Survey of Threatened Monkeys in the Iladyi River Valley Region, Southeastern Bioko Island, Equatorial Guinea

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Abstract: Bioko Island, Equatorial Guinea, is home to a diverse assemblage of anthropoid primates, making it one of the most important places in Africa for primate conservation. The only threat to the persistence of these primates on Bioko is illegal bushmeat hunting. Since October 1997, the rate of primate carcasses in the central market in the capital, Malabo, has increased significantly, with over 41,000 primates recorded through December 2012. However, the relationship between market dynamics and the status of wild populations is poorly documented and difficult to quantify. This is due, in part, to a lack of island-wide survey data, which detracts from the accuracy of both the population and range estimates of Bioko's monkey species. For instance, the range of the Critically Endangered, endemic Pennant's red colobus (Procolobus pennantii) is currently divided into what are believed to be two isolated populations: a core range in the southwest corner of Bioko, and an unconfirmed population in the Iladyi River valley (IRV) to the southeast. This study investigated the presence of *P. pennantii* in the IRV region and assessed the status of remaining monkey populations. We also evaluated temporal changes in the relative abundance and proportional representation of monkey species in the IRV region relative to surveys conducted in the same region in 2007. Although not proving its absence, we found no evidence of *P. pennantii* in the region, suggesting that the Iladyi population may be extirpated. Each of the other five monkey species known to these habitats were encountered, though primate abundance in the IRV region decreased since 2007, concurrent to an increase in hunting in the region. Our results suggest that the primate community may also be undergoing a compensatory shift towards smaller-bodied monkeys (Cercopithecus spp.), as larger species like P. pennantii are being hunted out. Effective enforcement of existing legislation to achieve a decrease in hunting is critical to the long term future of the primates of Bioko.

Key words: Africa, primate, bushmeat hunting, Bioko Island, Equatorial Guinea, shotgun, conservation

INTRODUCTION

Bioko Island, Equatorial Guinea (Figure 1) is among the highest priority sites in Africa for the conservation of primates (Oates 1996). The island is home to seven species of diurnal primates [drill (Mandrillus leucophaeus poensis), black colobus (Colobus satanas satanas), Pennant's red colobus (Procolobus pennantii), red-eared monkey (Cercopithecus erythrotis erythrotis), crowned monkey (Cercopithecus pogonias pogonias), putty-nosed monkey (Cercopithecus nictitans martini), and Preuss's

monkey (*Allochrocebus preussi insularis*)], all of which are threatened with extinction as either species and/or subspecies (IUCN 2012). This diversity notwithstanding, illegal hunting of primates, which represents the primary threat to these species, has increased dramatically over time, with primates comprising approximately 20% of the total bushmeat sold in Malabo, the capital of Equatorial Guinea (Albrechtsen *et al.* 2007; Morra *et al.* 2009; Cronin *et al.* 2010).

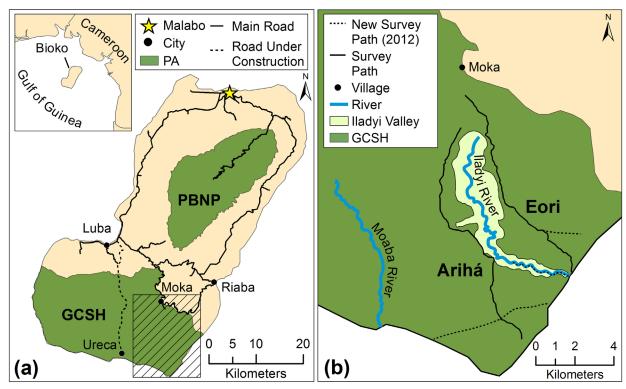


Figure 1: (a) Bioko Island, Equatorial Guinea, showing the major cities and roads on Bioko, as well as both protected areas (PA): Pico Basilé National Park (PBNP), and the Gran Caldera-Southern Highlands Scientific Reserve (GCSH). Ureca, the only village within the GCSH is also shown. The hash marked area depicts the location of the study area in southeastern Bioko. (b) The study area is shown with survey paths used, in both 2007 and 2012, to assess primate abundance and hunting pressure.

The relationship between market data and wild populations on Bioko is poorly documented, as there have been relatively few island-wide primate surveys since Butynski & Koster's (1994) extensive 1986 survey. Much of the work has been restricted to the remote Gran Caldera de Luba in the southwest sector of the island (Figure 1a); consequently, detailed primate distributions, like that of the critically endangered Pennant's red colobus (Procolobus pennantii), a species endemic to Bioko, remain approximations (Groves 2007). The core range of *P. pennantii* is estimated to be entirely within the Gran Caldera and Southern Highlands Scientific Reserve (GCSH), with relative abundance highest (up 0.5 groups/ km) (Cronin, unpublished data) in the immediate vicinity of the Gran Caldera de Luba to the southwest (Butynski & Koster 1994). A second, unconfirmed, allopatric population is believed to exist within the Iladyi River valley (IRV) in the southeast sector of the GCSH (Figure 1b) (Cronin et al. 2010; Oates 2011; IUCN 2012). Despite there being suitable habitat, numerous surveys have not resulted in any evidence of present-day connectivity between the two populations, supporting a hypothesis for allopatry if the second IRV population were to exist (Cronin, unpublished data). Nevertheless, the existence of the second population remains uncertain, as no surveys have been conducted in the immediate area of the IRV to confirm the presence of *P. pennantii*.

To address this dearth of information, in October 2012, we conducted a rapid assessment of primate abundance in the southeast sector of the GCSH (Figure 1b). The main objective of this survey was to confirm the presence of *P. pennantii* in the IRV. In addition, this study also aimed to: (1) document the presence and/or absence of primate species, (2) evaluate the geographic range for the primates, (3) assess the current status of the primates, and (4) quantify temporal changes of primate sighting frequencies by comparing results to surveys conducted in the same region in 2007 (Nowak & Rioso Etingue 2007).

METHODS

Study Area

Bioko Island (2,017 km²) is a volcanic, continental island in the Gulf of Guinea island chain located 37 km off the coast of Cameroon. The GCSH makes up the entire southern sector of Bioko (510 km²), encompassing a range of habitat types (monsoon forest, lowland forest, montane forest, Schefflera (Araliaceae) forest, and cultivation) and elevations that rise from sea level to two peaks, the Gran Caldera de Luba (2,261 m) in the west and Pico Biao (2,009 m) in the east, in less than 15 km (Butynski & Koster 1994). Human populations are

concentrated along the northern border of the GCSH (e.g., Moka, Riaba), and, with the exception of Ureca (< 80 individuals), the GCSH holds no permanent human settlement and has been largely protected from exploitation apart from hunting.

Data Collection

During October 2012, surveys of primate populations were conducted in the southeastern sector of the GCSH (Figure 1b). Primate surveys were conducted along established multiuse footpaths first described by Colell et al. (1994), the majority of which were comparable to those surveyed by Nowak and Rioso Etingue (2007). Reconnaissance, or "recce", walk methodology was used for all surveys, rather than straight line transects, which typically involve the creation of additional hunting paths. With recces, the researcher follows the path of least resistance through the forest (e.g., footpaths), cutting only what is necessary to maintain a general compass heading (Walsh & White 1999; Linder 2008). In this way, both the surveyed area and number of animals detected can be increased by allowing greater distances to be covered in an equivalent period of time (Walsh & White 1999; Linder 2008). Recce paths were located either on the northern (Eori) or southern (Arihá) ridge above the Iladyi River. We also conducted surveys opportunistically along the Iladyi River valley floor and across Punta Santiago (Figure 1b). A total distance of 36.17 km was surveyed (Eori-11.30 km; Iladyi River-5.00 km; Arihá-19.87 km). Surveys averaged 3.29 km in length (range: 1.03-6.20 km), and were walked between 7:00 and 16:00 h at a rate of 1.06 km/hr. The length of each survey varied relative not only to the difficulty of terrain and the presence and status of preexisting trails, but also to the presence of a useable water source, as the survey team changed camps daily.

All primate survey data were collected according to a methodology established by Schaaf et al. (1990). Due to dense vegetation, heavy hunting pressure, and a lack of habituation to human presence, which make detecting individuals exceptionally difficult, group counts are used to estimate primate abundance (Whitesides et al. 1988; Butynski & Koster 1994). We collected the following data for each primate encounter: time of encounter, location (GPS coordinates), elevation, species observed, number of individuals sighted, sex of individuals, estimated distance from the observer to the first individual sighted, sighting angle between the transect line and the observer-to-animal line, estimated group height in trees, polyspecific association (if within 50 m of another primate species), vocalization type, method of detection, and response of individuals to human presence. To quantify hunting pressure, all signs of hunting observed along each of the survey transects were recorded. Direct evidence of hunting included spent shotgun shells, discarded batteries, hunting camps, carcasses, and snares (Linder 2008). All survey data were collected via a Cybertracker (v3.248) data collection system developed for use on Bioko (Steventon 2002).

Data Analysis

Survey data for all primates were converted to sighting frequencies, calculated as the number of social groups (including solitary individuals) sighted per kilometer walked (Marshall et al. 2008). Sighting frequencies provide a measure of relative density and were used because of problems associated (e.g., violation of key assumptions) with absolute density calculations resulting from difficulties in detecting hunted primates in dense forest (Fashing & Cords 2000; Thomas et al. 2010; Linder & Oates 2011). Acoustic primate encounters are reported below, but were excluded from temporal analyses, as accurately identifying primate vocalizations becomes difficult at distances over 50 m or along deep ravines, and call frequency and volume differ between species (Linder & Oates 2011; Cronin, pers. obs.). Additionally, previous surveys conducted in the region did not report any acoustic encounters (Nowak & Rioso Etingue 2007). As a proxy for the relative intensity of hunting pressure along each transect, all observations of hunting signs were converted to a hunting sign encounter rate. Each individual sign was treated as a separate encounter (Linder & Oates 2011).

In addition to reporting the current status of both primate populations and hunting pressure in the southeastern sector of Bioko, we also quantified temporal changes of primate sighting frequencies in the region. We compared sighting frequencies from our study to those conducted in the same areas and along many of the same footpaths in 2007 (Nowak & Rioso Etingue 2007). In order to circumvent problems inherent in a direct comparison (small sample size; lack of replication; nonidentical transects), we grouped all surveys conducted north of the Iladyi River as the "Eori" region and all those south of the river as the "Arihá" region. This arrangement follows the general demarcation of Moka area hunting zones, B and C respectively, in Colell et al. (1994). Surveys conducted along the Iladyi River itself were not included in the comparison. In order to gauge variability among transects, surveys within each "region" were then portioned into 2 km sections, providing a unit of replication, with each section treated as a "survey transect." A survey length of two kilometers was chosen because we believe this distance represents a length likely to encompass more than local effects, but not so long that it includes the entire surveyed transect. Sighting frequencies for both 2007 and 2012 were then calculated for each region (Eori and Arihá).

Significant differences in sighting frequencies of primates were determined using Wilcoxon-Mann-

Table 1. Overall primate group encounters from all survey regions in the 2012 survey. Sighting Frequency considers only visual identifications, while Encounter Rate includes both visual and acoustic encounters.

		Prim	ate Encounte	r Data	
Scientific Name	Visual	Acoustic	Total Encounters	Sighting Freq. (grps/km)	Encounter Rate (grps/km)
Eori Region					
Cercopithecus nictitans	4	0	4	0.35	0.35
C. erythrotis	3	2	5	0.27	0.44
C. pogonias	1	6	7	0.09	0.62
Sciurocheirus alleni	1	0	1	0.09	0.09
Region Totals	9	8	17	0.80	1.50
Iladyi River					
C. erythrotis	2	2	4	0.40	0.80
C. pogonias	1	0	1	0.20	0.20
Region Totals	3	2	5	0.60	1.00
Arihá Region					
C. erythrotis	11	4	15	0.55	0.75
C. pogonias	8	7	15	0.40	0.75
Mandrillus leucophaeus	1	2	3	0.05	0.15
Colobus satanas	1	0	1	0.05	0.05
C. nictitans	1	1	2	0.05	0.10
S. alleni	1	0	1	0.05	0.05
Cercopithecus sp.*	1	0	1	0.05	0.05
Region Totals	24	14	38	1.21	1.91
Overall Totals	36	24	60	1.00	1.66

^{*}Cercopithecus sp. were positively identified to genus, but species identifications were not possible.

Whitney (WMW) tests. Tests were run two ways, using a default WMW test employing a continuity correction, and a permutation-based WMW using the "coin" package; both methods gave similar results (Hothorn *et al.* 2008). We present significance values of the default WMW, as it is slightly more conservative given the small sample size and the high frequency of zero counts. All statistical analyses were conducted using R (v2.14.2; R Core Development Team 2012).

RESULTS

Primate Abundance

Primate groups were encountered a total of 60 times resulting in an overall encounter rate of 1.66 groups/km. Visual identifications were confirmed for 36 encounters, resulting in a sighting frequency of 1.00 groups/km, while 24 groups were identified solely by vocalizations. The most commonly sighted monkey overall was *C. erythrotis*

(0.44 groups/km), followed by *C. pogonias* (0.28 groups/km), *C. nictitans* (0.14 groups/km), *M. leucophaeus* (0.03 groups/km), *S. alleni* (0.06 groups/km), and *C. satanas* (0.03 groups/km). We encountered no signs of either *P. pennantii* or *A. preussi* during the survey, though it should be noted that the majority of surveys (95%) took place at lower elevations (< 1,000 m), where *A. preussi* is less likely to be found (Butynski & Koster 1994). Four (11%) visual encounters were with polyspecific associations, however, all polyspecific associations included *C. erythrotis* (11% of all *C. erythrotis encounters*): 3 with *C. pogonias* (30% of all *C. pogonias encounters*); 1 with *C. satanas* (100% of all *C. satanas* encounters).

When both visual and acoustic encounters are considered, *C. erythrotis* and *C. pogonias* represented the majority of encounters in each of the three regions (Table 1). In the Eori region, however, *C. nictitans* were sighted at the highest frequency (0.35 groups/km), while *C. pogonias*, although heard often, were not seen as commonly as in other regions (Table 1). Both the overall

encounter rate (1.91 groups/km) and sighting frequency (1.21 groups/km) were higher for Arihá than for either Eori or the IRV. C. erythrotis (0.55 groups/km) and C. pogonias (0.40 groups/km) were sighted most often and made up 79% of all sightings (Table 1). The total number of primate species encountered was also higher in the Arihá region, as both M. leucophaeus and C. satanas were not encountered in Eori or the IRV. The IRV had the lowest encounter rate (1.00 groups/km) and sighting frequency (0.60 groups/km), but this number may be an underestimate due to the breadth of the valley floor (>50 m in parts) and loud ambient sound of the running river, which may have reduced our ability to detect primates. Only C. erythrotis and C. pogonias were encountered within the IRV.

Temporal Changes in Primate Abundance

There was a significant decrease in the overall primate sighting frequency from 2007 to 2012 in both the Arihá (W=83.50, p<0.02) and Eori (W=27.50, p<0.03) regions (Table 2). In Arihá, C. pogonias were sighted significantly less frequently (W=74.00, p<0.04) and represented fewer overall encounters. Sightings of C. erythrotis also declined (W=73.00, p<0.05), but accounted for a higher proportion of primate encounters. Relative to C. satanas, which increased in its proportional representation of primate encounters, both C. nictitans and M. leucophaeus accounted for fewer sightings. In Eori, both C. erythrotis (W=27.00, p<0.03) and C. pogonias (W=25.00, p<0.05) were sighted at significantly lower frequencies between years, accounting for 33% fewer overall primate group encounters; however, this decline was offset by a 27% increase in the proportion of *C. nictitans* encounters.

Hunting Activities

The number of hunting signs increased dramatically in Eori and Arihá since 2007 (Table 3). In Eori, the rate of gun hunting signs more than tripled, while in Arihá it more than doubled. This is largely due to very high numbers of spent shotgun cartridges, but there were also two hunting camps in Eori that were not present for the 2007 surveys. Encounter rates of snare hunting signs also increased in both regions, though not as steeply as signs of gun hunting (Table 3).

DISCUSSION

We encountered five of the seven diurnal primates present on Bioko in the study area; however, we did not encounter any evidence of a population of P. pennantii. Although this does not prove its absence, since we could not directly access a 7 km stretch of the Iladyi River (area < 10 km²), we believe that it is unlikely a viable southeastern population of P. pennantii persists. Where they do occur on Bioko, P. pennantii are relatively easy to detect, since they move in large, noisy groups, and, in valleys similar to the IRV, can often be heard vocalizing over great distances (Schaaf et al. 1990; Butynski & Koster 1994; Struhsaker 2005). As these traits make P. pennantii relatively easy to hunt, one would expect a considerable number of carcasses to originate in the region, though Colell et al. (1994) only reported one individual taken by Moka hunters during their study. This suggests that by 1992 the southeastern population of P. pennantii was already at low density, and given the absence of P. pennantii from subsequent surveys in both 2007 and 2012, is now likely extirpated.

In our survey, the Arihá region had the highest primate species richness and relative abundance, likely due to its location south of the IRV, which presents a major barrier to access to the region from the north. There is a history of human habitation to the north and also a network of trails that provide ready access to the Eori forests from Riaba, a major city on the eastern side of Bioko with a direct highway to Malabo. In contrast, there is only a single roadside access to the Arihá region, located in the mountain village of Moka, almost twice the distance by road from Malabo than Riaba. Greater accessibility in the Eori region and higher signs of gun hunting support the conclusion that hunting is a driving factor in the decline in primate abundance in the region.

The declines in primate abundance observed in both Arihá and Eori between the Nowak and Rioso Etingue (2007) surveys and this study (2012) can be linked to hunting as well, as there have been no substantial habitat alterations in the survey areas (Cronin, pers. obs.). Furthermore, since 2007, there has been an increase in the number of carcasses for sale in the Malabo bushmeat market, with an average of over 15 primates/market day, and some months reaching as high as 39 primates/market day (Cronin et al. 2010; Cronin, unpublished data). Given the reduction in the abundance of vertebrate fauna in northern Bioko, the majority of bushmeat supplied to the Malabo market now originates in southern Bioko, so much of the increased hunting should be manifested within the GCSH (Fa 2000; Fa et al. 2000; Albrechtsen et al. 2007).

The absence of P. pennantii combined with the low densities of M. leucophaeus and C. satanas, and the high proportion of Cercopithecus spp., also suggest that this region may currently be undergoing an ecological shift in its primate community. P. pennantii and other largerbodied species are particularly vulnerable to hunting and their loss or population decline is known to dramatically alter their ecosystems (Struhsaker 2005; Wilkie et al. 2011). As larger-bodied species were either absent or at low densities in our study, our observed species composition is likely to be reflective of historical hunting pressure, rather than natural distributions (Struhsaker

Table 2. Temporal change in sighting frequency of primate groups between surveys conducted in 2007 (Nowak & Rioso Etingue) and this study (2012). Note the number of group sightings. S.F. is the sighting frequency (groups/km surveyed). % represents the percent contribution of a species' encounters to the overall encounter total. Values in parentheses are standard errors. Values in italics are significant at p < 0.005.

	Eor	Eori Region							Arih	Arihá Region						
Species	2007	7		2012	2				2007			2012	2			
	z	S.F.	%	z	S.F.	%	>	d	z	S.F.	%	z	S.F.	%	×	ф
		(grps/km)			(grps/km)			1		(grps/km)			(grps/km)			•
Cercopithecus erythrotis	13	13 1.30 (0.34)	56.5	\mathcal{E}	0.25 (0.17)	33.3	27.00	0.03	26	1.06 (0.15)	39.4	11	0.56 (0.18) 45.8	45.8	73.00	0.05
C. pogonias	5	0.50 (0.16)	21.7	П	0.08 (0.08)	11.1	25.00	0.05	26	1.05 (0.27)	39.4	8	0.35 (0.14)	33.3	74.00	0.04
C. nictitans	4	0.40 (0.19)	17.4	4	0.33 (0.17)	44.4	16.50	0.84	6	0.33 (0.16)	13.6	1	0.06 (0.06)	4.2	59.00	0.29
Mandrillus leucophaeus	1	0.10 (0.10)	4.3	0	0.00	0.0	18.00	0.36	4	0.16 (0.09)	6.1	1	0.04 (0.04)	4.2	55.50	0.44
Cercopithecus sp.*	0	0.00	0.0	0	0.00	0.0	n/a	n/a	1	0.04 (0.04)	1.5	1	0.04 (0.04)	4.2	46.50	0.88
Colobus satanas	0	0.00	0.0	0	00.00	0.0	n/a	n/a	0	0.00	0.0	1	0.06 (0.06)	4.2	42.00	0.26
Procolobus pennantii	0	0.00	0.0	0	0.00	0.0	n/a	n/a	0	0.00	0.0	0	0.00	0.0	n/a	n/a
Allochrocebus insularis	0	0.00	0.0	0	0.00	0.0	n/a	n/a	0	0.00	0.0	0	0.00	0.0	n/a	n/a
Sciurocheirus alleni	0	0.00	0.0	1	0.13 (0.13)	11.1	12.50	0.47	0	0.00	0.0	1	0.05 (0.06)	4.2	42.00	0.26
Total	23	2.30 (0.56)		6	0.79 (0.36)		27.50	0.025	99	2.63 (0.37)		24	1.17 (0.42)		83.50	0.024

*Cercopithecus sp. were positively identified to genus, but species identifications were not possible.

Table 3. Temporal change in hunting sign encounters between surveys conducted in 2007 (Nowak & Rioso Etingue) and this study (2012).

	Survey Region				
Hunting Sign Type	Eori Region		Ariha Region		
	2007	2012	2007	2012	
Gun Hunting Signs					
Empty Cartridge	74	269	201	345	
Batteries	-	10	-	16	
Hunting Camp	-	2	1	1	
Gun Shot	1	-	-	1	
Carcasses	-	-	-	1	
Totals	75	281	202	364	
Snare Hunting Signs					
Snares	21	68	25	35	
Animal Traps	-	1	-	1	
Totals	21	69	25	36	
Total Hunting Signs	96	350	227	400	
Gun Sign Encounter Rates (km ⁻¹)	7.59	24.87	8.15	18.32	
Snare Sign Encounter Rate (km ⁻¹)	2.13	6.11	1.01	1.81	
Overall Hunting Sign Encounter Rate (km ⁻¹)	9.72	30.97	9.15	20.13	

1999). The increase in the proportional representation of C. nictitans in the Eori region relative to decreased encounters of C. erythrotis and C. pogonias is similar to that in Korup National Park, Cameroon, where a reduction in the abundance of other species led to an increase of C. nictitans via competitive release (Linder & Oates 2011). Although larger than both C. erythrotis and C. pogonias (Butynski et al. 2009), C. nictitans is often more cryptic and encountered in smaller groups; as well as being more ecologically flexible, allowing for exploitation of a wide range of habitats and diets (Linder & Oates 2011; Cronin, pers. obs.).

These results, though only a microcosm of the situation on Bioko, illustrate an increasingly desperate situation. Conservation strategies, beginning with legitimate enforcement of existing legislation, could greatly improve the current status of Bioko's primates. An island-wide reduction of hunting is necessary, with a focus on government-supported conservation efforts (e.g., training of national staff, sensitization of government, police, and military personnel, and conservation education programs), especially within the GCSH and Pico Basilé National Park. Effective conservation and management of the two protected areas can still secure a future for the biodiversity of Bioko.

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LITERATURE CITED

Albrechtsen, L., D. Macdonald, P.J. Johnson, R. Castelo & J.E. Fa. 2007. Faunal loss from bushmeat hunting: Empirical evidence and policy implications in Bioko island. Environmental Science and Policy 10:654-667.

Butynski, T.B., Y.A. de Jong & G. W. Hearn. 2009. Body measurements for the monkeys of Bioko Island, Equatorial Guinea. Primate Conservation 24:99-105.

Butynski, T.M. & S.H. Koster. 1994. Distribution and conservation status of primates in Bioko Island,

- Equatorial Guinea. *Biodiversity and Conservation* 3:893-909.
- 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* 3:939-950.
- 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.
- Fa, J.E. 2000. Hunted Animals in Bioko Island, West Africa: Sustainability and Future. In *Hunting for Sustainability in Tropical Forests*, J.G. Robinson & E.L. Bennett, eds. Columbia University Press, New York, NY. Pp: 168-198.
- Fa, J.E., J.E.G. Yuste & R. Castelo. 2000. Bushmeat markets on Bioko Island as a measure of hunting pressure. *Conservation Biology* 14:1602-1613.
- 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* 50:139-152.
- Groves, C.P. 2007. The taxonomic diversity of the Colobinae of Africa. Journal of Anthropological Sciences 85:7-34.
- Hothorn, T., K. Hornik, M.A. van de Wiel & A. Zeileis 2008. Implementing a Class of Permutation Tests: The coin Package. *Journal of Statistical Software* 28:1-23.
- IUCN. 2012. IUCN Red List of Threatened Species. Version 2011.2. www.iucnredlist.org, Date Accessed: 30 MAR 2012.
- Linder, J.M. 2008. The Impact of Hunting on Primates in Korup National Park, Cameroon: Implications for Primate Conservation. Dept. of Anthropology. City University of New York, New York, NY.
- 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* 144:738-745.
- Marshall, A.R., J.C. Lovett & P.C.L. White. 2008. Selection of line-transect methods for estimating the density of group-living animals: Lessons from the primates. *American Journal of Primatology* 70:452-462.
- Morra, W., G. Hearn & A.J. Buck. 2009. The market for bushmeat: *Colobus satanas* on Bioko Island. *Ecological Economics* 68:2619-2626.

- Nowak, K. & F. Rioso Etingue. 2007. Diurnal Primate Surveys in the Iladyi River Valley Region, Bioko Island, Equatorial Guinea. Bioko Biodiversity Protection Program.
- 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. 2011. Primates of West Africa: A Field Guide and Natural History. Conservation International, Arlington, VA.
- R Core Development Team. 2012. R: A Language and Environment for Statistical Computing. Version 2.14.0. R Foundation for Statistical Computing. Vienna.
- 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.
- Steventon, J. 2002. Cybertracker v. 3.284. Cybertracker Software.
- Struhsaker, T.T. 1999. Primate communities in Africa: The consequence of longterm evolution or the artifact of recent hunting. In *Primate Communities*, J.G. Fleagle, C. Janson, & K.E. Reed, eds. Cambridge University Press, Cambridge. Pp 289-294.
- Struhsaker, T.T. 2005. Conservation of red colobus and their habitats. *International Journal of Primatology* 26:525-538.
- Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques & K.P. Burnham. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47:5-14.
- Walsh, P. & L.J.T. White. 1999. What it will take to monitor forest elephant populations. *Conservation Biology* 13:1194-1202.
- Whitesides, G.H., J.F. Oates, S.M. Green & R.P. Kluberdanz. 1988. Estimating primate densities from transects in a West African rain forest: A comparison of techniques. *Journal of Animal Ecology* 57:345-367.
- Wilkie, D.S., E.L. Bennett, C.A. Peres & A.A. Cunningham. 2011. The empty forest revisited. *Annals of the New York Academy of Sciences* 1223:120-128.

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