Association of Body Mass with Price of Bushmeat in Nigeria and Cameroon

Article *in* Conservation Biology · October 2011

DOI: 10.1111/j.1523-1739.2011.01741.x · Source: PubMed

8 authors, including:

David Macdonald
University of Oxford
1,517 PUBLICATIONS **72,418** CITATIONS
SEE PROFILE

Paul J. Johnson
University of Oxford
192 PUBLICATIONS **6,623** CITATIONS
SEE PROFILE

Lise Albrechtsen
Norwegian Ministry of Foreign Affairs
15 PUBLICATIONS **793** CITATIONS
SEE PROFILE

Adam Dutton
Office for National Statistics
15 PUBLICATIONS **409** CITATIONS
SEE PROFILE

Conservation Biology

Contributed Paper

Association of Body Mass with Price of Bushmeat in Nigeria and Cameroon

DAVID W. MACDONALD,* PAUL J. JOHNSON,† LISE ALBRECHTSEN,* ADAM DUTTON,* SARAH SEYMOUR,† JEF DUPAIN,‡,§ AMY HALL,† AND JOHN E. FA†

*Wildlife Conservation Research Unit (WildCRU), Zoology Department, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon OX13 5 QL, United Kingdom

†Durrell Wildlife Conservation Trust, Les Augrès Manor, Trinity, Jersey JE3 5BP, United Kingdom, and ICCS, Division of Biology, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, United Kingdom

‡Centre for Research and Conservation, Royal Zoological Society of Antwerp, Koningin, Astridplein 26, 2018 Antwerp, Belgium

Abstract: *Spatially extensive patterns of bushmeat extraction (and the processes underlying these patterns) have not been explored. We used data from a large sample (*n = 87*) of bushmeat trading points in urban and rural localities in Nigeria and Cameroon to explore extraction patterns at a regional level. In 7,594 sample days, we observed 61,267 transactions involving whole carcasses. Rural and urban trading points differed in species for sale and in meat condition (fresh or smoked). Carcass price was principally associated with body mass, with little evidence that taxonomic group (primate, rodent, ungulate, or mammalian carnivore) affected price. Moreover, meat condition was not consistently associated with price. However, some individual species were more expensive throughout the region than would be expected for their size. Prices were weakly positively correlated with human settlement size and were highest in urban areas. Supply did not increase proportionally as human settlement size increased, such that per capita supply was significantly lower in urban centers than in rural areas. Policy options, including banning hunting of more vulnerable species (those that have low reproductive rates), may help to conserve some species consumed as bushmeat because carcass prices indicate that faster breeding, and therefore the more sustainable species, may be substituted and readily accepted by consumers.*

Keywords: bushmeat, conservation planning, mammals, trade, West Africa

Asociación de la Masa Corporal con el Precio de Carne Silvestre en Nigeria y Camerún

Resumen: *Los patrones espacialmente extensivos de extracción de carne silvestre (y los procesos relacionados con esos patrones) no han sido explorados. Utilizamos datos de una muestra grande (*n = 87*) de puntos de venta de carne silvestre en localidades urbanas y rurales en Nigeria y Camerún para explorar los patrones de extracción a nivel regional. En 7,594 días de muestreo observamos 61,267 transacciones involucrando cuerpos completos. Los puntos de venta rurales y urbanos difirieron en especies en venta y condición de la carne (fresca o ahumada). El precio del cuerpo se asoció principalmente con la masa corporal, con poca evidencia de que el grupo taxonómico (primate, roedor, ungulado o mamífero carnívoro) afectara el precio. Mas aun, la condición de la carne no se asoció consistentemente con el precio. Sin embargo, algunas especies individuales en la región fueron más caras de lo esperado por su tamaño. Los precios se correlacionaron positiva y débilmente con el tamaño del asentamiento humano y fueron más altos en áreas urbanas. La oferta no incrementó proporcionalmente a medida que incrementó el tamaño del asentamiento, tanto que la oferta per cápita fue significativamente menor en centros urbanos que en áreas urbanas. Opciones de políticas, incluyendo la prohibición de la caza de especies más vulnerables (aquellas que tienen bajas tasas reproductivas), pueden ayudar a conservar algunas especies consumidas como carne silvestre porque los pre-*

§¶ *email david.macdonald@zoo.ox.ac.uk Current Address: African Wildlife Foundation Conservation Centre, Ngong Road, Karen, P.O. Box 310, Code 00502 Nairobi, Kenya*

Paper submitted January 14, 2011; revised manuscript accepted April 12, 2011.

DOI: 10.1111/j.1523-1739.2011.01741.x

cios indican que especies de reproducción más rápida, y por lo tanto más sustentables, pueden ser sustituidas y aceptadas de buena gana por los consumidores.

Palabras Clave: África Occidental, carne silvestre, comercio, mamíferos, planificación de la conservación

Introduction

The number of wild animals killed for human consumption (i.e., bushmeat) is thought to be escalating in Central and West Africa, and at current levels of offtake may threaten the persistence of many species (Fa & Brown 2009). The rise in bushmeat consumption has been brought about by increased commercial hunting, which is associated with increased access to remote forests via logging roads (Wilkie et al. 2000) and to modern weapons (Bowen-Jones & Pendry 1999). At the same time, low incomes and lack of alternative sources of income are an impetus for hunters to sell bushmeat directly to nonlocal consumers or to others who sell it at distant, urban markets (Wilkie et al. 2000; Wilkie & Godoy 2001; Wilkie et al. 2005).

Counts of carcasses in bushmeat markets or at other trading points (i.e., bushmeat concentration points), which are found in almost every town and village in many parts of Africa, can be used to understand patterns of bushmeat consumption (Juste et al. 1995; Fa et al. 2000). These concentration points are part of a commodity chain in which bushmeat is a commodity and its harvest a commercial activity (Caspary 1999). Extraction of bushmeat persists because the actors in the trade benefit from it (Cowlishaw et al. 2005). Understanding mechanisms that influence the behavior of the different actors can help inform policies that can achieve a balance between supply and demand.

Food markets in the developing world may be structurally different from those in developed nations (Scarborough & Kydd 1992), but the same general principles of supply and demand are expected to prevail, whereby price is inversely related to supply. Price is also likely to be influenced by the availability of alternatives, by the preferences of customers, and by the flow of information among and within markets. For instance, price may not fluctuate as a function of availability of a particular type of meat if traders are unsure of how much is available to them or to other traders or if their knowledge of prices of this meat or alternatives offered by other traders is incomplete (Timmer 1987).

In bushmeat markets, as in others markets, scarcity increases prices, slows consumption, and encourages substitution with alternative products (Albrechtsen et al. 2007). Variation in demand for different types of bushmeat affects the potential success of policy options. For example, if all species were equally preferred by consumers, it might be possible to discourage hunting of endangered species and encourage hunting of species that are more likely to be harvested sustainably.

Few data are available on factors that affect bushmeat demand and supply in Central and West Africa. A number of studies have been conducted on bushmeat use and how use is influenced by consumer income. In Gabon, Wilkie et al. (2005) showed that bushmeat consumption is higher among wealthy households than poorer households. They also observed that bushmeat consumption falls as its price increases, whereas fish consumption rises as the price of bushmeat increases. They interpreted these data as evidence that bushmeat and fish are dietary substitutes. In Rio Muni, Equatorial Guinea, the association between wealth and bushmeat consumption is confined to urban areas and does not affect the type of meat eaten (Fa et al. 2009). The rarity of a species does not necessarily confer status as a luxury good (East et al. 2005).

Preference for meats of certain species on the basis of taste has been reported in West and Central Africa. In Congo, for example, frugivorous guenons (*Cercopithecus* spp.) are considered tasty (Butynski 2002), and rodents (including brush-tailed porcupine [*Atherurusa fricanus*]) are preferred to duikers (Anadu et al. 1988). Ethnic differences in bushmeat consumption and preferences also exist (Fa et al. 2002). Nonetheless, the results of most studies in African moist forests do not support the idea that hunters' pursuit of particular species is motivated by consumer preference, as has been shown for some Neotropical hunters (Koster et al. 2010). This may be because most hunters in African moist forests use wire snares and other indiscriminate trapping methods, which is not the case in the Neotropics (Fa & Peres 2001). Nonetheless, the species that are hunted and that are on sale in markets may differ because larger species are more often traded and smaller species tend to be eaten by the hunters or sold locally (Cowlishaw et al. 2005; Davies et al. 2007; Allebone-Webb et al. 2011). Despite this difference, demand for bushmeat may relate more to human settlement size than to species being supplied. If this is the case, as urban centers increase in size (highest urbanization rates are in Africa), hunting pressure on bushmeat species could rise proportionately (Bowen-Jones & Pendry 1999).

We quantified the supply of bushmeat across space within an area of high species richness in West Africa – the Cross-Sanaga region between Nigeria and Cameroon. Previous studies of the bushmeat trade have been geographically limited and offer only an incomplete understanding of bushmeat trade at a landscape scale. We ex-

amined the composition of bushmeat species supplied to urban and rural areas and whether composition varied as a function of human settlement size. We also explored whether prices were affected by type and size of species traded, by variation in their supply to the markets, and whether these patterns differed between rural and urban settlements. Our results may help shape future policies and programs aimed at promoting sustainable use of wild animals in the bushmeat trade.

Methods

Study Area

The border region between Nigeria and Cameroon, between the Cross and Sanaga rivers (Fig. 1), is approximately 35,324 km^2 (10,795 km^2 in eastern Nigeria and 24,529 km^2 in western Cameroon), most of which is covered by humid tropical forest (rainfall 2000–3000 mm/year). Humidity is high throughout the year and temperatures range from 15 °C to 33 °C. The wet season lasts from April to October.

Although the rate of forest loss has been high in the region (annual loss of approximately 2.6% in 1999 and 2000) (World Bank 2004), large areas of primary rainforest remain. The region is known for populations of endemic subspecies such as lowland gorillas (*Gorilla gorilla diehli*), chimpanzees (*Pan troglodytes vellerosus*), drills (*Mandrillusl eucophaeus*), and forest elephants (*Loxodonta cyclotis*) (Oates 1999). The Cross River National Park covers 3586 km^2 in Nigeria, and the Korup National Park in Cameroon is 1256 km^2. We estimate that approximately 5,200,000 people lived within the study area at the time of sampling (1,300,000 in Nigeria and 3,900,000 in Cameroon). We based these population estimates on the methodology described in Fa et al. (2006). The majority of inhabitants are concentrated around the cities of Calabar in Nigeria and Douala in Cameroon. In Nigeria 33% of the study area's population live in Calabar (>500,000), and in Cameroon 37% live in Douala (>3 million) (Fa et al. 2006).

Data Collection

Bushmeat is traded in practically all rural settlements and urban centers in the study area. We surveyed markets and other types of bushmeat-trading points within these settlements and centers. We considered a bushmeat market an area within a city or village in which stalls were

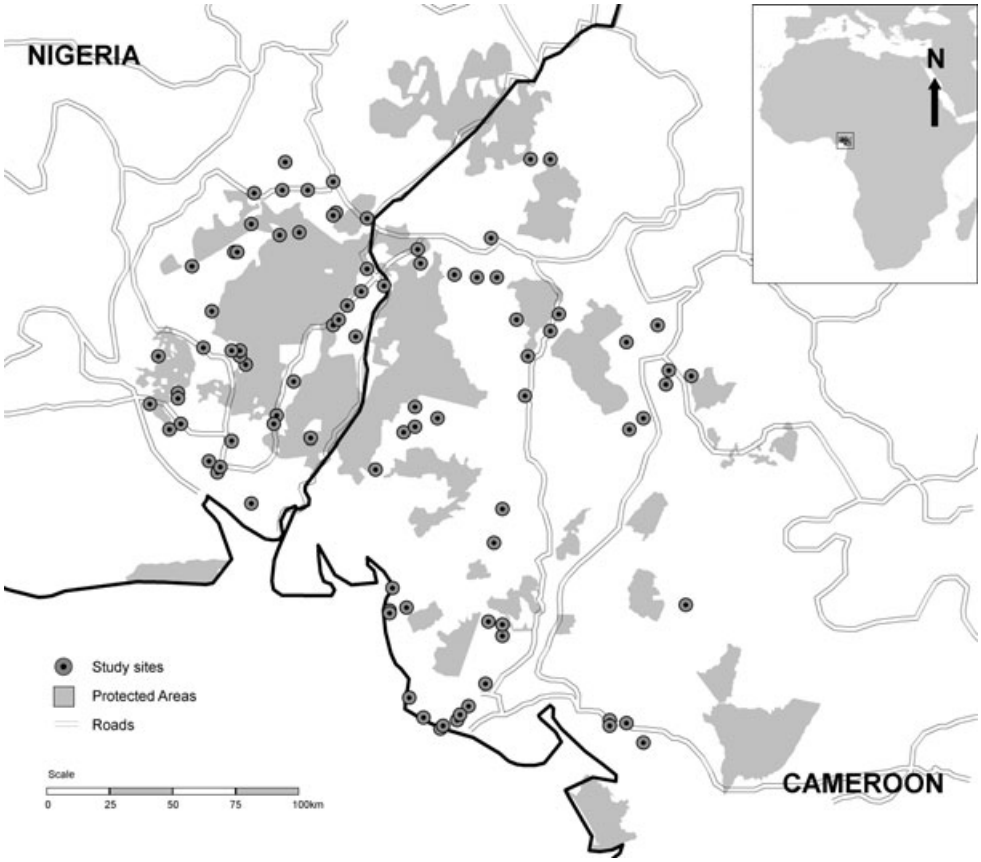

Figure 1. Location of the trading points where bushmeat carcasses were sampled and of protected areas and principal roads.

routinely laid out to display carcasses on sale to the public. Other trading points included known sellers' houses or places in villages where hunters deposited meat.

We visited over 100 rural settlements throughout the study area before the start of data collection. We chose sites that represented the main vegetation types (e.g., undisturbed primary forest, secondary forest, montane vegetation) and a gradient of human population densities. We selected 87 of these settlements for study (Nigeria 41 and Cameroon 46). Failure to find suitable assistants prevented use of the other settlements. Between August 2002 and January 2003, we gathered data in the rural settlements and from the main bushmeat markets in Calabar, Nigeria, and Douala, Cameroon. Estimated human settlement sizes around trading points at the time of sampling are in (Fa et al. 2006).

We grouped settlements into 6 clusters. Twelve teams (5 teams in Cameroon and 7 in Nigeria) were assigned to each settlement cluster. Each team was led by a research assistant, who recruited, paid, and monitored 4–9 local reporters (i.e., people who lived in or near to the settlement cluster). Research assistants were trained and managed by S.S. in Nigeria and by J.D. in Cameroon, who also assembled and ensured the information collected was correctly entered onto standardized datasheets. We sampled each of the 87 sites an average of 142.3 days (SD 5.0) (range 29-148) in Nigeria and 152.2 days (1.40) (range 100–167 days) in Cameroon for a total of 7594 site days (4936 in Nigeria and 2658 in Cameroon).

At each sampling site, local reporters recorded the identity of the vendor, species at the trading point, and condition of the meat (smoked or fresh). So few animals were alive that we did not include them in our analyses. Reporters also recorded the sale price (in Nigerian nira or Cameroonian cefa francs) for all carcasses. Carcasses could not always be identified to species, for example, because the carcass had been prepared for consumption. In both countries, monkeys in the genus *Cercopithecus* were frequently not identified to species. Thus, we grouped these carcasses by genus. Body masses of bushmeat species are from Fa and Purvis (1997).

Data Analyses

We used SAS software to analyze data (Littell et al. 1996). We converted sale prices to June 2002 U.S. dollar values (World Bank 2004). We derived a hedonic price function (Neshiem 2008) to estimate the strength of association between each covariate and carcass value. The application of this method in economics is based on the assumption that the price of a product can be explained by the product's characteristics. For example Mishili et al. (2009), used a hedonic price function to evaluate how the market value of a West African grain crop is affected by variation in the size, color, and texture of the grains.

For analyses of the composition of bushmeat at market, we considered only rodents, ungulates, primates, carnivores, and pangolins because other taxa were represented by very few carcasses (Table 1). We applied likelihood-ratio chi-squared tests to contingency tables.

For our price analyses, we used general linear modeling (GLM) with carcass price (log-transformed) as the response and country, taxon, location (urban or rural), and condition (smoked or fresh) as categorical covariates. In these analyses, taxon was a categorical covariate in which the categories were species (or genus) for which carcasses dominated the markets in each country (those that together composed > 90% of the total). An initial analysis identified country as a categorical covariate with 2 levels (Cameroon, Nigeria). For the analysis including country, we used data for only the 3 taxa that were very common in both countries (brush-tailed porcupine,

Table 1. The numbers and percentages of whole carcasses in different taxonomic groups traded in rural and urban markets in Cameroon and Nigeria.

	Cameroon				*Nigeria*			
	rural		*urban*		*rural*		*urban*	
Taxonomic group	n	%	n	%	n	%	n	%
Birds	20	0.2	64	0.3	81	0.3	0	0.0
Bats	5	0.0	0	0.0	43	0.2	0	0.0
Mammalian carnivores	555	4.7	381	1.9	1,694	6.3	21	0.9
Hyraxes	23	0.2	6	0.0	24	0.1	0	0.0
Pangolins	692	5.8	1,188	6.0	586	2.2	0	0.0
Primates	2,094	17.6	3,985	20.0	3,173	11.8	440	18.4
Rodents	3,362	28.2	7,663	38.4	12,751	47.2	1,130	47.2
Manatee	0	0.0	1	0.0	1	0.0	0	0.0
Ungulates	4,883	40.9	4,050	20.3	7,642	28.3	779	32.6
Reptiles	290	2.4	2,601	13.0	1,025	3.8	23	1.0
Snails	0	0.0	0	0.9	5	0.0	0	0.0
Total	11,924		19,939		27,011		2,393	

blue duiker [*Cephalophus monticola*], and *Cercopithecus* spp.). The term trading point nested in country was used as the denominator for the country F ratio (individual trading point was the correct unit of replication for comparing countries). When statistical interactions that included country were significant, we carried out separate analyses for each country (including those taxa comprising 90% of total carcasses for each country).

To quantify whether taxon was a reliable surrogate for body mass we also fit GLMs that predicted mean price for each taxon (regardless of condition) as a function of the taxon's body mass. We also explored whether taxonomic group explained substantial additional variance in a prediction of price on the basis of body size. For this latter analysis, we considered only the subset of taxa in the groups ungulate, rodent, mammalian carnivore, and primate (the number of taxa in other groups was too small). To explore regional consistency in pricing patterns, we compared deviations from the price–mass relation across different sectors of the region by comparing residuals from the price–mass relation. We compared the residuals between rural and urban Nigeria and Cameroon.

To explore the effect of condition further, we examined differences between mean carcass price for each taxon at only those trading points where the taxon occurred in both conditions; this ensured that any observed difference would be associated with condition alone, and not, for example, an effect of spatial variation in the occurrence of the condition type.

For the analysis of the effect of human settlement size, we determined the total biomass of bushmeat traded per day per inhabitant of the settlement associated with the trading point. Both this variable and settlement size were log transformed to linearize the relation and to meet the assumptions of GLM models.

Results

Urban and Rural Market Composition

In Nigeria 95.8% and 99.03% of carcasses (total n = 29,404) in rural and urban markets, respectively, were mammals. Almost half of these were rodents; ungulates and primates comprised the majority of the rest of the carcasses (Table 1). Taxonomic composition differed significantly between rural and urban markets (χ^2 = 462.2, df = 5, $p < 0.001$ for H_o of similar composition.) Compared with rural markets, urban markets offered a higher percentage of primates and a lower percentage of carnivores.

Cameroonian markets were also dominated by mammal carcasses (total n = 31,683; rural, 97.5%; urban 86.5%), and composition of carcasses differed significantly between rural and urban markets (χ^2 = 2305.2, df = 5, $p < 0.001$ for H_o of similar composition). Rodents comprised the highest percentage of carcasses in urban markets. Ungulates were relatively less abundant in urban markets. In Nigeria the proportion of mammalian carnivores was lower in urban markets.

Carcass condition varied considerably between rural and urban markets (Table 2). In Cameroon the percentage of fresh carcasses of pangolins, primates, ungulates, and reptiles was significantly higher in urban than in rural markets ($\chi^2 \geq 4.4$, df = 1, $p \leq 0.05$). The condition effect was more marked in Nigeria, where fresh carcasses of all taxonomic groups were much less common in urban markets ($\chi^2 \geq 25.2$, df = 1, $p \leq 0.001$; Table 2).

Few animals were sold alive in either country. In rural markets in Cameroon, 0.15% (n = 17) of whole carcasses were sold alive. Most of these were primates (8 drills, 2 gorillas, and 2 chimpanzees). The others were varanid lizards (n = 3) and 2 species of ungulates (*Cephalophus*). In urban markets, the proportion of live animals was greater (0.80%, n = 163) and the proportion of primates was lower than in rural markets (1.84%, n = 3, *Cercopithecus* spp.). Reptiles represented 84.7% of live items (n = 138). No live carcasses were recorded in Nigerian urban markets, and only 5 live animals (0.02%; 2 birds, 2 blue duikers, 1 pangolin) were recorded in rural markets.

In rural Nigerian markets, the 4 taxa with greatest relative abundances were brush-tailed porcupine (34.6%, n = 9333), blue duiker (18.4%, n = 4970), grasscutter

Table 2. Percentage of fresh bushmeat in different taxonomic groups sold in rural and urban markets.*

	Cameroon				*Nigeria*			
	rural		*urban*		*rural*		*urban*	
Taxonomic group	*fresh %*	n	*fresh %*	n	*fresh %*	n	*fresh %*	n
Mammalian carnivores	73.5	554	69.0	381	76.1	1537	28.6	21
Pangolins	53.0	691	93.3	1188	53.8	586	–	0
Primates	37.5	2075	46.5	3980	25.0	3173	7.7	440
Rodents	54.7	3362	52.7	7662	49.9	12751	11.7	1130
Ungulates	36.9	4037	47.6	4399	39.5	7642	7.6	779
Reptiles	54.1	491	94.5	2601	88.0	1025	0.0	23

**The* n *values are the total numbers of carcasses recorded for each taxonomic group (i.e., fresh and smoked carcasses). If* n *is less than n in Table 1, this means whether the meat was fresh or smoked was not recorded.*

Table 3. Prices per carcass* (in 2002 U.S. dollars) of taxa that represented more than 90% of carcasses in markets in each country.

Species (taxonomic group, mean body mass [kg])	*Location*	*Nigeria*				*Cameroon*			
		mean (SE)	n	*minimum*	*maximum*	*mean (SE)*	n	*minimum*	*maximum*
Atherurus africanus	rural	6.05 (0.02)	9341	0.38	22.56	6.64 (0.04)	2660	1.19	15.80
(rodent, 2.9)	urban	11.48 (0.09)	1018	0.75	22.56	10.33 (0.06)	4871	0.59	25.69
Cephalophus dorsalis	rural	11.58 (0.14)	1519	1.35	43.63	13.39 (0.63)	78	3.95	23.71
(ungulate,17.9)	urban	13.63 (1.30)	55	1.50	33.85	17.66 (1.14)	20	8.89	29.64
Cephalophus monticola	rural	5.67 (0.04)	4980	0.75	31.59	6.70 (0.04)	3461	0.99	15.81
(ungulate, 3.9)	urban	12.04 (0.13)	710	1.50	26.33	5.67 (0.04)	3238	1.98	19.97
Cephalophus spp	rural	11.57 (1.65)	16	4.51	26.33	8.86 (0.20)	493	2.57	31.61
(ungulate)	urban	–	–	–	–	28.75 (0.31)	515	2.77	39.52
Cercopithecus spp	rural	5.92 (0.07)	2582	0.75	45.31	7.24 (0.07)	1583	0.79	23.71
(primate, 3.9)	urban	11.72 (0.11)	500	4.89	23.32	11.81 (0.09)	2776	0.79	88.91
Cricetomys emini	rural	2.31 (0.06)	901	0.38	15.04	1.30 (0.11)	57	0.59	4.94
(rodent 1.95)	urban	9.21 (0.43)	45	2.26	13.54	2.46 (0.02)	2099	0.40	4.94
Manis spp	rural	3.44 (0.07)	584	0.53	11.28	4.93 (0.07)	691	0.40	17.78
(pangolin, 2.3)	urban	–	–	–	–	9.48 (0.08)	1193	0.99	20.75
Osteolaemus tetraspis	rural	9.18 (1.15)	10	5.27	15.04	9.58 (0.31)	171	0.49	35.57
(reptile, 10.0)	urban	8.84 (0.91)	24	2.63	18.80	25.17 (0.39)	922	1.98	98.79
Thryonomys swinderianus	rural	6.48 (0.06)	2424	0.15	22.56	6.93 (0.07)	644	0.40	16.79
(rodent, 5.05)	urban	13.47 (0.38)	70	1.28	20.31	10.46 (0.13)	667	0.79	17.78
Varanus niloticus	rural	4.66 (0.11)	473	0.75	18.80	9.77 (0.30)	91	3.95	19.76
(reptile, 9.0)	urban	–	–	–	–	12.56 (0.14)	1022	1.19	35.57

Data derived from Fa and Purvis (1997).

(*Thryonomys swinderianus*) (8.9%, $n = 2420$), and bay duiker (*Cephalophus dorsalis*) (5.6%, $n = 4970$), which together comprised 67.5% of the total carcasses (Supporting Information). In urban markets, carcasses were less diverse. The same 4 species comprised a total of 77.3% of carcasses (brush-tailed porcupine, 42.5%, $n = 1017$; blue duiker, 29.6%, $n = 708$; bay duiker, 2.3%, $n = 55$; grasscutter, 2.9%, $n = 69$) (Supporting Information).

In rural Cameroonian markets, the most abundant species were blue duiker (29.3%, $n = 3462$), brush-tailed porcupine (22.3%, $n = 2260$), and grasscutter (5.8%, $n = 691$). The percentage of brush-tailed porcupine was similar in rural and urban markets (24.4%, $n = 4864$), whereas blue duiker was relatively less abundant (16.2%, $n = 3229$) in rural markets than in urban markets. Pouched rat (*Cricetomys emini*) was more abundant in urban markets (10.5%, $n = 2097$) than in rural markets (0.5%, $n = 57$).

Market Location, Carcass Condition, and Price

The main effect of country as a predictor of price was not significant ($F = 0.07$; df = 1, 83; $p = 0.87$). However, all the 2-way interactions with country were statistically significant, complicating interpretation of the main effect of country. For example, prices were higher in Cameroon in rural than in urban markets (Table 2). Given these interaction effects, we applied separate GLMs to the data for each country.

For Cameroon 62.2% of the variability in carcass price ($n = 27,252$) was explained by the model that included taxon, location, and condition. After controlling for taxon (partial $r^2 = 50.4\%$), location explained 16.9% of the remaining variation (the condition effect was negligible by comparison: 0.1%). However, because all interaction effects in these country-level models were statistically significant ($p < 0.001$), we quantified the location effect by evaluating separate models for each combination of taxon and condition classes. All taxa were significantly more expensive in urban markets (Table 3 & Supporting Information).

In Nigerian markets, taxon, location, and condition explained 37.7% of the variability in carcass price. As for Cameroonian markets, taxon (partial $r^2 = 22.6\%$) explained the greatest variation in price. Location explained 4.6% of the remaining variation after controlling for taxon (compared with 0.01% explained by condition). The interaction terms were also statistically significant; thus, we conducted separate comparisons for each taxon. The magnitude and direction of price differences were similar in Cameroon and Nigeria (Table 3 & Supporting Information); prices were consistently higher in urban markets. The effects presented in Table 3 were statistically significant for all 10 taxa in Cameroon ($F \geq 9.8$; df = 1, ≥ 96; $p \leq 0.0023$) and for 6 of the 8 possible comparisons in Nigeria ($F \geq 281$; df = 1, ≥ 944; $p < 0.001$). Only for bay duiker and dwarf crocodile (*Osteolaemus tetraspis)* were the observed price differences not statistically significant ($F = 0.20$; df = 1, 1572; $p = 0.65$ and $F = 0.20$; df = 1, 32; $p = 0.60$ respectively). Condition did not explain significant variation in market price in either country for any of these taxa (Cameroon, $F = -0.03$; df = 1, ≥ 9; $p \geq 0.13$; Nigeria, $F = 0.03$; df = 1, ≥ 29; $p \geq 0.14$).

Carcass Size and Regional Preferences

In both countries, particularly Cameroon, taxon was strongly associated with carcass price (as shown by the values of partial r^2 in the analyses above). The more common taxa in markets (90% of market transactions) cost \$1.5–2.5/kg in rural markets and \$2.0–4.0/kg in urban markets (Supporting Information).

There was evidence that the relation between price and body size differed between rural and urban markets for both countries. The interaction between location and size was significant in both countries (Cameroon, $F = 4.4$; df = 1, 63; $p = 0.04$; Nigeria, $F = 40.4$; df=1, 52; $p < 0.001$). We therefore quantified the effect of body size separately for rural and urban markets.

In rural markets in both countries, price increased approximately as a function of the square root of carcass mass (Fig. 2). In urban markets, the relation differed between countries. In Cameroon, price increased more steeply as size increased than in rural markets (Fig. 2), whereas in the Nigerian urban markets size did not explain significant additional variation in price. Taxonomic group ($F = 1.37$; df = ≥ 4, ≥ 8; $p \geq 0.27$) and mean number of carcasses appearing per day ($F = 1.37$; df = 1, 11; $p \geq 0.06$) did not explain significant additionl variation in carcass price in either country.

Regional pricing of individual taxa in rural markets and in urban markets in Cameroon showed some consistent patterns after accounting for carcass mass. For example, pouched rats were consistently cheaper than we expected on the basis of body mass, and chimpanzees were more expensive. Meat of the servaline genet (*Genetta servalina*) was the most expensive item per unit mass in both rural and urban markets in Cameroon (\$10.6 and 6.7/kg respectively).

Settlement Size

The amount of bushmeat in markets was higher where human population size was higher, but the rate of increase was low (slope on log-log scale = 0.23, CI 0.14–0.32, where a slope of 1.0 is consistent with a constant supply per person). The slope did not differ significantly between countries (interaction term, $F = 1.2$; df = 1, 77; $p = 0.29$). Hence, bushmeat supply per capita declined steeply in both countries as a function of human population size (Fig. 3). The slopes on a log-log scale were −0.73 (CI −0.86 to −0.47) for Cameroon and −0.84 (CI −0.98 to −0.56) for Nigeria. Prices increased as population size increased, but the slopes for covariates that explained significant variation in price (on log-log scale) were all well below 1.0, which indicates these

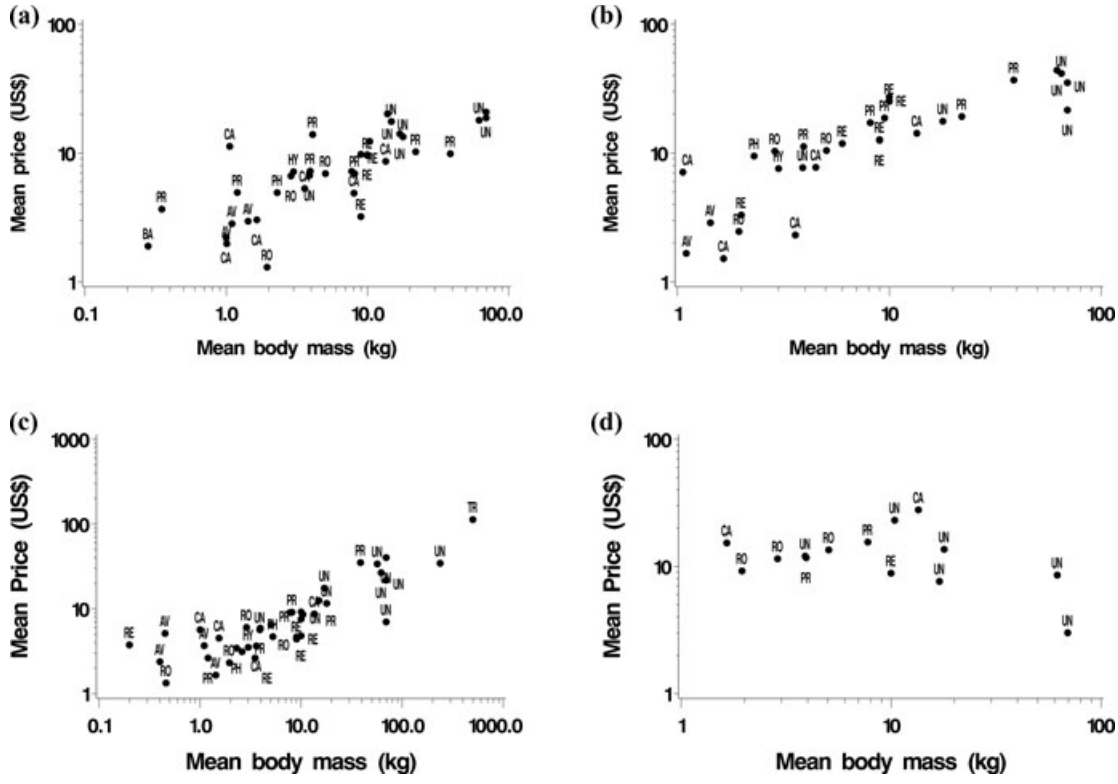

Figure 2. Relation of price and body mass for different taxonomic groups in markets in (a) rural (slope 0.46, CI 0.32–0.55) and (b) urban Cameroon (0.64, 0.49 to 0.79) and markets in (c) rural (0.45, 0.34 to 0.56) and (d) urban Nigerian (−0.19, −0.43 to 0.05) (CA, carnivore; UN, ungulates; PR, primates; Ph, pangolins; AV, birds; RE, reptiles; BA, bats).

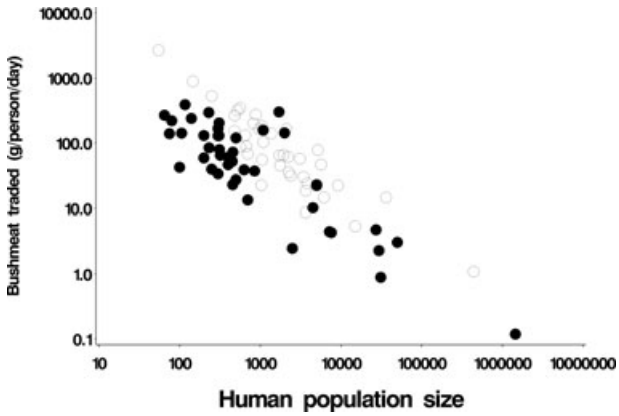

Figure 3. Per capita bushmeat traded and settlement size (open circles, Nigeria; closed circles, Cameroon; outlying point in Nigeria not included Fa et al. (2006)(slope, −0.71, CI −0.83 to −0.59).

increases were not a linear function of population size. This was true whether or not urban sites were included. For example, the slope for brush-tailed porcupine was 0.06 (SE0.02) for all sites and 0.05 (0.02) for rural sites alone.

Discussion

The cost of a carcass to a consumer in our study area was determined largely by the animal's size. Rarity (indexed by average abundance in the market) had no detectable effect on price, which is consistent with results of previous studies (Wilkie & Godoy 2001). Also, there was no evidence that taxonomic group was related to price. Taxa that are large and have low reproductive rates, such as primates, were not, taking into account their size, generally more expensive than rodents.

There were some consistent regional patterns in pricing, which we interpreted as preferences for individual taxa. Pouched rat, for example, was, in all markets, much less expensive than might have been predicted on the basis of its size (around 2 kg), and in Cameroon chimpanzees were the most expensive taxon. The higher price of endangered species was principally explained as a function of their body size (generally larger than species that were not endangered). Thus, policies that encourage hunting of species that can withstand high levels of harvest (e.g., blue duikers and rodents such as pouched rats, brush-tailed porcupines, and grasscutters) and minimize hunting of primates and large ungulates may help provide protein sources for the rural inhabitants and deflect attention from the most vulnerable species (Bennett et al. 2007). Increased supply of a less attractive good will not necessarily reduce demand for more desirable ones. But if consumers choose bushmeat independent of rarity, enforcement of legislation aimed at minimizing hunting of endangered species would be effective. If rare and common species are dietary substitutes, relatively minor disincentives to trading in and consuming rare species (e.g., small fines for possessing primates) may elicit the substitution.

Carcass prices were higher in settlements with more people, although this effect was small. If the relation between price and distance to market is explained by the cost of transport, as in Ghana (Cowlishaw et al. 2005), then enforcement along known transport routes from sources to markets is likely to reduce the bushmeat trade. The higher percentage of smoked carcasses in urban than in rural markets in Nigeria is consistent with inadequate transport to urban markets. Meat is more often moved along forest paths in Nigeria than in Cameroon, where it is moved via road and rail (Fa et al. 2006). As has been observed previously (Willcox & Nambu 2007), there was little effect of carcass condition on price.

We were surprised by the weak association between settlement size and both the supply and price of bushmeat, at least to established markets. Demand for bushmeat may be lower in urban areas where alternatives are more available and cheaper than in rural areas (Willcox & Nambu 2007). Bushmeat may be considered more of a luxury item in urban areas. Regardless, the relation between settlement size and supply does not support the idea that human migration to towns promotes the bushmeat trade; the biomass of bushmeat traded per person was lowest in the urban centers.

Supporting Information

A complete list of taxa sampled and their mean prices is available online (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Acknowledgments

This study was funded by the U.K. Government's Darwin Initiative Fund (project 162/10/004). We are grateful to our locally recruited staff in Cameroon and Nigeria. L.A. acknowledges and appreciates the support given to her by the Biological Diversity Program of the Norwegian Research Council. We also thank other members of Wild-CRU for valuable discussions.

Literature Cited

Albrechtsen, L., Macdonald, D. W., Johnson, P. J., Castelo, R. and J. E. Fa. 2007. Faunal loss from bushmeat hunting: empirical evidence and policy implications in Bioko Island. Environmental Science and Policy **10:**654–667.

Allebone-Webb, S. M., N. F. Kümpel, J. Rist, G. Cowlishaw, J. M. Rowcliffe, and E. J. Milner-Gulland. 2011. Use of market data to assess bushmeat hunting sustainability in Equatorial Guinea. Conservation Biology **25:** 597–606.

Anadu, P. A., P. O. Elamah, and J. F. Oates. 1988. The bushmeat trade in southwestern Nigeria: a case study. Human Ecology **16:**199–208.

Bennett, E. L., E. Blencowe, et al. 2007. Hunting for consensus: reconciling bushmeat harvest, conservation, and development policy in west and central Africa. Conservation Biology **21:**884–887.

Bowen-Jones, E. and S. Pendry. 1999. The threat to primates and other mammals from the bushmeat trade in Africa, and how this threat could be diminished. Oryx **33:**233–246.

Butynski, T. M. 2002. Conservation of the guenons: an overview of status, threats, and recommendations. Pages 411–424 in M. E. Glenn and M. Cords, editors. In The Guenons: diversity and adaptation in African monkeys. Kluwer, New York.

Caspary, H.-U. 1999. Wildlife utilization in Côte d'Ivoire and West Africa—potentials and constraints for development cooperation. Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Germany.

Cowlishaw, G., S. Mendelson, and J. M. Rowcliffe. 2005. Structure and operation of a bushmeat commodity chain in southwestern Ghana. Conservation Biology **19:**139–149.

Davies, G., B. Schulte-Herbruggen, N. F. Kumpel, and S. Mendelson. 2007. Hunting and trapping in Gola Forest, south Eastern Sierra Leone: bushmeat from fallow and forest. G. Davies and D. Brown, editors. In Bushmeat and Livelihoods: Wildlife Management and Poverty Reduction. Blackwell, Oxford.

East, T., N. F. Kümpel, E. J. Milner-Gulland, and J. M. Rowcliffe. 2005. Determinants of urban bushmeat consumption in Rio Muni, Equatorial Guinea. Biological Conservation **126:**206–215.

Fa, J., and D. Brown. 2009. Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. Mammal Review **39:**231–264.

Fa, J. E., and C. A. Peres. 2001. Game vertebrate extraction in African and Neotropical forests: an intercontinental comparison. Pages 203-241 in J. Reynolds, G. Mace, J. G. Robinson and K. Redfords, editors. Conservation of Exploited Species. Cambridge University Press, Cambridge, United Kingdom.

Fa, J. E., and A. Purvis. 1997. Body size, diet and population density in afrotropical forest mammals: A comparison with neotropical species. Journal of Animal Ecology **66:** 98–112.

Fa, J. E., L. Albrechtsen, P. J. Johnson, and D. W. Macdonald. 2009. Linkages between household wealth, bushmeat and other animal protein consumption are not invariant: evidence from Rio Muni, Equatorial Guinea. Animal Conservation **12:**599–610.

Fa, J. E., C. A. Peres, and J. Meeuwig. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. Conservation Biology **16:**232–237.

Fa, J. E., S. Seymour, J. Dupain, R. Amin, L. Albrechtsen, and D. W. Macdonald. 2006. Getting to grips with the magnitude of exploitation: bushmeat in the Cross-Sanaga Rivers region, Nigeria and Cameroon. Biological Conservation **129:**497–510.

Fa, J. E., J. E. G. Yuste, and R. Castelo. 2000. Bushmeat markets on Bioko Island as a measure of hunting pressure. Conservation Biology **14:**1602–1613.

Juste, J., J. E. Fa, J. P. Delval, and J. Castroviejo. 1995. Market dynamics of bushmeat species in Equatorial-Guinea. Journal of Applied Ecology **32:**454–467.

Koster, J. M., J. J. Hodgen, M. D. Venegas, and T. J. Copeland. 2010. Is meat flavor a factor in hunters' prey choice decisions? Human Nature **21:** 219–242.

Littell, R., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina.

Mishili, F. J., J. Fulton, M. Shehu, S. Kushwaha, K. Marfo, M. Jamal, A. Kergna, and J. Lowenberg-DeBoer. 2009. Consumer preferences for quality characteristics along the cowpea value chain in Nigeria, Ghana, and Mali. Agribusiness **25:**16–35.

Neshiem, L. 2008. Hedonic prices. S. N. Durlauf and L. E. Blume, editors. The new Palgrave dictionary of economics. Palgrave Macmillan, Hampshire, United Kingdom.

Oates, J. F. 1999. Myth and reality in the rain forest: how conservation strategies are failing in West Africa. University of California Press, Berkeley.

Scarborough, V., and J. Kydd. 1992. Economic analysis of agricultural markets: a manual. Natural Resources Institute, Chatham, United Kingdom.

Timmer, C. P. 1987. Food marketing and price policy. Pages 65-75 in D. Elz, editor. Agricultural marketing strategy and pricing policy. The International Bank for Reconstruction and Development and World Bank, Washington, D.C.

Wilkie, D. S., and R. A. Godoy. 2001. Income and price elasticities of bushmeat demand in lowland Amerindian societies. Conservation Biology **15:**761–769.

Wilkie, D. S., E. Shaw, F. Rotberg, G. Morelli, and P. Auzel. 2000. Roads, development, and conservation in the Congo Basin. Conservation Biology **14:**1614–1622.

Wilkie, D. S., M. Starkey, K. Abernethy, E. N. Effa, P. Telfer, and R. A. Godoy. 2005. Role of price and wealth in consumer demand for bushmeat in Gabon, Central Africa. Conservation Biology **19:**268–274.

Willcox, A. S., and D. M. Nambu. 2007. Wildlife hunting practices and bushmeat dynamics of the Banyangi and Mbo people of Southwestern Cameroon. Biological Conservation **134:**251–261.

World Bank. 2004. African development indicators. The World Bank, Washington, D.C.