Conservation strategies for understanding and combating the primate bushmeat trade on Bioko Island, Equatorial Guinea

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Short Title: Combating bushmeat hunting on Bioko

Research Highlights: We summarize results from multifaceted primate conservation efforts on Bioko Island, detail the negative impact bushmeat hunting has had on primate populations, and discuss what strategies have worked and how we should move forward.

Abstract

Bioko Island, Equatorial Guinea is among the important places in Africa for the conservation of primates, but a cultural preference for bushmeat and a lack of effective law enforcement has encouraged commercial bushmeat hunting, threatening the survival of the remaining primate population. For over 13 years we collected bushmeat market data in the Malabo market, recording over 35,000 primate carcasses, documenting "mardi gras" consumption patterns, seasonal carcass availability, and negative effects resulting from government intervention. We also conducted forest surveys throughout Bioko's two protected areas in order to localize and quantify primate populations and hunting pressure. Using these data, we were able to document the significant negative impact bushmeat hunting had on monkey populations, estimate which species are most vulnerable to hunting, and develop ecological niche models to approximate the distribution of each of Bioko's diurnal primate species. These results also have allowed for the identification of primate hotspots, such as the critically important southwest region of the Gran Caldera Scientific Reserve, and thus, priority areas for conservation on Bioko, leading to more comprehensive conservation recommendations. Current and future efforts now focus on bridging the gap between investigators and legislators in order to develop and effectively implement a management plan for Bioko's Gran Caldera Scientific Reserve and to develop a targeted educational campaign to reduce demand by changing consumer attitudes towards bushmeat.

Using this multidisciplinary approach, informed by biological, socioeconomic, and cultural research, there may yet be a positive future for the primates of Bioko.

KEYWORDS: bushmeat, hunting, red colobus, ecological niche models, conservation, Bioko

Introduction

The hunting of wildlife for human consumption is common in tropical forests throughout the world, as bushmeat plays a prominent economic and dietary role for many rural populations [Fa et al., 2002b; Milner-Gulland and Bennett, 2003; Robinson and Bennett, 2000], and has been positively linked to improved childhood nutrition and overall human health [Fa et al., 2015b; Golden et al., 2011], despite high risk and repeated incidents of zoonotic disease transmission between humans and wildlife [Leroy et al., 2004; Peeters et al., 2002; Rouquet et al., 2005]. Hunting, however, poses a significant threat to wildlife throughout the tropics, as it has become predominantly commercially-driven and unsustainable [Bennett et al., 2002; Fa and Brown, 2009; Milner-Gulland and Bennett, 2003; Robinson and Bennett, 2000], and wildlife declines and, in some cases extirpations, have been well documented [Butynski et al., 1997; McGraw, 1998; Oates et al., 2000; Robinson and Bennett, 2000; Wilkie and Carpenter, 1999]. In the Gulf of Guinea forests of central Africa in particular, bushmeat hunting is especially extensive. This region contains some of the highest human population densities in all of Africa (e.g., > 500 people/km^2) [Oates et al., 2004], and the volume of bushmeat for sale in its markets is estimated at approximately 12,000 tons per year [Fa et al., 2006]. Based on estimates of maximum sustainable production, most taxa hunted for bushmeat are overexploited; potentially more than six times sustainable levels [Bennett, 2002; Bennett et al., 2002; Fa and Brown, 2009]. However,

not all wildlife species are equally threatened by hunting. Factors such as ecological flexibility (e.g., broad dietary breadth, ability to exploit numerous habitats), anti-predator behavior, and life history traits can influence species' vulnerability to hunting [Linder and Oates, 2011; McGraw, 2007; Struhsaker, 1999]. Diurnal primates, for example, are particularly threatened, with over 70% of species in the region thought to be hunted unsustainably [Fa and Brown, 2009], despite most species receiving at least some level of legal protection under both national and international legislation (e.g., CITES, African Convention on the Conservation of Nature and Natural Resources). Primates play a vital role in ecosystem functioning in terms of seed dispersal, and the preservation of primate populations is critically important for the maintenance of forest structure and forest regeneration [Chapman and Onderdonk, 1998; Poulsen et al., 2001; Wrangham et al., 1994]. Declines and/or losses of these species can lead to cascading negative ecological consequences, including reductions in the number of large hardwood trees, a transition towards fast-growing, low-density pioneer species, and declines in the overall tree community diversity, threatening the persistence of the ecosystems they inhabit and the people who depend on them [Abernethy et al., 2013; Chapman and Onderdonk, 1998; Effiom et al., 2013; Laurance et al., 2012; Terborgh et al., 2008; Vanthomme et al., 2010].

Hundreds of millions of dollars have been spent on conservation in central Africa, leading to the development and implementation of numerous strategies to better understand and combat the bushmeat trade, which have been met with varied levels of success [Pailler, 2005; Pyhälä et al., 2016]. Development objectives, such as poverty alleviation, are widely utilized and have improved livelihoods of some of those dependent on forest resources, but real conservation effectiveness is rare and often not evaluated [Roe et al., 2015], and as stand-alone measures, development objectives have had minimal success in reducing bushmeat consumption [Astaras,

2009; Oates, 1999; Robinson and Bennett, 2002]. In the Oban Division of the Cross River National Park, for example, despite a proposed budget of 18.43 million European Currency Units over a seven-year period (most of which went to development projects and international consultants), high-intensity unregulated hunting in the park led to low mammal densities [Oates, 1999]. Heavy hunting in the park has continued since Oates' account, resulting in extremely low mammal densities, and local communities in the vicinity of the park are now 'somewhat antagonistic' due to unfulfilled development promises stemming from the creation of the park [Morgan et al., 2013; Morgan et al., 2011]. Furthermore, many development projects struggle to meet their own objectives due to limited funds, capacity, and available time [Wicander and Coad, 2015]. Forest guard patrols in protected areas have shown to be successful at reducing hunting [Bruner et al., 2001; Campbell et al., 2011; Corlett, 2007; de Merode and Cowlishaw, 2006; Hilborn et al., 2006; Rowcliffe et al., 2004; Tranquilli et al., 2012], but they do not fully address the problem of bushmeat demand. These patrols often lack adequate financial resources [Njuh Fuo and Memuna Semi, 2011; Oates et al., 2004], can be ineffective if improperly implemented, and, in some cases, have contributed to conflicts with local communities [Pyhälä et al., 2016]. Blanket criminalization of hunting and consumption could deter hunting if properly enforced, but enforcement regimes are often ineffective or absent, and, as such, have been relatively unsuccessful in reducing the overall trade [Barnes, 1996; Biggs et al., 2013; Burton, 1999; Miron, 1998; Rivalan et al., 2007]. Domestication of bushmeat species has been proposed as a way to alleviate demand [Cooper, 1995; Grande Vega et al., 2013; Jori et al., 1995], but it has been shown to be economically inviable in the absence of enforcement, while wild meat remains essentially a free good [Brooks et al., 2010; Mockrin et al., 2005; Nasi et al., 2008]. Despite readily available protein alternatives at cheaper prices, taste and cultural preferences for

bushmeat contribute to the persistence of its high demand [Bowen-Jones and Pendry, 1999; East et al., 2005; Kümpel et al., 2007; Morra et al., 2009; Reid et al., 2005; Schenck et al., 2006]. Education in order to change perceptions towards wildlife and conservation may have long lasting impacts, but societal change is often a slow process, and too many species require solutions in the short-term in order to ensure their persistence. Thus, education and outreach should be critical components of any comprehensive strategy, but they do not address the inherent immediacy of the bushmeat crisis. What is clear is that there is no panacea for the bushmeat crisis and that our understanding of how to most effectively solve the problem remains unclear, largely due to the extremely complex nature of the bushmeat trade, spanning from individual actors to national and international-level policy considerations. No single solution can stand alone in the face of such an intricate problem; rather, we need to address the bushmeat trade from as many angles as possible.

It has long been said, however, that conservation is a crisis discipline [Soulé, 1985], and some of the best laid theories often fall victim to limitations of funding, logistics, and the realities on the ground [Cronin et al., 2014b; James et al., 1999b]. Due to these limitations, researchers in central Africa have often focused their efforts on a particular niche, e.g. socioeconomics or ecology [Brashares et al., 2011; Foerster et al., 2012], with the aim of contributing data to an overarching conservation effort. Recent studies (e.g., Fa et al. [2015a]; Nasi and Van Vliet [2011]; and Ziegler et al. [2016]) have begun to broaden the focus to provide regional understanding and scope, while still providing great specificity in the details of their findings. However, there have been few instances where it has been possible to develop and implement a long-term multidisciplinary approach tailored to a particular site; where both

research and conservation activities could be implemented in an area small enough to feasibly manage multiple projects as well as monitor progress.

Bioko Island, Equatorial Guinea provides a unique opportunity to study the bushmeat trade and its effects on primate populations in central Africa. The Bioko Biodiversity Protection Program (BBPP), an academic partnership between Drexel University and the Universidad Nacional de Guinea Ecuatorial (UNGE), has carried out research and conservation activities and has been spearheading conservation efforts on Bioko since its inception in 1998. In recent years however, the BBPP has developed and implemented a more comprehensive approach to biodiversity conservation on Bioko, leveraging the strength of its long-term conservation and monitoring programs to shift to a more results-based approach that encompasses current education, research, and planning techniques. In this paper, we aim to 1) detail the multifaceted conservation framework (Fig. 1) currently being employed by the BBPP, 2) synthesize recent BBPP research to summarize current knowledge on the status of wildlife and conservation on Bioko, 3) demonstrate how we are aggregating results to prioritize conservation efforts, and 4) provide conservation recommendations to improve protection of Bioko's primate populations.

Bioko Island: A bushmeat case study

Bioko Island, Equatorial Guinea (2,017 km^2) is a small volcanic island in the Gulf of Guinea, just 37 km off the coast of Cameroon (Fig. 2). The island has been recognized as a hotspot for biodiversity [Myers et al., 2000; Oates et al., 2004], owing in part to its small size, location, and biogeographic history, as well as its seven diurnal primate taxa (Table 1), which make it one of the highest priority sites in Africa for the conservation of primates [Oates, 1996]. Human population density varies widely on Bioko, from >100 people/km^2 in Malabo in the north

to <10 people/km^2 in the south [Albrechtsen et al., 2006]. Much of the island's biodiversity occurs within two protected areas that comprise approximately 40% of the island, Pico Basilé National Park (PBNP) (330 km^2) and the Gran Caldera Scientific Reserve (GCSR) (510 km^2). Since the late 1990s, urban development surrounding Malabo has expanded greatly, but due to a combination of rugged terrain, isolation, heavy rainfall, and an island-wide ban on logging activities [Republic of Equatorial Guinea, 1991], large swaths of intact forests remain, especially within PBNP and GCSR [Zafra-Calvo et al., 2010]. Despite the readily available intact habitats and biological wealth of Bioko, there are neither management plans for its protected areas, nor detailed enforcement strategies in place with which to effectively conserve its biodiversity.

Bioko Island provides a unique opportunity for the study of the bushmeat trade. Bushmeat hunting is the primary threat to the persistence of primates on Bioko. Government attempts to regulate the bushmeat trade in Equatorial Guinea have so far focused on reducing supply by regulating hunting [Republic of Equatorial Guinea, 1988], banning hunting inside protected areas [Republic of Equatorial Guinea, 2000; Republic of Equatorial Guinea, 2003], and prohibiting the hunting, sale, and consumption of primates [Republic of Equatorial Guinea, 2007]. Each of these legislative efforts have ultimately been toothless, however, as objectives have been too broad, unfeasible (e.g., no staff/infrastructure to enforce laws in protected area), and/or lacking detailed strategies for funding and implementation. As a result, forests and protected areas are entirely unmanaged and hunting is extensive throughout the island, both outside (legally) and inside (illegally) of protected areas [Cronin et al., 2013; Cronin et al., 2016; Grande-Vega et al., 2016; Grande Vega et al., 2013]. This hunting is conducted nearly exclusively for profit, predominantly by commercial hunters from the mainland sector of Equatorial Guinea [Albrechtsen et al., 2007; Grande Vega et al., 2013; Hearn et al., 2006; Reid et

al., 2005]. The market structure and taxonomic profile are relatively similar to other regional markets [Albrechtsen et al., 2007; Cronin et al., 2015b; Fa et al., 2000]. The bushmeat trade on Bioko is confined to a relatively small, contained (insular) system (barring easily identifiable imports from the mainland), with simple transport routes [Fa, 2000], and consumption primarily restricted to Malabo [Albrechtsen et al., 2007]. Malabo's population is not dependent on bushmeat, as alternative protein sources are readily available, and bushmeat contributes an insignificant proportion of the population's minimum protein requirement [Albrechtsen et al., 2006; Grande Vega et al., 2013; Morra et al., 2009; Reid et al., 2005] and fulfills only a fraction of the economic needs for relatively few individuals [Albrechtsen et al., 2006; Reid et al., 2005]. Rather, it seems that consumption of bushmeat, and especially of primates, is associated with wealth and status [Albrechtsen et al., 2006; Cronin et al., 2015b; Reid et al., 2005]. As a result, larger vertebrates, specifically monkeys, are in decline on Bioko [Cronin et al., 2010; Cronin et al., 2015a; Cronin et al., 2013; Grande-Vega et al., 2016; Hearn et al., 2006]. This situation is exacerbated by the recent completion of a new highway bisecting the GCSR (Fig. 2), providing easy access to previously inaccessible areas, creating new opportunities for illegal exploitation of wildlife and forest resources, stimulating new interest in development activities at Ureca, and facilitating establishment of (unregulated) tourism in the GCSR.

Bushmeat Market Surveys

At the time of the first contemporary conservation assessment of primates on Bioko, primate populations were relatively abundant, but researchers also documented the existence of a bushmeat market on Bioko and warned of the potential negative impacts hunting could have on the island's primates [Butynski and Koster, 1994]. Subsequent studies documented the extent of

211 the market, and demonstrated that throughout the 1990s and early 2000s, wildlife on Bioko was
212 heavily exploited, with some species, including primates, hunted unsustainably [Albrechtsen et
213 al., 2007; Fa et al., 1995; Hearn et al., 2006; Juste et al., 1995; Morra et al., 2009]. These studies
214 formed a critical baseline for conservation planning, but lacking a true temporal component,
215 were only able to provide general 'snapshot' details of market characteristics and trends. Cronin
216 et al. [2015b], however, conducted a comprehensive bushmeat market study using long-term data
217 collected between October 1997 and September 2010, which allowed for the detection of short-
218 and long-term effects of market interventions, species-specific hunting patterns within taxonomic
219 groupings, and seasonality in hunting patterns across several years. Market data were classified
220 into groups (e.g., primates) and analyzed relative to three distinct periods based on conservation
221 activities, government interventions, and notable market changes using an intervention model
222 [Box and Tiao, 1975] and suite of time series analyses (See Cronin et al. [2015b] for an in-depth
223 description of methodology).

224 Over 197,000 carcasses from 45 different taxa were recorded during the course of the
225 study. More than 35,000 of these carcasses were primates, making up about 18% of the entire
226 volume of the market [Cronin et al., 2015b]. The overall market grew significantly over time
227 concurrent to a transition towards increased shotgun hunting. The volume of primate carcasses in
228 the market also increased gradually until October 2007 (Fig. 3a), when the hunting, sale, and
229 consumption of primates were banned by Presidential Decree [Republic of Equatorial Guinea,
230 2007]. As a result, the primate carcass rate temporarily dropped to nearly zero carcasses/market
231 day, but then swiftly increased to rates 3-4 higher than pre-ban, reaching a maximum of 37.42
232 carcasses/market day in April 2010. Cronin et al. [2015b] termed this pattern a 'mardi gras'
233 mentality in relation to attempted conservation interventions, in which bushmeat volume actually

234 increased following implementation of the intervention largely due to a lack of enforcement as
235 market players sought to maximize their gains before the potential effects of the legislation could
236 take hold. Not all primate taxa were hunted equally, however, as interspecific differences
237 revealed via trend analyses shed light on the drivers of the rapid increase in the overall primate
238 carcass rate following the decree. Five of the seven primates occurred in the market at a
239 significantly greater rate in the period following the primate hunting ban, but two species (*P.*
240 *pennantii* and *C. nictitans*) did not follow the same pattern (Fig. 3b). As a result of both
241 environmental factors and a history of unrestricted hunting, populations of these two species are
242 restricted to the remote southern extent of Bioko within the GCSR (Fig. 3c) [Butynski and
243 Koster, 1994; Cronin et al., 2015a; Cronin et al., 2013; Cronin et al., 2016], suggesting that a
244 combination of isolation and long-term BBPP conservation activities focused on the area, have
245 provided at least passive protection from hunting. Furthermore, due to their limited geographic
246 range, these species can serve as indicator species, alerting us to hunting activity in particular
247 areas of the GCSR.
248
249 *Forest Surveys*
250 While many bushmeat studies have been conducted on Bioko, there have been fewer
251 comprehensive field surveys for primates. Rather, the emphasis has been on maintaining a
252 localized, yet regular, long-term monitoring and research effort [Cronin et al., 2010; Hearn et al.,
253 2006; Hearn et al., 2004] in order to provide passive protection in key areas. Although there have
254 been myriad conservation benefits to this program, more broadly-focused, systematically
255 designed surveys were necessary to better estimate the status of primate populations and hunting
256 intensity. In order to investigate the impact of hunting on wild primate populations, targeted

forest surveys were conducted throughout the GCSR at three sites representative of differing levels of human access and activity: Moraka Playa, Ureca, and Belebu (Fig. 2) [Cronin et al., 2016]. Moraka Playa, in the remote southwest, had very little hunting and was over 30 km on foot from the nearest road. Ureca, the only village within the GCSR, was located about 22 km over land from the nearest road and at the time had a population of approximately 80 people. Ureca was considered to have moderate levels of human activity due to military personnel hunting in the area and extensive trapping by the villagers. Belebu, on the northern boundary of the GCSR, was a village of several hundred people and served as the primary access point for the GCSR via paved roads from Luba. The area around Belebu was extensively hunted and regularly organized bushmeat transports brought offtake to Malabo [JMEE, pers. obs.]. There also has been a long history of plantation agriculture around Belebu, so in addition to the loss of primary forest in the area, shotguns were widely used to both hunt bushmeat and control agricultural pests [Butynski and Koster, 1994]. It should be noted that these surveys took place between January 2011 and February 2012 and, as aforementioned, direct access to Ureca and the southern beaches via the new road has changed patterns of hunting pressures in the reserve (Fig. 2).

Unsurprisingly, primate abundance was negatively associated with shotgun hunting [Cronin et al., 2016]. Primate encounter rates were significantly lower at Belebu than at either of the other two sites, while concurrently shotgun hunting was highest at Belebu (Table 2). Although these data indicated that hunting was adversely impacting the overall primate population, they did not explain how individual species were affected by differing levels of hunting pressure. A “hunting response index” (HRI) was developed in order to infer species-specific vulnerability (Fig. 4). An HRI has been used before (e.g., Linder and Oates [2011]) to provide an estimate of vulnerability to hunting by comparing relative differences in species’

encounter rates between highly and lowly hunted forests while controlling for habitat type. HRI values of less than one suggest that a species is vulnerable to hunting, values greater than one suggest the species may be resilient, and a value equal to one suggests no effect from hunting. Both *C. erythrotis* and *C. nictitans* exhibited some resiliency to hunting, which in the case of *C. nictitans* supports results from Linder and Oates' [2011] study in Korup National Park in Cameroon, as well as reports of relatively high densities of *C. nictitans* in other heavily hunted forests throughout the region [Garcia and Mba, 1997; Matthews and Matthews, 2002; Muchaal and Ngandjui, 1999]. In contrast, the other four primate species were all vulnerable to hunting, as each was encountered less in heavily hunted forests (Fig. 4). *P. pennantii* was most vulnerable to hunting, a trait it shares with many other highly threatened forms of red colobus across Africa [Struhsaker, 2005]. This vulnerability has been attributed to its high degree of ecological specialization (e.g., limited dietary and habitat flexibility), as well as its large body and group size, and slow and ineffective anti-predator responses [González-Kirchner, 1997; McGraw, 2007; Struhsaker, 1999].

Biomonitoring and Research Presence

Forest guards can be beneficial in combating the illegal harvesting of wildlife [Bruner et al., 2001; Campbell et al., 2011; Corlett, 2007; de Merode and Cowlishaw, 2006; Hilborn et al., 2006; Rowcliffe et al., 2004; Tranquilli et al., 2012], and are believed to be the most cost-effective and expeditious solution to poaching, as well as an integral part of effective long-term protected area planning [Bennett, 2011]. On Bioko, however, there are no management strategies for the island's protected areas, nor have any governmental enforcement activities, such as forest patrols, been implemented. Since 1998, the BBPP has sought to fill that role by employing a

community-based research and monitoring program within the GCSR. Teams of trained monitors, all of whom are hired locally, collect data on the status of hunting, primate populations, and nesting marine turtles throughout the GCSR. In addition to collecting vital data on the status of wildlife and hunting in the reserve, their presence in the forests has proven successful as a deterrent to hunting, despite lacking any official enforcement capacity (CR, pers. obs.). Employment of the monitoring and research teams has also provided an alternative livelihood for the local communities of Ureca and Moka (Fig. 2), and, in doing so, converted a number of former hunters to enthusiastic conservationists. Furthermore, data collected by the monitoring teams have been vital to BBPP's efforts, contributing to a number of reports and publications advancing the cause of biodiversity conservation on Bioko [Cronin et al., 2010; Cronin et al., 2015a; Cronin et al., 2013; Cronin et al., 2016; Fitzgerald et al., 2011; Hearn et al., 2006; Rader et al., 2006], as distilling data into formats understandable to policy makers as well as the general population is key to the development of successful wildlife management plans.

Ecological Niche Models

One of the most significant inhibitions to our greater understanding of primate ecology and abundance on Bioko is access. Bioko's climate is one of the wettest in the world with over 10,000 mm of rain annually [Font Tullot, 1951; Nosti, 1947], and its rugged terrain has left steep and deep ravines unexplored, and restricted potential areas for primate surveys, especially during the wet season, when access and mobility are extremely limited. As a result, our inferences about primate distributions could not adequately account for inaccessible areas and/or range shifts. We have been able to overcome these hurdles by generating ecological niche models (ENMs) using the program Maxent [Phillips et al., 2006]. ENMs were developed specifically to maximize the

utility of presence-only data collected in similar situations [Elith et al., 2011], and have been used successfully elsewhere to model primate distributions [Blair et al., 2013; Etiendem et al., 2013; Sesink Clee et al., 2015]. Using forest survey data collected between 2008 and 2014, we developed species distribution models for each of Bioko's 7 diurnal primate species [Cronin et al., 2015a]. In order to best inform overall primate conservation, we combined individual species distributions to create a heat map depicting hotspots of primate species richness on Bioko (Fig. 5a) [Cronin et al., 2015a]. The modeling of primate abundances and distributions in a scientifically accurate manner clearly illustrates the importance of the GCSR to the conservation of primate diversity on Bioko and has proven to be an effective tool for the communication of the importance of priority conservation zones on the island (Fig 5b). The southern slope of Bioko, from the peaks of the Gran Caldera and Pico Biao down to the southern beaches, is likely to be the only remaining place where over 5 species of diurnal primates remain on the island. Even more critical is the Gran Caldera itself, the last vestige of truly remote forest on Bioko, which maintains populations of all 7 species in an area of under 15 km^2.

Understanding Human Use

In order to fully understand the bushmeat trade on Bioko, or indeed anywhere the trade occurs, it is important to understand the socioeconomic and cultural drivers that motivate people to hunt illegally and consume wildlife. Despite the wealth of data gained from studies of the market and wild primate populations, a lack of contemporary data on these drivers following the dramatic expansion of the Equatoguinean economy since the late 1990s [Central Intelligence Agency, 2016; The World Bank, 2016] has limited our ability to effectively target education, outreach, and conservation strategies. In an attempt to fill these gaps in our understanding of the bushmeat

trade on Bioko, we conducted a series of questionnaires, a methodology which has proven useful in elucidating patterns of bushmeat consumption and preferences [East et al., 2005; Jenkins et al., 2011; Kümpel et al., 2010; Schulte-Herbrüggen et al., 2013]. Over 700 public surveys were conducted between June 2013 and September 2014 at various sites in Malabo and in villages throughout Bioko [Bocuma Meñe, 2016]. Results suggested that bushmeat consumption on Bioko is indeed driven by cultural preferences, predominantly in the two major ethic groups, Fang and Bubi, which make up the majority of the island's population. Fang and Bubi respondents consumed bushmeat at a similar frequency ($DF = 3$; $p > 0.05$), and reported that bushmeat was their preferred protein source ($DF = 1$; $p > 0.05$). However, differences existed among ethnic groups in regards to preferred bushmeat type; Fang respondents had a higher preference for primates (Fisher's Exact Test; $p < 0.05$). These findings were similar to Fa et al. [2002a] in which they reported that in 1990-1991 the Fang also had a significant preference for primates. This suggests that certain cultural preferences may transcend significant economic growth and changes in the bushmeat market [Cronin et al., 2015b], and the erosion of other seemingly entrenched societal norms related to consumption (e.g., a taboo on eating *Colobus satanas*) [Colell et al., 1994; Kümpel et al., 2008]. In a comparison of two hunting villages, one Bubi and one Fang, Grande Vega et al. [2013] also found that only Fang hunters targeted monkeys. However, this may be confounded by the fact that Fang hunters had guns, while Bubis have had limited gun ownership since 1998 [Grande Vega et al., 2013]. These findings highlight the importance of understanding the heterogeneity of local cultures as they relate to variability in bushmeat market drivers, and, as a result, how best to tailor conservation approaches to account for these differences[Walters et al., 2015]. For example, our results suggest that education and

outreach efforts aimed at reducing primate hunting and consumption through behavioral change should be tailored to address Fang cultural preferences.

Discussion

A broad-based holistic understanding of the status of primates and conservation on Bioko is required in order to engage with policy makers to design and implement effective conservation priorities. To that end, our goal is to leverage the strengths of the BBPP: (*i*) numerous longitudinal datasets, (*ii*) a successful academic partnership with UNGE, long-term history in the villages of both Ureca and Moka, (*iii*) and a continuous research and biomonitoring presence in the GCSR, to 'kick start' the movement towards government-led conservation.

Focusing Conservation Efforts: Primates as Umbrella Species

A good example of our strategy in practice is the case of Pennant's red colobus (*P. pennantii*), which illustrates the biological importance of the GCSR and the utility of using primates as umbrella species for conservation on Bioko. *P. pennantii* is perennially considered among the world's most endangered primates [Cronin et al., 2014a; Mittermeier et al., 2007; Mittermeier et al., 2010]. Previous work has suggested that *P. pennantii* is the only primate species endemic to Bioko [Groves and Ting, 2013; Groves, 2007; Oates, 2011], despite high subspecific endemism among the other 6 species [Oates, 2011], and that it is also the most vulnerable primate to the impacts of hunting on the island [Cronin et al., 2016]. Forest surveys have suggested that the population size of *P. pennantii* has declined significantly since 2006 [Cronin, unpublished data], and that its geographic distribution [Cronin et al., 2015a; Cronin et al., 2013; Cronin et al., 2016] is restricted entirely within the boundaries of the GCSR to an area

almost half the size of previous estimates [IUCN, 2016; Oates, 2011]. Furthermore, the distribution of *P. pennantii* encompasses not only the areas with the highest species richness of monkeys on Bioko, but also much of the critical sea turtle nesting habitat along the southern beaches of the GCSR (Fig. 6). Thus, if *P. pennantii* can be effectively conserved, it will serve as an umbrella for the conservation of many other threatened taxa (e.g., white-bellied pangolins, [*Phataginus tricuspis*]; Ogilby's duiker [*Cephalophus ogilbyi ogilbyi*]; and leatherback turtles [*Dermochelys coriacea*]) and habitats, including the Gran Caldera itself and a large swath of contiguous forest along an elevational gradient from sea level to over 2,200 m.

Conservation Recommendations

Securing the long-term future of the GCSR will require a multifaceted approach including (*i*) the development and implementation of an adaptive, evidence-based management plan; (*ii*) strengthening of the legal basis for protection of the GCSR; (*iii*) the empowerment of the National Institute of Forestry Development and Protected Area Management (INDEFOR-AP) and the Ministry of Forests and the Environment, the federal entities tasked with management of protected areas; (*iv*) increased law enforcement effectiveness; and (*v*) committed involvement from the Government of Equatorial Guinea in order to not only stop illegal hunting, but also to mitigate impacts from its own development plans.

A critical problem that must be addressed is the commitment of the Equatoguinean government to biodiversity conservation, namely through support for protected areas and their management. Equatorial Guinea is far from unique in this situation, as many African rain forest protected areas are underfunded by 50-80% of their necessary annual operating costs [Bruner et al., 2004; Wilkie et al., 2001], and at least 75% lack a secure, long-term funding program

417 [Struhsaker et al., 2005]. In a comprehensive analysis, Struhsaker et al. [2005] estimated that the
418 annual cost of operating a protected area in African rain forests was between 23 and 208 USD
419 per km^2, noting however, that these levels were believed to be insufficient, and that even
420 doubling estimates to about 400 USD per km^2 would still have left the costs significantly lower
421 than protected areas in developed nations [James et al., 1999b]. Blom [2004] had similar results,
422 estimating that the average yearly expenditure to achieve effective management at numerous
423 protected areas across Cameroon, Equatorial Guinea, Gabon and Central African Republic was
424 approximately 212 USD per km^2. Given the high abundance and diversity of species in these
425 forests [e.g., Oates et al., 2004], this suggests that investment in African rain forest protected
426 areas is highly cost-effective [Bruner et al., 2004]. Using the doubled approximations from
427 Struhsaker et al. [2005], 400 USD per km^2 would be approximately 495 USD per km^2 after
428 adjusting for inflation, resulting in an annual operating cost of just 415,800 USD for Bioko's two
429 protected areas [Cronin et al., 2014b]. Assuming a gross domestic product (GDP) for Equatorial
430 Guinea of 15.53 Billion USD [The World Bank, 2014], of which the forestry sector comprises
431 approximately 1.3% (~201.9 million USD) [Bizimana et al., 2014], the effective operation of
432 Bioko's protected areas represent only 0.003% of the annual GPD and 0.22% of the forestry
433 sector. It should be noted, however, that both above estimates assume that there is at least some
434 existing infrastructure with which Bioko's protected areas could be operated effectively (e.g.,
435 equipment and personnel). Despite the minimal costs relative to overall government
436 expenditures, and the strong motivation of INDEFOR-AP to expand their management and
437 conservation efforts, protected areas currently have insufficient infrastructure, personnel, and
438 capital with which to operate in any impactful manner on Bioko. As a result, it is perhaps more
439 realistic to estimate that in the near-term, initial investments must be higher to develop sufficient

infrastructure and capacity with which to begin to actively manage protected areas. This serves to illustrate the scale of underinvestment in protected areas and their management in Equatorial Guinea despite its globally recognized biological wealth and the government's declaration of environmental conservation as one of the country's 'Five Pillars' of reform [Quorvis Communications, 2010].

Far from simply detrimental to Bioko's primates and other flora and fauna, this also represents a significant economic loss at both local and national scales, which if acknowledged could help tip the scales in favor of improved conservation. Bioko's ecosystems provide services that are of vital importance to the well-being, health, and prosperity of the country and its citizens, yet they are often overlooked due to the enigmatic nature of valuating ecosystem services. In a global assessment, Costanza et al. [2014] posited that tropical forests should be valued at 5282 USD/hectare/year for their services. Based on this estimate, the services provided by Bioko's two PAs should be valued at approximately 452 million USD/year. Furthermore, James et al. [1999a] estimated that roughly 10 billion USD per year are spent safeguarding the world's protected areas, from which approximately 600 billion USD/year is generated in direct in-country expenditure from visitors to these areas [Balmford et al., 2015]. Unfortunately, visitors to Equatorial Guinea are scarce, as it is considered among the least visited countries in the world [Mark, 2015], meaning generating large-scale profits from ecotourism will be difficult in the near-term. However, if some policies were amended to make it easier to visit and transit throughout the country, there is significant potential for ecotourism on Bioko due to its intact forests, expansive beaches, and abundant wildlife, including high densities of both diurnal primates and marine turtles. We recognize that these values are rough estimates and that there are inherent limitations in detailed valuations of ecosystem services or potential future tourism

463 expenditures, but, in general, evidence suggests that increased investments in protected areas and
464 their management could yield substantial returns.

465 Given the current conditions and the task ahead, government-led conservation efforts
466 should be prioritized on Bioko in order to concentrate efforts how and where they are likely to
467 have the maximum possible conservation benefit. Initial efforts should focus on the protection of
468 primates and marine turtles, the taxa most threatened by current offtake patterns. The optimal
469 scenario for the preservation of primates would be a complete ban on shotgun hunting, which
470 accounts for over 90% of all primate carcasses [Cronin et al., 2015b; Grande Vega et al., 2013].
471 Albrechtsen et al. [2004] tested this policy in a model based on Bioko, which also included
472 manipulating market prices for larger animals and increased incomes from alternative
473 livelihoods. The gun hunting ban performed best, not just for the protection of large animals, but
474 also for the conservation of small animals and for reducing the size of the hunting population.
475 Guns have been confiscated previously on Bioko in 1974 [Butynski and Koster, 1994], to the
476 benefit of wildlife, and more recently Grande Vega et al. [2013] reported that during her study,
477 no primates were killed in the village of Basilé Bubi, where there are no guns. It seems, then, that
478 if enacted and effectively enforced, that a ban on gun hunting would considerably improve the
479 long-term viability of Bioko's primate populations.

480 Other measures, such as enforcement of existing legislation, could also be rapidly
481 implemented by the Government of Equatorial Guinea, and may significantly reduce the amount
482 of primate hunting by effecting barriers to the bushmeat trade. The primate hunting ban, for
483 instance, includes prohibitive fines (approximately 200-1000 USD/monkey) [Republic of
484 Equatorial Guinea, 2007], which could disincentivize hunting by threatening a significant portion
485 of hunters' annual hunting income (~480 to 1868 USD/year) [Fa et al., 2000; Grande Vega et al.,

2013]. Enforcement could begin in the immediate future at preexisting roadblocks on the two direct routes between catchment areas and Malabo where travelers are already required to stop and periodically show documentation (Fig. 5b). These checkpoints should be supplemented with personnel from INDEFOR-AP tasked with randomized vehicle searches, and supported by military personnel trained in environmental legislation and enforcement. Additional motivation for search and seizure of the citizens may have pitfalls (i.e. the potential for extortion by military staff), but if individuals were supported sufficiently enough to promote compliance with the law, these checkpoints would be well suited to stemming the transport of the majority of bushmeat to Malabo.

Perhaps the most practical solution would be the implementation of forest guards [Bennett, 2011], which has been successful elsewhere in reducing hunting and improving the effectiveness of protected areas [Bruner et al., 2001; Campbell et al., 2011; Corlett, 2007; de Merode and Cowlishaw, 2006; Hilborn et al., 2006; Rowcliffe et al., 2004; Tranquilli et al., 2012]. Intensive monitoring for bushmeat hunting could be conducted by these forest guards (or in the immediate future, the trained military personnel) stationed at 'ranger bases' situated at key protected area access points, and by randomized searches of those transiting into and out of protected areas by INDEFOR-AP staff. By focusing on these natural 'choke points,' guards may be more effective than with a more generalized enforcement scheme. The development and implementation of a 'ranger base' or restricted access point at Belebu is especially important to the long-term future of the GCSR (Fig. 5b). It provides the only vehicular access into the GCSR and to the southern extent of Bioko. The highest richness and densities of wildlife are found in this area, providing a biological incentive for protection, but the southern beaches area also a major tourist attraction, and the inability to control access and to generate profits that could then

509 be put back into the management of the GCSR represents a significant missed economic
510 opportunity.

511 A more broadly-focused, systematic program of regular forest patrols covering the
512 entirety of Bioko's protected areas should also be implemented in the long-term, but in the
513 beginning, we recommend that patrol efforts be prioritized following the conservation
514 prioritization framework we developed using our ecological niche model results (Fig. 5b). This
515 framework was created to maximize conservation effectiveness based on amounts of total
516 coverage, as well as the estimated relative investment necessary to effectively patrol the area. We
517 also recommend that forest guard positions eventually be staffed by people living in or alongside
518 protected areas (e.g., Ureca, Moka, Belebu, Moeri, Basilé Fang), as they are best suited for the
519 positions given their local knowledge of the area they will be patrolling. This will aid in the
520 success of the guard program by attaching an economic value to the stewardship of wildlife, and
521 by helping to empower and engage local communities in the process of conservation.

522 The highest priority zone is the southwestern sector of the GCSR, which should be
523 considered a 'critical zone' in each of the following management strategies (Fig. 5b). Using
524 patrols to make this area a 'no-take zone' could be enforced more easily than any offtake
525 restrictions [Milner-Gulland and Bennett, 2003], as it is already protected passively via isolation,
526 difficult terrain, and limited access from the ocean. This area contains all seven diurnal primate
527 taxa at densities higher than elsewhere on Bioko, and has significantly less hunting than other
528 sites [Cronin et al., 2015a; Cronin et al., 2016]. It also holds the highest densities of *M.*
529 *leucophaeus* and *C. satanas* on the island, as well as the entire population of *P. pennantii*
530 [Cronin et al., 2015a; Cronin et al., 2016; Cronin, unpublished data]. In addition to primates,
531 conservation of this zone would protect most of the critical nesting habitat of the four species of

marine turtle that nest on the island, as the two 'ranger camps' (Moraka and Moaba) are also the only safe sites for landing small boats, a tactic employed by both terrestrial and marine poachers (Fig. 5B). Thus, by concentrating anti-poaching efforts in the region, guards would be able to maximize conservation benefits at minimal cost.

The second priority zone is, in effect, an extension of the first zone to include the entire southern extent of Bioko (Fig. 5b). This would be potentially more of an investment to monitor as it is a larger area, but delineation would be slightly less arbitrary than the first priority zone, and thus, may be easier to enforce. This zone is delineated with a relatively straight line from east to west across the spine of the southern highlands, encompassing the northern rim of the Gran Caldera, but passing below the pastures on the slopes of Pico Biao. This conservation zone would contain an identical faunal species assemblage, but would likely also encompass the entire range of *C. nictitans*. Protecting this zone would also conserve the entirety of the unique monsoon forest habitat type as well as afromontane formations on the two peaks.

The third priority would be to simply protect the currently delineated protected areas (Fig. 5b). This is, perhaps, the best place to start, as the protected areas already legally exist, and would require no new designation. This strategy is aided, like the previous two, by the fact that they were originally created since much of the terrain they encompass was deemed inferior for agriculture and overly difficult to access and exploit. In spite of their legal status and difficult terrain, development continues to gradually progress inside Bioko's protected areas with little consideration of their status. Future projects occurring within the protected areas should be subjected to an environmental impact assessment and/or oversight by INDEFOR-AP in order to promote INDEFOR-AP's legal mandate to manage Equatorial Guinea's protected areas and to

554 ensure it meets the conservation and development goals of the protected areas' management
555 plans.

556 Finally, given the extensive territorial waters of Equatorial Guinea, the commercial
557 fishing sector represents a much underutilized resource, but also an opportunity to reduce
558 pressure on Bioko's terrestrial wildlife. Fish availability and bushmeat demand have been shown
559 to be directly linked [Brashares et al., 2004], thus increased availability of fresh fish may help to
560 alleviate demand for terrestrial wildlife. Malabo consumers have a preference for fresh meat
561 [Reid et al., 2005], but the only sources of meat currently 'produced locally' are bushmeat and
562 fish [Albrechtsen et al., 2006], as well as the occasionally available '*cebu*' beef (humped cattle).
563 The organization and improvement of the Equatoguinean national fishing fleet may reduce
564 pressure on Bioko's terrestrial wildlife. Furthermore, increasing numbers of non-African fleets
565 are fishing in the Gulf of Guinea, heavily exploiting stocks to the point of decline [Pauly et al.,
566 2014; Pauly and Zeller, 2016], and forcing small scale fisheries to compete with industrial fleets
567 [Belhabib et al., 2015; Pauly and Zeller, 2016]. If fish stocks do not begin to be managed more
568 effectively for the Equatoguinean population, the supply of fish will decline, likely leading to
569 increased demand for bushmeat [Brashares et al., 2004].
570

571 ## *Cultivating a Culture of Conservation*

572 Despite the significant issues discussed above and Equatorial Guinea's rapid and ongoing
573 development, there are still many reasons to remain optimistic about the future of conservation
574 on Bioko. Human population densities remain low throughout much of the island, and large areas
575 of forest remain intact and relatively inaccessible. Over the last 15 years, UNGE's School of
576 Environmental Sciences has grown from an annual enrollment of fewer than 15 students to over

400, and the school is UNGE's most successful and productive academic unit. There are increasing indicators that the Equatoguinean government, via INDEFOR-AP and the Ministry of Forests and the Environment, is interested in taking a more active role in preserving its natural heritage. INDEFOR-AP has recently become more proactive on Bioko, designating Conservators for the two protected areas, partnering with BBPP to deploy INDEFOR-AP ecoguards in Ureca and along the southern beaches, and collaborating with both BBPP and Ecoguinea to train a cadre of future ecoguards from villages around the borders of Bioko's protected areas. There have been periodic confiscations of captured wildlife and bushmeat [Ayecaba and Ortega, 2014], as well as an outreach campaign which distributed pamphlets explaining the primate hunting ban [Republic of Equatorial Guinea, 2007] and the dangers of hunting monkeys. The Equatoguinean government has also made commitments to work with partners, including the BBPP, Ecoguinea, the United Nations Development Program–Global Environmental Facility (UNDP-GEF) and the Wildlife Conservation Society (WCS), to improve management of protected areas, to develop a comprehensive national strategy for management of its protected areas, and to work towards gaining recognition for Bioko Island as UNESCO Biosphere Reserve [Engonga Osono et al., 2015].

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Figure Captions

Figure 1: In order to effectively understand and combat the bushmeat trade, it is critical that a multidisciplinary approach, such as this example employed by the BBPP, is implemented.

Figure 2: Distribution of major cities (including Ureca), main roads, and protected areas on Bioko Island.

Figure 3: (A) Time series plot of the overall primate carcass rates (carcasses/market day). Vertical lines delineate breaks between periods of distinct market activity identified via intervention analysis [Box and Tiao, 1975]. The second break (between "Pre-ban" and "Post-ban") coincides with the October 2007 Presidential Decree banning primate hunting [Republic of Equatorial Guinea, 2007]. Adapted from Cronin et al. [2015b]. **(B)** Average change in carcass rate per month (slopes) and 95% confidence intervals for each of the diurnal primate species. Adapted from Cronin et al. [2015b]. **(C)** Species range estimation for *P. pennantii* and *C. nictitans* derived from the ecological niche models developed using Maxent, both of which are restricted to the southern extent of Bioko within the GCSR. Adapted from Cronin et al. [2015a].

Figure 4: Hunting response index values (HRI) for six of the seven diurnal primate species on Bioko. *Allochrocebus preussi* was not encountered along transects used for in the HRI analysis, and was excluded from the analysis. HRI values above 1 suggest a relative tolerance to hunting pressure, while values below 1 indicate susceptibility of the species to hunting. Adapted from Cronin et al. [2016].

Figure 5: Using forest survey data, the BBPP developed ecological niche models for each of Bioko's monkey species [Cronin et al., 2015a], which allowed for the identification of **(A)** hotspots of primate species richness. Using these primate hotspots and existing infrastructure as a guide, we designated **(B)** priority areas for primate conservation on Bioko, as well as a series of 'Ranger Bases' at principal protected area access points and 'Bushmeat Checkpoints' that would utilize existing infrastructure at key transit 'choke points' to serve as bushmeat inspection points. Also designated were two remote camps, Moraka and Moaba, both long used by the BBPP, but also key sites for landing small boats, from which forests guards could monitor and protect two of most important beaches on the southern coast.

Figure 6: Bioko Island showing the past [IUCN, 2016] and present [Cronin et al., 2015a] estimated geographic distribution of *P. pennantii*, as well as the overlap between the estimated range of *P. pennantii* and the five (A-E) marine turtle nesting beaches along the southern coast.

Tables

Table 1: The diurnal primates of Bioko Island, Equatorial Guinea and their degree of threat status at the species and subspecies levels [IUCN, 2016]. Taxonomic classification follows Grubb et al. [2003], except for Preuss's monkey, which is allocated to the genus *Allochrocebus* following Grubb [2006]. Table adapted from Cronin et al. [2016].

Common Name	Binomial Name	Red List Category	
		Species	Subspecies
Bioko black colobus*	*Colobus satanas satanas*	Vulnerable	Endangered
Bioko red colobus*†	*Procolobus pennantii pennantii*	Critically Endangered	Endangered
Bioko drill*	*Mandrillus leucophaeus poensis*	Endangered	Endangered
Bioko Preuss's monkey*	*Allochrocebus preussi insularis*	Endangered	Endangered
Bioko red-eared monkey*	*Cercopithecus erythrotis erythrotis*	Vulnerable	Vulnerable
Crowned monkey	*Cercopithecus pogonias pogonias*	Least Concern	Vulnerable
Bioko putty-nosed monkey	*Cercopithecus nictitans martini*	Least Concern	Vulnerable

* Recognized by Grubb et al. [2003] as subspecies endemic to Bioko.
†Recognized by Groves (2007; *Piliocolobus pennantii*) and Oates (2011; *Procolobus pennantii*) as a species endemic to Bioko.

Table 2: Measurements of gun hunting intensity and primate abundance across three survey sites within the Gran Caldera Scientific Reserve. The number of primate group sightings is in parentheses. Table adapted from Cronin et al. [2016].

Survey Transect	Hunting Intensity (signs/km)	Survey Effort (km)	Species sighting frequency (groups/km)*								Sighting Frequency (groups/km)
			Mle	Csa	Ppe	Cer	Cpo	Cni	Apr	Unk	
Moraka	0.05	210.48	0.11 (19)	0.22 (36)	0.49 (111)	0.64 (133)	0.62 (131)	0.05 (13)	0 (0)	0.12 (26)	2.24 (469)
Ureca	0.29	99.25	0.10 (9)	0.04 (5)	0.19 (16)	0.93 (95)	0.44 (43)	0.05 (6)	0 (0)	0.06 (6)	1.82 (180)
Belebu	2.89	106.67	0 (0)	0.02 (1)	0 (0)	0.11 (9)	0.05 (6)	0 (0)	0.01 (1)	0 (0)	0.18 (17)

*Mle -*Mandrillus leucophaeus*; Csa - *Colobus satanas*; Ppe - *Procolobus pennantii*; Cer - *Cercopithecus erythrotis*; Cpo - *Cercopithecus pogonias*; Cni - *Cercopithecus nictitans*; Apr - *Allochrocebus preussi*; Unk – Unidentified