Contributed Paper

Contrasts in Livelihoods and Protein Intake between Commercial and Subsistence Bushmeat Hunters in Two Villages on Bioko Island, Equatorial Guinea

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Abstract: *Across West and Central Africa, wildlife provides a source of food and income. We investigated the relation between bushmeat hunting and household wealth and protein consumption in 2 rural communities in Bioko Island, Equatorial Guinea. One village was dedicated to commercial hunting, the other trapped game primarily for food. We tested whether commercial-hunter households were nutritionally advantaged over subsistence-hunter households due to their higher income from the bushmeat trade and greater access to wild-animal protein. We conducted bushmeat-offtake surveys in both villages (captures by hunters and carcasses arriving to each village). Mammals (including threatened primates: black colobus [*Colobus satanas*], Preussi's guenon [*Allochrocebus preussi*], and russet-eared guenon [*Cercopithecus erythrotis*]), birds, and reptiles were hunted. The blue duiker (*Philantomba monticola*), giant pouched rat (*Cricetomys emini*), and brush-tailed porcupine (*Atherurus africanus*) contributed almost all the animal biomass hunted, consumed, or sold in both villages. Monkeys and Ogilbyi's duikers (*Cephalophus ogilbyi*) were hunted only by commercial hunters. Commercial hunters generated a mean of US$2000/year from bushmeat sales. Households with commercial hunters were on average wealthier, generated more income, spent more money on nonessential goods, and bought more products they did not grow. By contrast, households with subsistence hunters spent less on market items, spent more on essential products, and grew more of their own food. Despite these differences, average consumption of vegetable protein and domestic meat and bushmeat protein did not differ between villages. Our results highlight the importance of understanding the socioeconomic and nutritional context of commercial and subsistence bushmeat hunting to correctly interpret ways of reducing their effects on threatened species and to enable the sustainable offtake of more productive taxa.*

Keywords: Bioko, household expenditure, offtake, protein intake, wealth

Contrastes en el Sustento y la Ingesta de Proteínas entre Carne de Caza de Subsistencia y Comercial en Dos Aldeas en Isla Bioko, Guinea Ecuatorial

Resumen: *En África Central y Occidental la fauna silvestre es una fuente de ingresos y alimento. Investigamos la relación entre la carne de caza, la economía familiar y la ingesta de proteínas en dos comunidades rurales en la Isla de Bioko, Guinea Ecuatorial. Una aldea se dedicaba a la caza comercial mientras que la otra cazaba principalmente para autoconsumo. Comprobamos si las familias que practicaban la caza comercial tenían ventajas nutricionales sobre las familias que practicaba una caza de subsistencia debido a sus mayores ingresos por el comercio de la carne y mayor acceso a proteínas procedentes de la fauna silvestre. Realizamos encuestas para conocer la extracción de carne de caza en ambas aldeas (capturas por cazadores y piezas que llegaban a cada aldea). Se cazaron mamíferos (incluyendo primates amenazados: colobo negro Colobus*

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satanas, cercopitecos de Preuss Allochrocebus preussi y cercopitecos de orejas rojas Cercopithecus erythrotis), aves y reptiles. El cefalofo o duiquero azul Phillantomba maonticola, la rata gigante de Emin Cricetomys emini y el puercoespín africano Atherurus africanus resultaron ser la mayoría de la biomasa animal cazada, consumida o comercializada en ambas aldeas. El duiquero de Ogilby Cephalophus ogilbyi y otros monos fueron cazados solamente por los cazadores comerciales. Éstos generaron un promedio de US$2000 al año con las ventas de la carne. Sus familias tuvieron una economía más saneada, mayores ingresos, gastaron más dinero en bienes no esenciales, comprando más productos en vez de cultivarlos. Por el contrario, las familias de los cazadores de subsistencia gastaron menos dinero en bienes de mercado y más en productos esenciales y cultivaron sus propios alimentos. A pesar de estas diferencias, el consumo medio de proteínas vegetales y animales (domésticos y carne de caza) no fue diferente entre ambas aldeas. Nuestros resultados resaltan la importancia de entender el contexto socioeconómico y nutricional en el que se desarrolla la caza comercial y de subsistencia para poder interpretar correctamente las vías para reducir sus efectos sobre las especies amenazadas y permitir una extracción sostenible de los taxones más productivos.

Palabras Clave: Bioko, extracción, gastos domésticos, ingesta de proteínas, riqueza familiar

Introduction

In African tropical forests, meat of wild animals (bushmeat) commonly satisfies basic protein requirements for many rural communities (Wilkie & Carpenter 1999). Many families also use hunting to supplement short-term cash needs because bushmeat is an easily traded, high value-to-weight ratio resource. As such, the distinction between subsistence and commercial use of wild meat is often blurred, with meat from the forest supplementing both diets and incomes (Kümpel et al. 2010). Identifying interactions between income generation and food security for communities dedicated to professional or subsistence hunting may guide appropriate management approaches to protect threatened animals but also to guarantee human livelihood sustainability.

For people of the tropics, gathered plant foods are primarily dietary supplements to their starchy staple diet, and bushmeat is their primary protein source (Froment et al. 1993; Pagezy 1993; Ntiamoa-Baidu 1997). However, the contribution bushmeat makes to rural household diets may vary substantially (e.g., 30–80% in Central Africa) (Koppert et al. 1993). Such a wide range of consumption of wild-animal protein may be affected by whether bushmeat is a subsistence product or is sold for profit; the sale of bushmeat can be a "stepping stone to greater prosperity" for some households (Solly 2004).

In general, wealth is an important predictor of consumption of animal protein (Wilkie et al. 2005). Moreover, employment alternatives for hunters, access to hunting equipment (guns, snares), or even livelihood activities and location may influence availability of bushmeat and its consumption (Jenkins et al. 2011). However, how bushmeat incomes are used by hunters and households may affect not only wealth accumulation, but also household nutritional status and food security. Thus, if hunting incomes are not used for purchasing essential components of household economies, then a reduction in the commercial bushmeat trade may not have a significant effect on hunter livelihoods (Starkey 2004; Coad et al. 2010). However, if hunting incomes are used for the purchase of subsistence items, then declines in hunting income could greatly affect hunter livelihoods (Elliott 2002).

Although it is well known that bushmeat may simultaneously be a safety net or an important source of income for hunter households (Brashares et al. 2011), we focused on explaining how hunting for commercial urban markets or for subsistence-based consumption affects protein consumption of households. We obtained data from 2 matched hunter-type villages in Bioko Island, Equatorial Guinea. In one village, hunting and sale of bushmeat to Malabo, the main town on the island and the country's capital, were the main livelihood activities for men, whereas in the second village, animals were primarily hunted for consumption by the villagers. We interviewed household members in both villages and collected data on household wealth, assets, and income sources, as well as daily consumption of bushmeat and other protein sources (animal and vegetable). We also estimated volume and biomass of bushmeat hunted or traded within each village from daily records of prey items brought to the villages. We used these different data sets to examine the relation between hunter types (subsistence or commercial) and household wealth; how wildlife consumption is related to the consumption of alternative protein sources at the household level; and the effect of commercial hunting versus subsistence hunting on threatened species in the study area. From a biological diversity conservation perspective, our results highlight the need to understand the individual contribution of bushmeat to income and food security so as to identify their implications on achieving sustainability.

Methods

Study Sites and Household Selection

Bioko is a volcanic continental island (69 × 32 km, 2017 km^2) in the Gulf of Guinea, 32 km off the Cameroon coast (Fig. 1). We gathered nutrition and livelihood data in Basilé Bubi (BB) and Basilé Fang (BF) villages.

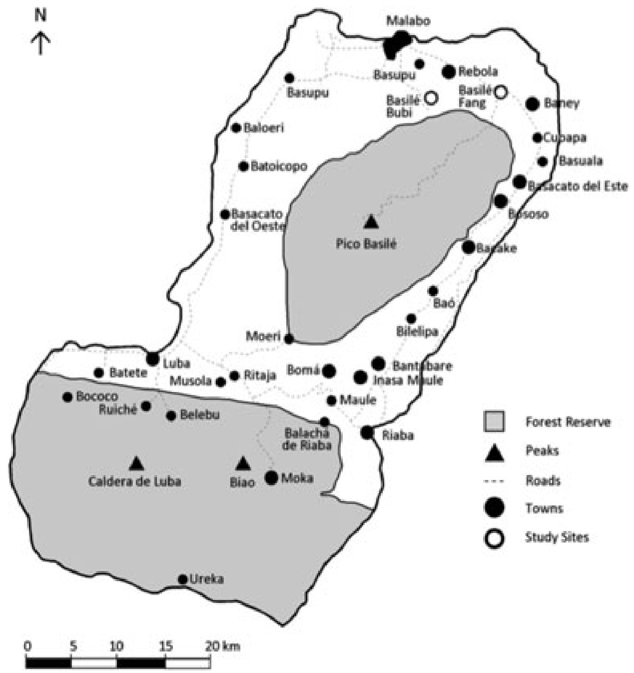

Figure 1. Distribution of human settlements, roads, and forest reserves (protected areas) and location of study villages, Basilé Bubi and Basilé Fang, in Bioko Island.

Both villages are on Pico Basilé Mountain (northeastern Bioko) 10–15 km south of the country's capital, Malabo (population around 211,000 in 2001 [Dirección General de Estadística y Cuentas Nacionales 2012]). BB is a long-established village (population 110 in 2010). It probably dates back to the early settlement of the indigenous Bubi ethnic group, who colonized the island from mainland Africa around 50 BC. BF was founded in 2005 by ethnic Fang, who are professional hunters from continental Equatorial Guinea, Rio Muni. This village (population 150 in 2010) is on the main Malabo to Riaba road and at the base of a paved road that leads to the summit of Pico. Pico Basilé (3011 m) is the largest and highest of 3 overlapping volcanoes that form the island. The area was declared a national park in 1988 (Fa 1991).

Average temperatures are around 25 °C in the lowlands, but reach a minimum of 5 °C at the highest elevation. Average annual rainfall is <2000 mm (Terán 1962), mostly concentrated between April and October (Juste & Fa 1994; Clemente Muñoz et al. 2006). We gathered information on overall food consumption from July to November 2009 in both villages. For all households surveyed, we collected information on household composition (number, age, and sex of all household members), education, income, and wealth. All households (28 in BB and 27 in BF) were visited and encouraged to participate in our study. Around half these (14 in BB and 13 in BF) completed our food-consumption surveys accurately and were included in our analyses.

Gun hunting and trapping were the primary hunting methods in BF. Only trapping was practiced in BB because gun ownership by the Bubis is prohibited since a Bubi rebellion against the government in January 1998.

Household Income, Wealth, and Expenditure

We carried out structured household interviews in both villages to assess the comparative wealth of each household on the basis of their assets (Morris et al. 2000). The female head of the household was asked about household ownership of 23 asset items, including the number owned and each item's individual price. These goods covered a wide range, from relatively cheap subsistence goods, such as cooking pots, to expensive items (e.g., refrigerators, music players, televisions, mobile phones, electric fans, air conditioners, vehicles). We also ascertained the value of the property (or houses) owned by the family by asking the household head or by estimating its value on the basis of building materials used and dwelling size.

To estimate transitory income, we asked all working household residents to recall the amount of income from salaries, wages, bonuses, pensions, donations, commercial activities, sale of forest goods, gifts, and remittances over the past year. We requested each interviewee to provide us with specific details of frequency and income from work, sale of goods such as annual crops, or monetary gifts received during a typical month. From these data, we calculated the annual income per household.

Annual household expenditure was determined from the amount spent during a typical month on food; education (tuition, school supplies, transport to school); members of the immediate family or other dependents; and fuel, telephone, rent, home repairs, extraordinary expenses, travel, and contracted personnel per month. This information was obtained from interviews with the head of each household.

We recorded income, expenditure, and assets in local currency (Central African franc [CFA]). To facilitate comparison with other locations, we use U.S. dollars as the monetary unit where appropriate. We used the purchasing power parity (PPP) conversion factor between CFA and U.S. dollars for 2010–2011, which was 508.82 CFA/PPP per US$1 (World Bank 2012).

Protein Consumption

To compare food consumption among households some measure of household size is needed. The simplest measure is the number of individuals in the household, but this does not take into account the relative contributions of different members of the household with regard to energy needs (Sellen 2003). We used a measure of adult male equivalence to account for differences in energy requirements on the basis of age and sex. We used reference adult (RA) units (ILCA 1981), as in Sellen (2003). RA units are a type of AME (adult male equivalent): 1.0 RA for an adult male (>16 years of age), 0.86 for an adult female (>16 years of age), and 0.96, 0.85, and 0.52, respectively, for children 11–15, 6–10, and 0–5 years old. These ratios are based on estimates of energy requirements in FAO et al. (1991).

We asked the female head of each household to note all produce, natural resources, and manufactured goods consumed (purchased, hunted, caught, or otherwise obtained) every day for 7 d. Respondents were trained on how to complete the food diaries, and we gave an incentive gift to each family after completion. We derived the weight of all consumed items by weighing a sample (>10 units) of each item. Because a proportion of food items were used whole (e.g., piece, leg, head, pile, cup), we derived the average weight for these items by weighing a sample of each. For each item consumed, household respondents also provided the value in CFA and the number of units of that good bought.

For each meal, all ingredients consumed and quantities eaten (which we transformed into grams) were noted by the female head of the family. We also recorded the sex and age of all persons eating each meal from which we obtained the number of RAs at each meal. We also asked the interviewee how many meals were consumed outside the home and who ate them. We did not ask what was consumed during these meals.

Daily animal and vegetable protein consumed per RA were determined by multiplying the amounts eaten of the different foods during each meal by their respective protein content. Hence,

$$\mathrm{PIRA} = \sum (A_{a \ldots n} \times P_{a \ldots n})/\mathrm{RA}, \qquad (1)$$

where PIRA is the protein intake per RA during a single meal, A is the total amount (in grams) consumed of food items $a \ldots n$, and P is the protein content (grams of protein per grams of the food item), and RA is the total number of RAs consuming that meal. The total daily protein intake per RA was derived by adding all PIRAs for each sampled day.

Protein contents of all foods were obtained from published nutrient composition tables. Data for protein contents of commonly eaten plant foods were taken from Oguntona and Akinyele (1995), Okeke et al. (2010), Odebunmi et al. (2009), and Zumbado et al. (1992); for bushmeat species from Malaisse and Parent (1982), Ajayi and Tewe (1983), and Oyarekua and Ketiku (2010); and for fish from Oguntona and Akinyele (1995).

Bushmeat Offtake

We estimated the volume of bushmeat extracted by hunters per year in each village from incoming carcasses over 16 months in BF (August 2010 to November 2011) and over 6 months in BB (July 2011 to December 2011). We sampled bushmeat extraction over 9 wet and 7 dry season months in BF and over 3 wet and 3 dry season months in BB. It was not possible to collect individual data for all hunters in BF; we had a male research assistant record the number of animals entering the village and ownership of the animals over 327 d. Animals that were not seen because they had been consumed in camps by members of the hunter's household or discarded were not included. In BB animals trapped by all village hunters were recorded over 158 sample days. In both villages, a team member (M.G.V.) regularly visited our 2 field assistants to ensure completeness, legibility, and accuracy of the data being recorded. Despite a ban on primate hunting since 2007 (Hearn & Morra 2006), hunters allowed us to record monkeys brought to the collection site.

For each carcass observed, we noted species and condition (fresh, alive, or smoked) and whether it was for personal consumption or whether it was to be sold. In most cases, we were able to record the price offered by the hunter to middle persons and to calculate annual income per hunter and per species. When possible, we weighed carcasses to the nearest 10 g on a direct-reading spring balance (capacity 25,000 g). We weighed 219 carcasses of all species (except Preuss's guenon [*Allochrocebus preussi*] and Palm Nut Vulture [*Gypohierax angolensis*]) from which we calculated the mean adult body mass (male and female combined) for each species.

In BF hunted animals were brought to the village after a hunting trip. Each batch of animals observed by our assistant during a sample day was attributed to an individual hunter. From this, we derived the proportion of sample days during which incoming carcasses were recorded for each hunter. We then used this proportion to estimate the number of hunting days undertaken by a particular individual in a year. Because hunters were likely to hunt during any day of the year, we multiplied the observed proportion of hunting days per hunter by 365. We multiplied the estimated annual number of hunting days per hunter by the median number of animals recorded per sampled day for each hunter. We used the median because the number of animals hunted per day was positively skewed for all sampled hunters.

Because only 7 hunters operated in BB, we were able to record all animals trapped by each hunter during the sampling period. We used the median number of animals per species harvested per day per hunter to calculate the number of carcasses per hunter per year by multiplying the median by 365 d. The BB hunters were likely to hunt any day of the year.

We calculated annual biomass of bushmeat extracted by species, hunter, and village by multiplying each animal's average body mass, derived from carcasses weighed in the field (except for 2 species, Table 2), by the number of animals extracted. The total number of carcasses and biomass traded or hunted per village per year was

Table 1. Results of univariate tests and mean (SE) household income, expenditure, and protein consumption in Basilé Fang and Basilé Bubi, Bioko Island, Equatorial Guinea.

Variables	*Basilé Fang*	*Basilé Bubi*	*Test (p)*[a]
Households			
income (US$)	7044 (1500)	3,441 (1,043)	$F_{(1,19)} = 3.133$ (0.094)
expenditure (US$)	3453 (928)	914 (365)	$F_{(1,19)} = 4.602$ (0.046)
assets (US$)	3809 (1,212)	1213 (264.84)	$F_{(1,19)} = 2.943$ (0.103)
hunting income (US$)	1,868.41 (441.55)	not estimated (< 1% sold)	
Protein consumption[b]			
Total ($g \cdot RA^{-1b} \cdot d^{-1}$)	142.63 (22.53)	119.08 (12.92)	$F_{(1,26)} = 0.853$ (0.365)
vegetable ($g \cdot RA^{-1} \cdot d^{-1}$)	48.57 (4.94)	52.77 (5.18)	$F_{(1,26)} = 0.342$ (0.564)
animal ($g \cdot RA^{-1} \cdot d^{-1}$)	94.06 (20.60)	65.14 (9.55)	$F_{(1,26)} = 1.701$ (0.204)
bushmeat ($g \cdot RA^{-1} \cdot d^{-1}$)	18.47 (6.67)	10.49 (6.48)	$Z = -1.868$ (0.062)
bushmeat protein (%)	11.35 (3.06)	7.64 (3.64)	$F_{(1,26)} = 0.601$ (0.446)

[a] *All tests are analysis of variance (ANOVA) except for grams per reference adult (RA) per day (*).*
[b] *Reference adult units were calculated according to the ILCA system (ILCA 1981), by which an adult male represents 1.0 RA unit, an adult female represents 0.86 RA units, and children in the 0–5, 6–10, and 11–15 age groups represent 0.52, 0.85, and 0.96 units, respectively.*

obtained by summing the values for all species and all hunters in each village.

Statistical Analyses

We investigated differences in hunting activity, income and expenditure, wealth, and protein consumption between BF and BB households with univariate statistical analyses. We first tested data normality by means of a Kolmogorov-Smirnov test. We used a one-way analysis of variance (ANOVA) for variables with normal data and a Mann-Whitney *U* test for non-normal data (Fowler & Cohen 1992). We used regression analyses (Sokal & Rohlf 1997) to explore possible relations between protein consumption and household incomes and expenditure and to test relations between household income and expenditure.

We used a generalized linear model (GLM) with a normal error distribution and an identity link function (Crawley 1993) to examine the relations and interactions between household expenditure (dependent variable) and villages and items purchased as factors associated with sources of variation (independent variables). All data were log transformed (Fowler & Cohen 1992). All analyses were performed with SPSS (version 15.0).

Results

Household Wealth, Income, and Expenditure

Mean annual income and assets per household were higher in BF than in BB, but not statistically so (Table 1). Variation in income was large: $1,428–15,362 in BF and $493–9,071 in BB. Mean household assets ranged from $19 to 11,234 in BF and from 687 to 2,598 in BB. Mean expenditure per household was significantly higher in BF than in BB (Table 1).

Annual income from the sale of bushmeat was 32.8% and 1.2% in BF and BB, respectively. Income from bar-shop trade (trade from an establishment that sells groceries and other goods, as well as cooked meals and alcohol) was higher in BF (28.7%) than in BB (17.7%). Five BF and 2 BB households had bar-shop businesses (start-up costs of these businesses are high). Wages from work outside the village contributed 40.6% and 11.0% of total earned income in BB and BF, respectively. The sale of products (e.g., taro [*Colocasia esculenta*], cassava [*Manihot esculenta*]) from household gardens accounted for <1% and 12.4% of the income in BB and BF, respectively. Distribution of income from hunting per hunter in BF was right skewed. At one extreme, 5 particularly successful hunters had a total catch and income that far exceeded any other hunter in the village. The majority of hunter incomes fell into the lowest income category. Income derived from the bushmeat-offtake survey revealed that hunters in BF earned on average $1,868 (median = $636)/year (range $14 to a $13,526 [Supporting Information]). Income from hunting in BB was negligible because only a small proportion of animals hunted were sold and animals were always sold within the village itself.

Most hunting income was derived from the sale of relatively small-bodied prey species. Blue duiker (*Philantomba monticola*) contributed 82.9% of the estimated annual income per hunter (Supporting Information) and 8 times more than the next-most important species, the brush-tailed porcupine (*Atherurus africanus*). However, the 4 larger-bodied species (>5 kg) (black colobus [*Colobus satanas*], Preuss's guenon, russet-eared guenon [*Cercopithecus erythrotis*], and Ogilby's duiker [*Cephalophus ogilbyi*]) contributed 6.5% (SE 2.5) to a hunter's annual income.

Protein Consumption

Entries in food diaries were for 195 d in both villages (mean [SE] = 7.22 d/household [0.11], range 6–9). We recorded 120 food items consumed in 1791 meals during

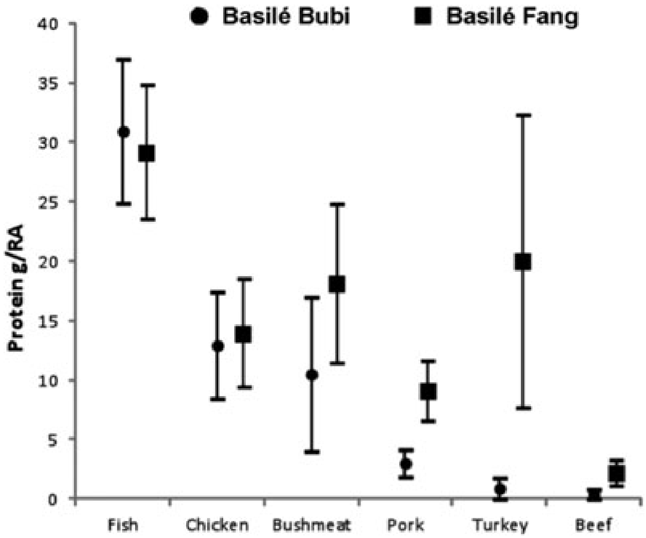

Figure 2. Mean (SE) grams of animal protein from different sources consumed by households in Basilé Bubi and Basilé Fang (RA, reference adult, units of which are a type of adult male equivalent unit [ILCA 1981]).

the study period in both villages. In BB 78 food items were consumed in 547 meals. In BF 98 food items were consumed in 1244 meals. Twenty-two and 47 foods were exclusive to BB and BF, respectively. Seventy meals (5.63%, 4 families) in BF were eaten outside the home, and 26 meals (4.75%) were eaten outside the home (2 families) in BB. There was no significant difference between BF and BB in total protein consumption (Table 1). Mean consumption of vegetable protein was slightly higher in BB than BF, whereas mean consumption of animal protein in BF was greater that in BB (Supporting Information).

Bushmeat was not a major component of protein eaten (Fig. 2). Mean consumption of bushmeat protein did not differ significantly between villages (Table 1). Bushmeat protein contributed 7.64% (SE 3.64) 11.35% (SE 3.06) of all protein consumed in BB and BF, respectively. Bushmeat protein was 14.90% (SE 6.61) and 16.67% (SE 4.07) of the animal protein eaten in BB and BF, respectively. Frozen fish was the most commonly consumed animal protein in both villages, followed by chicken in BB and turkey in BF and bushmeat and frozen pork and beef in both villages (Fig. 2).

For both villages together, household income was significantly correlated with daily consumption of total protein (adjusted $R^2 = 0.\ 18$, df $= 19$, $p = 0.04$). At lower incomes, households consumed less protein, but above a certain income threshold, protein consumption was high (polynomial regression model, adjusted $R^2 = 0.\ 66$, df $= 19$, $p = 0.001$). However, daily amounts of animal, vegetable, or bushmeat protein consumed per RA were not affected by household incomes. Household expenditure and protein consumption were also not correlated. Within sites, we did not find a significant correlation between income and protein consumption or between income and bushmeat protein consumption. These results suggest that in both villages bushmeat is not the preferred protein source.

Expenditure differed significantly among all items purchased by households in both villages (Wald = 958.03; df = 14; $p < 0.001$). Amount spent on different foods differed significantly between villages (Wald = 77.78; df = 14; $p < 0.001$), and there was a significant interaction effect between village and items bought (Wald = 37.30; df = 14; $p = 0.001$). Meat, poultry, and eggs made up around 30% of food expenditure in both villages, followed by cereals and cereal products, and fish and seafood (Fig. 3). These 3 food groups together made up over 60% of food expenditure in both villages. However, BF households spent more money on high-sugar foods (beverages, soft drinks, preserves, and sugar or syrup) and on milk or milk products, fruits, vegetables, and vegetable products (Fig. 3). Overall, households with higher income spent significantly more on domestic meats and fish (adjusted $R^2 = 0.\ 36$, df $= 18$, $p = 0.004$).

Bushmeat Offtake

We gathered offtake data on 51 hunters (gun hunters and/or trappers) of the 88 adult males (>16 years) in the 2 villages. Of the 44 BF hunters 26 used shotguns. Of these, 6 owned their weapons, all others either hired or borrowed them. No gun hunting was observed in BB during the study period. All hunted species in BB were snared, except reptiles, which were killed with a machete.

We recorded 4186 animals hunted in BF (4147 carcasses of 9 mammals, 33 carcasses of 2 birds, 6 carcasses of 2 reptiles) and 529 animals hunted in BB (505 carcasses of 4 mammals and 24 carcasses of 2 reptiles) (Table 2). The blue duiker made up 88% of all animals observed in BF, whereas the giant pouched rat (*Cricetomys emini*) predominated (62%) in BB (Table 2). For all species, the proportion of adult animals harvested was high, and <7% were juveniles (Table 2). Three largely arboreal species (2 primates, the russet-eared guenon and Preussi's guenon, and 1 bird, the Blue Plantain Eater [*Corythaeola cristata*]) were harvested with guns. Squirrels and the black colobus were primarily shot; only a small proportion (<2%) were snared. By contrast, 4 terrestrial species (Ogilby's duiker, brush-tailed porcupine, giant pouched rat, and tree hyrax [*Dendrohyrax dorsalis*]) were almost exclusively snared. The blue duiker was harvested in almost equal proportions with snares and guns.

The average number of animals and biomass traded per day was significantly higher in BF than in BB, but mean body mass and total biomass harvested did not differ between villages (Table 3). Mean number of animals

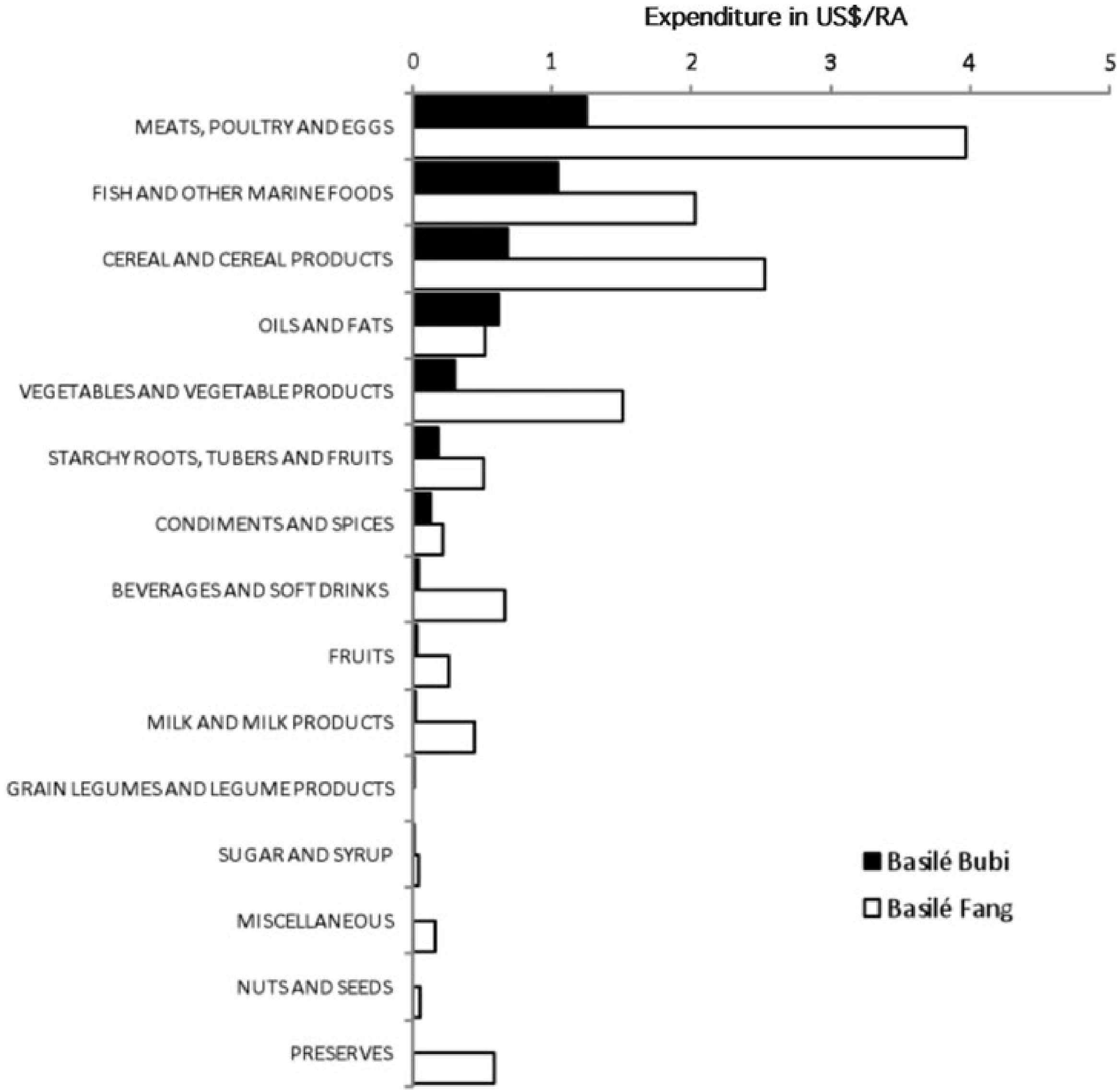

Figure 3. Distribution of expenditure per reference adult (RA) (defined in legend of Fig. 2) in Basilé Fang and Basilé Bubi, Bioko Island, on food in 14 groups (Oguntona & Akinyele 1995) (CFA, Central African francs).

harvested and the biomass extracted per hunter per year were significantly higher in BF than in BB (Table 3). The estimated annual offtake was 3650 and 482 animals in BF and BB, respectively. On average, BF hunters took fewer hunting trips in a year than hunters in BB (Table 3). However, hunting trips in BF were longer (1–7 d), whereas they were 1 d in BB.

We found that the proportion of animals shot during the wet season was lower (44.69% [SE 4.57], $n = 9$) than during the dry season (52.08% [SE 5.66], $n = 7$), although not significant. However, there were also no significant seasonal differences in the number of animals hunted per hunter trip in BF (dry: 2.81 [SE 0.13] animals/hunter trip, $n = 69$; wet: 2.75 [SE 0.07] animals/hunter trip, $n = 250$; Mann-Whitey U, $Z = -0.55$, $p = 0.59$). In BB, by contrast, significantly more animals were trapped during the dry season than during the wet season (dry: 6.00 [SE 0.41] animals/hunter trip, $n = 27$; wet: 3.26 [SE 0.20] animals/hunter trip, $n = 87$; $Z = -5.33$, $p < 0.001$).

Discussion

Subsistence and commercial bushmeat hunters obtain a product from nature that provides not only a source of protein but also income, and consumers are willing to pay a higher price for bushmeat than domestic meats (Chardonnet et al. 1995; Trefon 1998). The implications of protein intake of households that participate in subsistence or commercial hunting have been little

Table 2. Body mass, sale price, and offtake levels of species hunted in Basilé Fang and Basilé Bubi villages, Bioko Island, Equatorial Guinea.

			Offtake variables per species per village													
			Basilé Fang							*Basilé Bubi*						
Group (species)	*Mean body mass (kg)* (n, *SE*)	*Mean price (US$)* (n, *SE*)	n	*adult[a] ratio*	*sample days[b]*	*proportion sample days[c]*	*days/ year[d]*	*animals harvested /year*	*biomass harvested (kg)/year*	n	*adult ratio*	*sample days*	*proportion sample days*	*days/ year*	*animals harvested /year*	*biomass harvested (kg)/year*
Birds																
Blue Plantain Eater (*Corythaeola cristata*)	1.16 (11, 0.06)	11.57 (32, 0.89)	32	0.93	16	0.05	18.02	36.05	41.82	–	–	–	–	–	–	–
Palm Nut Vulture (*Gypohierax angolensis[e]*)	1.6 (1, 0.00)	6.88 (1, 0.00)	1	–	1	0.003	1.13	1.13	1.92	–	–	–	–	–	–	–
Reptiles																
snakes (*Bitis* and *Naja* spp.)[f]	1 (4, 0.05)	–	1	–	60	0.19	67.59	67.59	805.03	24	–	9	0.08	28.81	28.81	28.81
python (*Python sebae*)	–	21.29 (2, 1.64)	3	–	3	0.01	3.38	3.38	6.76	–	–	3	0.03	9.61	9.61	9.61
Hyrax																
tree hyrax (*Dendrohyrax dorsalis*)	2.61 (3, 0.23)	15.92 (10, 1.93)	10	0.9	10	0.03	11.27	11.27	29.4	–	–	–	–	–	–	–
Pangolin																
African white-bellied pangolin (*Phataginus tricuspis*)	1.80 (2, 0.22)	–			3	0.01	3.38	3.38	6.08	–	–	–	–	–	–	–
Primates																
Preuss's guenon (*Allochrocebus preussi*)[g]	4.5	28.50 (2, 4.91)	3		3	0.01	3.38	3.38	15.21	–	–	–	–	–	–	–
russet-eared guenon (*Cercopithecus erythrotis*)	6.20 (16, 0.52)	30.44 (45, 1.16)	52	0.81	3	0.01	3.38	3.38	20.95	–	–	–	–	–	–	–
black colobus (*Colobus satanas*)	10.23 (26, 0.47)	29.48 (19, 1.84)	20	1	15	0.05	16.9	16.9	172.87	–	–	–	–	–	–	–
Rodents																
brush-tailed porcupine (*Atherurus africanus*)	3.01 (17, 0.13)	39.64 (100, 0.70)	107	0.97	67	0.21	75.48	75.48	227.19	1	–	1	0.01	3.2	3.2	9.64
forest giant pouched rat (*Cricetomys emini*)	1.99 (30, 0.09)	9.48 (207, 0.31)	222	0.85	76	0.23	85.62	171.23	340.76	157	0.8	69	0.61	220.92	441.84	879.27
squirrels (*Scuiridae[h]*)	1.18 (12, 0.04)	7.95 (124, 0.19)	127	0.88	23	0.07	25.91	77.73	91.72	30	0.8	23	0.2	73.64	73.64	86.9
Ungulates																
Ogilby's duiker (*Cephalophus ogilbyi*)	11.91 (26, 0.49)	59.53 (101, 1.32)	106	0.81	31	0.1	34.92	34.92	216.52	–	–	–	–	–	–	–
blue duiker (*Philantomba monticola*)	3.65 (116, 0.05)	23.05 (3300, 0.04)	3,464	0.94	292	0.9	328.95	3289.5	12006.7	26	0.8	22	0.19	70.44	70.44	257.1

[a] *Adult ratio refers to the proportion of sexually mature individuals in the sample.*
[b] *Actual number of days during which the species was recorded.*
[c] *Proportion of days the species appeared out of the 327 d sampled during the study.*
[d] *Estimated number of days in a year during which the species was expected to appear in Basilé Fang village.*
[e] *Body mass from Dunning (2008).*
[f] *Snakes such as the forest cobra (*Naja melanoleuca*), Rhinoceros viper (*Bitis nasicornis*), and rhinoceros horned viper (*Bitis nasicornis*).*
[g] *Body mass from Butynski et al. (2009).*
[h] *Mostly the larger African giant squirrel (*Protoxerus stangeri*) but also scaly-tailed squirrels (*Anomalurus spp.*).*

Table 3. Mean (SE) of species harvested, hunting activity, and offtake in Basilé Fang and Basilé Bubi, Bioko Island, Equatorial Guinea.

Variables	*Basilé Fang*	*Basilé Bubi*	*Test* (p)*
Animals traded/day	12.94 (0.54)	4.64 (0.28)	$Z = -10.919$ (0.001)
Biomass harvested/day (kg)	47.48 (2.04)	4.12 (0.47)	$Z = -13.445$ (0.001)
Mean body mass of harvested animals (kg)	3.59 (0.79)	1.64 (0.34)	$F_{(1,25)} = 2.962$ (0.098)
Total biomass harvested /year (kg)	910.58 (737.22)	52.19 (34.06)	$Z = -1.267$ (0.205)
Hunting trips/year	13.22 (2.60)	67.56 (7.03)	$Z = -3.974$ (0.001)
Offtake/hunter/ year	91.00 (19.64)	190.23 (21.56)	$Z = -2.616$ (0.007) **
Biomass of offtake/hunter/year	366.67 (79.98)	70.99 (12.18)	$Z = -1.446$ (0.155)

The* Z *values are derived from Mann-Whitney* U *tests and the* F *value from an analysis of variance (p < 0.05; ***p < 0.0001).*

reported. We postulated that because commercial hunters have greater access to wild meat and generate more income from the sale of bushmeat, the average protein intake per person for these commercial-hunter households would be higher than in subsistence-hunter households. We found no significant differences in overall protein intake between commercial- and subsistence-hunter households.

Bushmeat was not a noteworthy protein source in either village. This may indicate that protein security is possible in subsistence- and commercial-hunting settings. In both study villages, primarily smaller-bodied more productive species were hunted, namely the blue duiker and large rodents. Commercial hunters harvest larger species, and this could lead to the extinction of these species (particularly primates and Ogilbyi's duikers) if their offtake remains high, as has been observed in other localities (e.g., Ghana [Cowlishaw et al. 2005]). Primates hunted in our study area and elsewhere on the island are endemic subspecies and are threatened with extinction on the island (Hearn & Morra 2001, 2006). That these primates still occur in the area is good news; some authors claim that some of these species have been extirpated (Hearn & Morra 2006).

Despite an official ban since 2007, monkeys were hunted by BF hunters because only BF hunters owned guns, which are essential for pursuing diurnal primates and large duikers (Kümpel et al. 2010). Income from hunting monkeys is only a small proportion of BF hunters' earnings given that 22 of the 44 BF hunters shot monkeys during the study. Moreover, only 2 hunters would have >50% of their annual incomes affected if primates were not hunted. Hunters would need to be persuaded that their income would not be seriously affected by concentrating on smaller and more abundant species. Moreover, smaller species and core elements of the bushmeat trade throughout the Congo Basin can withstand high offtake levels.

There were large differences in wealth, income, and expenditure between villages, BF were households substantially better off than households in BB. This difference was a direct result of commercial hunting income in BF; on average commercial BF hunters earned $1,868/year (around 33% of the household income; range $14 to $13,500/year). These hunting-revenue figures were much higher than the average $545 recorded for hunters in Rio Muni (Kümpel et al. 2010). In Gabon hunting incomes range from 15% to 72% of the total household income (Starkey 2004), and hunting incomes in villages in Cameroon are well above the national average (Gally & Jeanmart 1996). By contrast, BB hunters derived most of their revenue from salaried work.

The average amount of total protein consumed by inhabitants of both villages, 120–140 $g \cdot RA^{-1} \cdot d^{-1}$, is above sub-Saharan averages and over the recommended amount of 52 g/d to meet dietary needs (Fa et al. 2003). We estimated bushmeat consumption of 10–20 $g \cdot RA^{-1} \cdot d^{-1}$ in both villages. These amounts are within the lower end of the spectrum of reported amounts of bushmeat protein consumed in other parts of West and Central Africa. Cowlishaw et al. (2005) reported consumption of 33 $g \cdot person^{-1} \cdot d^{-1}$ in rural communities and 44 $g \cdot person^{-1} \cdot d^{-1}$ in urban areas in Ghana. Wilkie and Carpenter (1999) for Central Africa and Starkey (2004) for Gabon calculated bushmeat consumption of 130 $g \cdot person^{-1} \cdot d^{-1}$ and 268 $g \cdot AME^{-1} \cdot d^{-1}$, respectively. We found a clear relation between wealth and protein consumption for both villages pooled. The correlation was curvilinear between protein consumption and wealth, indicating that consumption rises dramatically after a threshold income of $480 /year is reached. That wealth is correlated with wildlife consumption is not new (Brashares et al. 2011). But, the higher consumption of frozen meats and fish and of high-sugar foods and drinks in the wealthier BF households may point to the nutrition-transition phenomenon already taking place in low-income and middle-income countries (Popkin & Gordon-Larsen 2004). Moreover, there were only 4 families in BF and 1 in BB that ate outside the home; in both villages around 5% of all meals recorded. We considered the effect of meals consumed outside the home on our protein-consumption estimates was minimal.

Because our villagers had easy access to imported animal products, livestock, and fish, our findings are unlike any other studies conducted in rural areas in West or Central Africa, although our results are similar to those of studies conducted in urban areas (Albrechtsen et al.

2006). Fish was by far the most important supply of animal protein in both villages. Protein consumption of fish was 53% of protein intake in BB and 31% of protein consumption in BF. This dependence on fish as a main source of protein was not unexpected because fish is 22% of protein intake in sub-Saharan Africa (FAO 2011). This level of fish consumption, however, can exceed 50% in the poorest countries (especially where other sources of animal protein are scarce or expensive). In West African coastal countries, for instance, where fish has been a central element in local economies for many centuries, the proportion of dietary protein that comes from fish is high (World Fish Center 2004). This is the case for Equatorial Guinea (East et al. 2005; Fa et al. 2009).

In BB food production in home gardens was substantially higher and expenditure on food was less than in BF. The lack of home gardens in BF was reflected by their higher expenditure on fruits, vegetables, and vegetable products in comparison with BB. Animal production was not high in either village. This is likely related to economic bottlenecks (e.g., high costs of start up, feed, and veterinary care) and lack of technical expertise. Subsistence agriculture was a major contributor to overall household production in BB, but it contributed little to household income. This may be less true in villages in the more populous areas of the country, where wildlife is depleted and agriculture plays a larger role in livelihoods (Allebone-Webb 2009).

There is a case for the development of a well-regulated bushmeat industry that is linked to good governance of broader forest resources at the country level. An essential prerequisite of this is to clearly identify possibilities for legal and legitimate trade in bushmeat (Nasi et al. 2008). At the same time, stopping hunting of threatened species, which do not provide a significant proportion of bushmeat income or biomass, should be an urgent concern. These species should be protected through law enforcement and by raising awareness of hunters and consumers. In Bioko the ban on primate hunting is important to enforce adequately as suggested by Hearn and Morra (2006), although regulating the trade of large rodents and blue duiker may have more positive repercussions than the imposition of measures aimed only at primates. Adequate management of the protected areas on the island remains a fundamental task because these contain source populations for many nonthreatened taxa and are essential refugia for larger threatened species. Local wildlife management and planning for economic development and food security can gain much from considering what motivates hunters. Our comparison of a village dedicated to subsistence hunting with a village dedicated to commercial hunting revealed much about the dynamics of each system and can contribute to the development of better tools for natural resource governance and long-term sustainability of bushmeat hunting.

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Supporting Information

Estimated bushmeat offtake and income for hunters (Appendix S1) and protein consumption in sampled households (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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