertracker Software.
- Struhsaker, T. 1999. Primate communites in Africa: the consequence of long-term evolution or the artifact of recent hunting? *Primate Communities* 1: 289-294.

- Struhsaker, T. 2005. Conservation of red colobus and their habitats. *International Journal of Primatology* 26(3): 525-538.
- de Terán, M. 1962. Sintesis Geografica de Fernando Poo, Madrid, Espana: Insituto de Estudios Africanos.
- Walsh, P. D. & L. J. T. White. 1999. What it will take to monitor forest elephant populations. *Conservation Biology* 13(5): 194–202.
- Whitesides, G.H., J. Oates, S. Green & R. P. Kluberdanz. 1988. Estimating primate densities from transects in a West African rain forest: a comparison of techniques. *Journal of Animal Ecology* 57(2): 345–367.
- Wright, S. J., K. E. Stoner, N. Beckman, R. T. Corlett, R. Dirzo, H. C. Muller-Landau, G. Nuñez-Iturri,

C. A. Peres & B. C. Wang. 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* 39(3): 289-291.

- Wright, S. J., H. Zeballos, I. Domínguez, M. M. Gallardo, M. C. Moreno & R. Ibáñez. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology* 14(1): 227-239.
- Ziegler, S., J. E. Fa, C. Wohlfart, B. Streit, S. Jacob & M. Wegmann. 2016. Mapping bushmeat hunting pressure in Central Africa. *Biotropica* 48(3):405-412.

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