

Economic and geographic drivers of wildlife consumption in rural Africa

Justin S. Brashares^{a,b,1}, Christopher D. Golden^a, Karen Z. Weinbaum^a, Christopher B. Barrett^c, and Grace V. Okello^b

^aDepartment of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720; ^cCharles H. Dyson School of Applied Economics and Management, Cornell University, Ithaca, NY 14853; and ^bBushmeat Monitoring Network, University of California, Berkeley, CA 94720

Edited by Alexander J. Travis, Cornell University, Ithaca, NY, and accepted by the Editorial Board May 23, 2011 (received for review September 3, 2010)

The harvest of wildlife for human consumption is valued at several billion dollars annually and provides an essential source of meat for hundreds of millions of rural people living in poverty. This harvest is also considered among the greatest threats to biodiversity throughout Africa, Asia, and Latin America. Economic development is often proposed as an essential first step to win-win solutions for poverty alleviation and biodiversity conservation by breaking rural reliance on wildlife. However, increases in wealth may accelerate consumption and extend the scale and efficiency of wildlife harvest. Our ability to assess the likelihood of these two contrasting outcomes and to design approaches that simultaneously consider poverty and biodiversity loss is impeded by a weak understanding of the direction and shape of their interaction. Here, we present results of economic and wildlife use surveys conducted in 2,000 households from 96 settlements in Ghana, Cameroon, Tanzania, and Madagascar. We examine the individual and interactive roles of wealth, relative food prices, market access, and opportunity costs of time spent hunting on household rates of wildlife consumption. Despite great differences in biogeographic, social, and economic aspects of our study sites, we found a consistent relationship between wealth and wildlife consumption. Wealthier households consume more bushmeat in settlements nearer urban areas, but the opposite pattern is observed in more isolated settlements. Wildlife hunting and consumption increase when alternative livelihoods collapse, but this safety net is an option only for those people living near harvestable wildlife.

bushmeat harvest | panel analysis | poverty traps | wildlife conservation

Wildlife from land and sea is the primary source of meat and income for hundreds of millions of people in economically developing countries (1). The harvest, sale, and consumption of terrestrial wildlife comprise a trade valued at several billions of dollars annually (1, 2). This “bushmeat trade,” as it is popularly known, occurs across the planet and includes animals that vary in size from elephants to ants (2). Given its significance and scale, it is not surprising that the bushmeat trade is viewed by many observers as among the greatest threats to biodiversity, particularly in the tropics (1–3). Indeed, case studies illuminate a multitude of locations where once vibrant wildlife communities are harvested to a state of defaunation (2–4). There is general agreement among researchers that unsustainable harvest can have catastrophic consequences for ecosystems and the services and livelihoods that they provide (1–4). However, despite this, we have only a vague understanding of the economic, social, geographic, or other factors that determine the scale of human reliance on wildlife. Such an understanding is an essential first step for any effort to assess the indirect effects of economic development on biodiversity as well as to predict the consequences of biodiversity loss for local economies and livelihoods.

Two somewhat contrasting hypotheses are often put forward to explain broad patterns of wildlife consumption in the developing world (1, 2, 5). We call the first hypothesis the “bushmeat as inferior good hypothesis.” This hypothesis, based on the common observation that poorer, rural households typically consume more bushmeat than do wealthier, urban households, maintains that

wildlife provides a cheap and accessible source of food and income during times of economic or other hardship (i.e., shocks) to the poorest members of society (6) but also, that it is an option of last resort that is consumed less as a household’s wealth grows. In this context, bushmeat is the safety net that protects impoverished rural households from chronic malnutrition. This hypothesis has clear predictions about the relationships between wealth, alternative foods supply, and wildlife consumption. Specifically, consumption of bushmeat should be highest among the least wealthy households and where alternative sources of meat are scarce and/or prohibitively expensive (6–9). Importantly, this hypothesis also predicts that poverty alleviation should lead to reduced reliance on wildlife and therefore, improved prospects for biodiversity conservation. If true, the inferior good hypothesis suggests that targets for poverty alleviation and biodiversity conservation should be aligned and that improvements on either front will benefit the other. However, it suggests also that reduced access to wildlife, either through use restrictions or unsustainable harvest, will create a positive feedback in which increased resource scarcity drives and, in turn, is exacerbated by increased economic desperation (i.e., a poverty trap) (10).

A second hypothesis, which we call the “bushmeat as normal good hypothesis,” poses that the demand for bushmeat, like most household goods, increases as household wealth grows (5, 7–9, 11–14). If true, the normal good hypothesis suggests that efforts for poverty alleviation and biodiversity conservation may be opposed but also, that the local collapse of wildlife populations or their strict protection through conservation efforts may have only limited direct effects on rural livelihoods and food security.

The dichotomy presented in the two hypotheses above oversimplifies what are likely to be complex and highly variable relationships among economics, geography, politics, and culture. In fact, wildlife consumption is embedded within a web of interacting and dynamic factors whose variability impedes efforts to identify a unifying theory for wildlife use or even management guidelines with general applicability. In particular, wealth is related with many other variables that matter to hunting and bushmeat consumption patterns. What appears as a negative (unconditional) relationship between bushmeat consumption and wealth, generating the inferior good hypothesis, may arise because poorer rural areas have greater access to wildlife, rural residents’ opportunity cost of time spent hunting is lower, and the price of bushmeat relative to alternative foods is lower. Because those effects also matter and are correlated with spatial differences in wealth, it becomes easy to conflate different factors and mistakenly infer that greater bushmeat consumption in

Author contributions: J.S.B., C.D.G., and K.Z.W. designed research; J.S.B., C.D.G., K.Z.W., and G.V.O. performed research; J.S.B., C.D.G., K.Z.W., and G.V.O. analyzed data; and J.S.B., C.D.G., K.Z.W., and C.B.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. A.J.T. is a guest editor invited by the Editorial Board.

¹To whom correspondence should be addressed. E-mail: brashares@berkeley.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1011526108/-DCSupplemental.

poorer rural areas is caused by rural poverty and thus, that economic development will naturally relax pressure on wildlife by reducing bushmeat demand. The complexity and fine-scale geographic variation are likely responsible for the incongruous results from studies that have explicitly examined the interactions of wealth, alternatives, and wildlife consumption in the tropics (6–13). Indeed, the setting chosen by any given study may differ from others in many aspects, including local culture, population density, poverty, habitat, wildlife abundance, market access, and law enforcement. Considering this variability among studies, it is not surprising that our understanding of the drivers of wildlife consumption remains murky.

Here, we combine multiyear datasets from four countries in Africa in an attempt to decipher patterns in the drivers of wildlife consumption amid a large amount of geographic, economic, cultural, and other variation. Specifically, we analyze data on wealth, alternatives, access, opportunity costs, and wildlife consumption for 2,000 households in 96 distinct settlements in Ghana, Cameroon, Tanzania, and Madagascar (Fig. 1). Our sampling within each country occurs largely in rural areas* but includes settlements that vary in their geographic setting, proximity to harvestable wildlife populations and urban markets, traditions, taboos, law enforcement, and economic activity. Within settlements, our sampling quantified variation in household wealth, access to bushmeat alternatives, and bushmeat consumption. In addition to settlement and household-level data, we also collected information on opportunity costs of hunting and the commodity chain of harvested bushmeat by following 47 hunters in Ghana and Tanzania. We used these data at the scales of settlement, household, and hunter to ask three questions. (i) What is the relationship between household wealth and wildlife consumption and is this relationship similar in rural and more urban areas? (ii) How does proximity to harvestable wildlife populations affect prices of bushmeat relative to alternative food sources and rates of consumption at the settlement level? (iii) To what extent is the fate of harvested wildlife determined by a hunter's access to urban bushmeat markets? Last, in an effort to compare the relative contributions of these and other factors as drivers of wildlife consumption and to integrate longitudinal data resulting from repeat visits to a subset of households in Ghana and Tanzania, we combined household wealth, access, enforcement, and market price as predictors in mixed-effect panel regressions (15).

Results and Discussion

Wildlife Consumption and Household Wealth. Our pair-wise comparison of household wealth and wildlife consumption across all 2,000 households and 96 settlements in four countries revealed only a weak negative interaction ($r = -0.04$) (Fig. 2A). Overall, wealthier households consumed only slightly less bushmeat than others. However, remarkably more insight was gained when proximity to urban area was added as a covariate in the analysis. The effect of this addition is made stark by separating the 2,000 households into the 500 most rural and 500 most urban (separated as quartiles based on geographic distance to a nearest urban area) and then, testing for a link between consumption and wealth in each of these subgroups. Such a test shows that the least wealthy households consistently consume the most bushmeat in rural settings ($r = -0.71$, $P < 0.001$) (Fig. 2B), whereas wealthier households show higher rates of consumption in urban settings ($r = 0.56$, $P < 0.001$) (Fig. 2C). These results show that



Fig. 1. Map of the location of the four countries and eight regions sampled in this study. Black stars show the location of the capital of each country, and white patches identify the approximate locations of households included in our sampling.

the interaction of wealth and consumption will change in different geographical situations within the same country. The co-occurrence of these relationships obscured our effort to identify wealth–consumption patterns across the entire urban–rural gradient and as has been suggested elsewhere (7–9, 11, 16), may explain the conflicting results of similar studies in these and other countries. As we now report, this finding likely reflects considerable spatial variation in access to wildlife, bushmeat prices relative to those of alternative foods, and opportunity costs of time spent hunting, all of which are correlated with wealth measures.

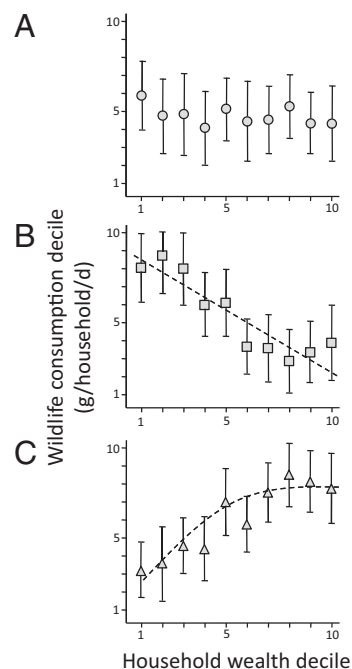


Fig. 2. Household wealth is only weakly linked to wildlife consumption (slope = -0.06 ; $r = -0.04$) for the complete dataset of 2,000 households and 96 settlements (A), but it is significantly and negatively related to consumption ($r = -0.71$, $P < 0.001$) for the 500 most rural households (B) and positively related to consumption ($r = 0.56$, $P < 0.001$) for the 500 most urban households (C). Values shown are means \pm SD for each graph.

*Our study focused on smaller, generally rural bushmeat harvest and markets. Although our methods account for the transport of bushmeat to and from our study sites, our sampling did not account for group hunting or larger-scale harvest efforts involving the transport of individuals from urban centers. Such hunting was, to our knowledge, non-existent among our study sites in Madagascar and rare within our study areas in Tanzania, Cameroon, and Ghana (although it is common in other regions of Ghana).

Wildlife Consumption and Proximity. One previously suggested (7–9) explanation for these patterns is that bushmeat in many rural areas is purchased close to its source of capture and thus, is likely to be less expensive than alternatives. Similarly, bushmeat sold in urban markets is likely to have traveled some distance from its source after being sold to middlemen and therefore, will have a higher price (16). To examine the potential influence of proximity to harvestable wildlife on consumption and price, we calculated the mean distance from each settlement to its nearest consistent source of bushmeat, as reported by hunters, and then compared this distance with average wildlife consumption per settlement. Our results show that households in settlements close to harvestable wildlife populations consume significantly more bushmeat than those households farther away ($r = -0.48$, $P < 0.001$, $n = 96$ settlements) (Fig. 3A). However, our analysis also suggests that this distance effect disappears at distances of 30 km or more (i.e., consumption rates in settlements as close as 30 km to a wildlife harvest area were similar to those as far as 150 km away) (Fig. 3A).

Our comparison of bushmeat prices across settlements with different proximity to wildlife in Ghana and Tanzania also supports the spatial price gradient hypothesis. Comparing price data for bushmeat and domestic meat and fish in 52 markets, we found that bushmeat was significantly cheaper than alternatives in areas close to harvestable wildlife ($r = 0.78$, $P < 0.001$, $n = 52$) (Fig. 3B). Furthermore, the price of bushmeat relative to alternative meat increased with increasing distances from hunting areas. When transported 90 km or more from its source, bushmeat cost nearly 50% more than fish and fowl (Fig. 3B).

Wildlife Harvest and Access to Urban Markets. Because bushmeat prices increase with proximity to urban areas, those hunters who harvest game meat nearer cities should gain relatively more from selling their catch than those hunters in more remote areas and thus, should be more likely to sell rather than consume bushmeat. We compiled data on the fate of 782 bushmeat items harvested by 47 hunters over a 3-y period. Specifically, we tested

if isolation of settlements from road networks and urban markets (measured as distance by road to nearest urban center) predicted whether bushmeat was more or less likely to be consumed locally. A high proportion (75–95%) of wildlife harvested in the settlements most isolated from commerce networks was consumed locally by the hunter's household or neighbor (Fig. 4). In contrast, hunters who lived within 10 km of an urban market sold more than 80% of their catch to outsiders.

Wildlife Harvest and Opportunity Costs. Regardless of who consumes it, bushmeat is predominately supplied by hunters plying their trade in rural forests and savannas. This finding naturally raises the question of how access to alternative livelihoods influences the behavior of individuals currently engaged in hunting. Put another way, as the opportunity costs of time spent hunting increase, does it discourage wildlife harvest, as recent research suggests (13, 14, 16–18)? In fact, wildlife management authorities and conservation organizations in Ghana, Tanzania, and other countries are known to target the most active local hunters for employment in nonhunting positions as a direct and efficient means of reducing harvest. The most reliable and widespread source of employment in rural Africa comes seasonally through agriculture. In most areas included in our study, agricultural activity comes in two strong pulses: the first pulse at the time of clearing/tilling and planting and the second pulse at crop harvest. To gain insight on opportunity costs of hunting, we collected daily activity reports from 47 hunters in Ghana and Tanzania over 18 mo and thereby, tracked their hunting effort in association with other activities. Our summary of activity budgets showed that hunting and household bushmeat consumption declined sharply at times of peak agricultural activity and increased again when less time was needed for agricultural activities (Fig. 5).

Integrated Assessment of Wildlife Harvest and Consumption. Our pair-wise comparisons provide insight on the economic and spatial determinants of bushmeat use and reveal patterns that are largely consistent across the four countries and 96 settlements included in our study. However, these analyses (i) poorly account for colinearity among our predictors, (ii) provide only a vague assessment of the relative importance of individual predictors, and (iii) fail to take advantage of longitudinal (repeat sampling) data available for nearly one-half of the households that we surveyed. To address these issues and provide a more integrated analysis, we conducted two unbalanced mixed-effect panel regressions (15) in which country, settlement, and household were included as fixed effects while we tested for best models of wildlife consumption using (i) household wealth, (ii) distance from wildlife, (iii) distance from urban centers, and for

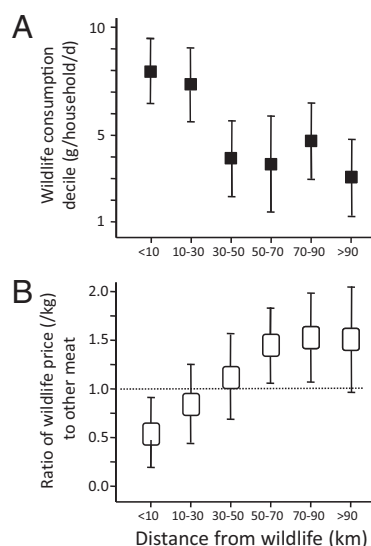


Fig. 3. Distance of human settlements from harvestable wildlife populations in Ghana, Tanzania, Madagascar, and Cameroon was a strong predictor of the amount of bushmeat that households in those communities consume annually ($r = -0.48$, $P < 0.001$, $n = 96$ settlements) (A). Distance from wildlife also was positively related ($r = 0.78$, $P < 0.001$, $n = 52$ settlements) to the price that consumers paid for bushmeat in Ghana and Tanzania. Values shown are means \pm SE (B). Geographic distances are shown here as raw values, but they were rank-transformed for each country for statistical analysis.

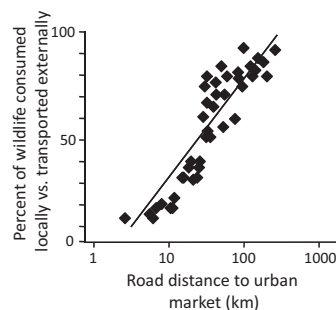


Fig. 4. Relative distance of settlements from urban areas in Ghana and Tanzania strongly predicted whether harvested wildlife would be consumed within the hunter's home community or exported to external markets ($r = 0.72$, $P < 0.001$, $n = 47$ hunters and 762 harvested animals). Geographic distances are shown here as raw values, but they were rank-transformed for each country for statistical analysis.

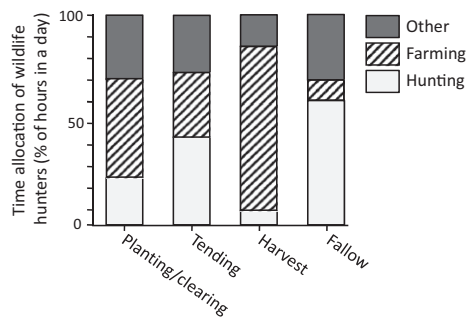


Fig. 5. Time allocation of 47 hunters surveyed weekly in Ghana and Tanzania was tied closely to employment or commitment to farming-related activities, with hunting levels peaking during periods when farms were fallow ($P < 0.01$ for ANOVAs of hunting and farming across the four time periods). Sleep was excluded from time budget calculations. Average daily bushmeat consumption in households provisioned by hunters included in this analysis declined by 68% (± 17) during months of peak farming activity.

model 2 only, (iv) bushmeat market prices. Results of these analyses show that wealth has no statistically significant independent effect on bushmeat consumption, although it does have a significant effect in amplifying the effects of distance from wildlife and attenuating the effects of relative bushmeat price and distance from urban center (Table 1; models including supply of alternative foods as a predictor of bushmeat use are provided in Table S1). These findings are qualitatively similar to those findings of our pair-wise analyses and strongly suggest that the juxtaposed inferior-normal good hypotheses that pervade the literature conflate wealth effects with more powerful correlated effects because of geographic proximity, relative prices, and although not feasible to include in the regression summarized in Table 1, opportunity cost of time spent hunting.

The patterns that we observe between rural and more urban settlements initially appear to contrast sharply, but in fact, both can be explained within a single economic framework. Three key characteristics of this framework are that (i) hunting is labor/time intensive and relies on access to wildlife, (ii) bushmeat is a normal good in more urban settings such that demand for it increases as a household's income increases, and (iii) there are significant costs to obtaining and marketing bushmeat. There are several implications of these three characteristics, and they are supported by our analyses. Individuals with low (perhaps only seasonal) labor productivity rationally reallocate their time to hunting, which we show with activity budgets from Ghana and Tanzania (Fig. 5), and thus, harvest more bushmeat than otherwise identical people

whose labor is productively absorbed in other activities offering at least comparable returns. When alternative livelihoods are seasonally unavailable or if they fail because of stochastic events, people turn to hunting to generate income and food. However, reallocation of labor to hunting is only an option for those people who live close (roughly within 30 km) to harvestable wildlife (Fig. 3A). Furthermore, where a hunter lives far from market, the costs of exchanging bushmeat for other foods are relatively high (Fig. 3B), and therefore, hunters and households within their settlements tend to eat their harvest (Fig. 4). Beyond areas where hunting is an option, bushmeat becomes purely a consumption good, and therefore, conventional income effects of the consumer dominate: individuals who have expendable income eat more than those individuals who do not. In summary, in rural areas, the effects of labor returns and geographic access dominate, in part, because of the costs of marketing meat. In urban areas, the dynamics of wildlife consumption are dominated by consumer income effects, because a shortage of local wildlife makes hunting an unrealistic option.

Biodiversity Conservation, Poverty Alleviation, and Poverty Traps.

In this study, we offer insights on drivers of wildlife consumption by analyzing data from a large number of households and settlements across a broad range of geographic locations that vary in levels of isolation from urban areas, access to wildlife, law enforcement, political systems, and wealth. Our sampling was relatively even in the number of households and settlements included for each country, but it was biased to rural areas. Nevertheless, our analyses suggest a clear pattern of wildlife consumption that is best explained by an interaction of wealth, price, and geographic factors. As discussed elsewhere (1, 2, 7, 8), we suggest that wildlife consumption in Africa may be viewed as a continuum from subsistence-based rural consumption to mixed subsistence-commercial hunting to hunting for commercial urban markets to the extreme case of hunting for the international trade in bushmeat. Not surprisingly, the price of bushmeat increases with each step that it is taken away from its source. For example, the price of one smoked red-flanked duiker in Brooklyn, New York is 17–25 times the cost of the same species sold near its source in eastern Ghana. As the price of bushmeat rises with its movement across the rural to urban gradient, the characteristics of the consumer change as well. Thus, the “poor” person's meat in the country becomes the “rich” person's meat in the city.

Our finding that bushmeat may simultaneously be a rural safety net and also, be governed by conventional income effects may surprise few who study these issues closely. However, noticeably little work has attempted to quantify variation in drivers of consumption over large areas and test mechanisms that may account

Table 1. Predictors of household wildlife consumption (grams per day per household) in Ghana, Tanzania, Cameroon, and Madagascar from 2004 to 2008 using mixed-effect panel regression models

Explanatory variable	Model 1	Model 2
Household wealth (decile)	-0.011 (0.62)	-0.043 (0.18)
Distance from harvested wildlife (km)	-0.074 (<0.01)	-0.142 (<0.01)
Distance from urban center (km)	0.061 (0.01)	0.133 (0.01)
Wealth × distance from harvested wildlife	0.29 (<0.01)	0.299 (<0.01)
Wealth × distance from urban center	0.16 (<0.01)	0.188 (<0.01)
Relative bushmeat price (ratio)		-0.122 (<0.01)
Wealth × relative bushmeat price		0.354 (<0.01)
Constant	2.9 (<0.01)	2.2 (<0.01)
Full model R^2	0.47	0.57

Model 1 includes a sample of 2,000 households from 96 settlements in the four countries. Model 2 includes a subset of 994 households from 54 settlements in Ghana and Tanzania for which weekly price of bushmeat (relative to other meats) was collected. Values shown represent coefficient estimates with associated probabilities in parentheses. Household was included as a fixed effect in both models.

for that variation (8, 9, 16). Furthermore, from the perspective of biodiversity conservation, our results highlight the need to understand the individual contribution of rural and urban consumption if we are to identify which source of demand is more crucial to achieving sustainability. For example, the international trade in bushmeat receives great attention (1, 2) but by most accounts, represents a small fraction of the volume sold domestically. How do absolute amounts of rural and urban consumption compare within a country? Unfortunately, our study included too few truly urban households to address this question, but we highlight it as a knowledge gap. Ultimately, the relative contribution of rural and urban consumption will determine the degree to which poverty alleviation and more broadly, economic development can expect to benefit biodiversity (11).

We focused on absolute levels of household wildlife consumption in this study, but great insight can be gained as well from looking at bushmeat consumption relative to other sources of meat. From this perspective, our data show that the relative contribution of bushmeat is most important from a food supply and livelihoods perspective to the rural poor. Specifically, although total bushmeat consumption was only weakly linked to wealth ($r = -0.04$), bushmeat consumption measured as a percent of total meat consumed was significantly and negatively related to wealth ($r = -0.43, P < 0.001$). This finding suggests that, although efforts to conserve harvested wildlife will need to address both rural and urban consumers, the costs of wildlife conservation will be borne most heavily by the rural poor. Conservation without mitigation may drive vulnerable rural households into poverty traps as traditional avenues for escaping poverty become illegal. However, it is critical to recognize that prolonged, unsustainable harvest of wildlife may leave those same households in a similar or worse economic predicament (2, 19, 20).

Methods

Data Collection. Madagascar. Household surveys were designed and piloted by C.D.G. and conducted by C.D.G. and two local research assistants in the Makira Protected Area of Madagascar in 24 settlement sites from January to December 2006. Settlements were chosen randomly throughout the region by attempting to cluster series of villages along designated trade routes. Research assistants met with village chiefs and other villagers to discuss village-level information and gain permission for conducting surveys in 2004 and 2005. We surveyed 18–100% (mean = 28%, median = 37%) of village households in each of the 24 villages included in our study for a total of 548 households. Household wealth was measured by adding the value of products sold, wages earned, and items bartered. Information regarding the annual use of bushmeat was collected through comparison of daily diet diaries with annual recalls of the consumption of 23 locally occurring mammal species. Additional details on assessments of bushmeat consumption, household wealth, and other variables are provided in *SI Text* and a recent work (21).

Cameroon. Household surveys were designed and piloted by K.Z.W. and conducted by eight local postgraduate students in the Center and East Regions of Cameroon in 20 town and village sites in October and November of 2007. Towns were chosen at the head of the four major road axes in the region, and villages were chosen randomly for cluster sampling of households using semistructured survey methods. Survey enumerators first conducted focus group meetings with village chiefs and other villagers to discuss village-level information and gain permission for conducting surveys. Approximate village population sizes were ascertained and used to determine the spacing of household sampling to allow 16 household surveys per village and 25 household surveys per town (given logistical constraints). A total of 478 complete surveys were retained. Household wealth was estimated using household assets. Annual wildlife consumption was measured through annual recalls of hunting and/or purchase by weekly, monthly, or seasonal frequency. Biomass was obtained by multiplying estimated annual consumption by the average adult body mass of each species or species group using weights from the PanTHERIA database (22). Access to wildlife was reported by respondents as the maximum distance traveled from village to hunting activities. Global Positioning System coordinates of all village locations were taken. Road distances to urban market were calculated using ArcGIS 9.1. Additional details are provided in *SI Text*.

Ghana. Five hundred three households were sampled using structured surveys conducted from January to November in 2004, 2005, and 2008 by five Ghanaian researchers in association with J.S.B. Sampling occurred in 24 distinct settlements in the Volta and Upper East regions to quantify bushmeat consumption and characterize relative wealth, food supply, access to markets, and alternative livelihoods among other social and economic factors. Consumption was estimated from daily and weekly recalls and also recorded through meat purchases at local markets. Recalls were verified against daily direct observation of meat consumption for a subsample of households (Fig. S1). Settlements included in our study ranged in size from 200+ to 3 households. Among larger settlements (i.e., 30+ households), the number of households sampled was roughly proportional to settlement size. Additional details are provided in *SI Text*.

Tanzania. Surveys of wealth, food supply, bushmeat consumption, hunting, and livelihoods were conducted by G.V.O. and seven research assistants from June 2007 to January 2009 in 491 households from 28 settlements in the Dodoma, Morogoro, Iringa, Shinyaga, and Tabora regions. These regions are characterized by mixed savannah and forest habitat. Survey methods and selection of settlements and houses followed the methods described above for Ghana. The number of households sampled per settlement was approximately proportional to settlement size. Additional details are provided in *SI Text*.

Definitions. Throughout our analyses, wealth was quantified as annual income plus property, livestock, and other holdings either bought or bartered. We focused our wealth assessments on a standard basket of owned assets for each settlement; however, the items in this basket varied between countries. For households in Madagascar, wealth calculations added the total value of products sold, wages earned, and items bartered to the standard basket. Wildlife consumption was measured through a combination of recalls and daily records (details in *SI Text*). Typically, households were asked to recall the amount of wildlife consumed over the last week, month, and year, and these results were compared against daily diet logs as well as data collected from local bushmeat markets (Ghana and Tanzania) (Fig. S1). The values used in our analyses represent grams consumed per day per household. Alternatives were measured as the daily amount consumed of primarily fish, fowl, goat, beef, pork, and eggs. Access to wildlife is a value assigned to each settlement that represents the mean distance traveled by hunters to the nearest harvestable wildlife population. In some cases, hunting occurred with high success rates in areas immediately adjacent to settlements, whereas in other places, the closest hunting areas were 100 km or more from the settlement. Our definition of access is intentionally simplistic and focused on geographic considerations, not social or political dimensions, so that it can allow for cross-regional and -cultural comparison. Our definition does not include locally specific sociopolitical barriers to access that may act differentially on the heterogeneous mix of individuals in each respective village. Price of wildlife and alternatives was collected only for Ghana and Tanzania, where markets in 46 settlements were visited weekly over 18 mo. Only the prices of the most common forms of bushmeat, specifically ungulates and rodents, were included in calculating the cost ratio of wildlife to alternatives. The fate of hunted animals and the time budgets of hunters were determined through weekly follows of 47 men in Ghana and Tanzania, each of whom self-identified as hunters at the start of our study. These men were asked each week to report (i) the fate of animals that they captured (i.e., consumed by the household, sold or bartered locally, or sold to middlemen for transport to urban markets) and (ii) the amount of time they spent in each 24-h period on hunting, agriculture, or other activities. Road distance to urban market is measured from the center of each settlement, and urban is defined as settlements greater than 5,000 people.

Data Transformation and Analysis. Several variables central to this study showed significant differences in mean, median, and range between countries. For example, not surprisingly, absolute values of wealth and wildlife hunting and consumption differed among Madagascar, Cameroon, Ghana, and Tanzania. Thus, to allow a metaanalysis of the multicountry dataset, we transformed raw country data into relative scales that allowed direct comparison. Specifically, for each country, we divided values of wealth, wildlife consumption, and availability of alternative sources of animal protein into deciles. This process meant that the wealthiest households or settlements in Madagascar, for example, would have the same decile value as the wealthiest households in Ghana, despite that, in absolute terms, the households in the two countries may differ greatly in wealth. Linear regressions were used for pair-wise comparisons unless data were nonnormally distributed, in which case rank correlations were applied. Multiple regression analyses followed the mixed-effect panel model as described by Frees (15) and was conducted in related studies of household bushmeat consumption (8). Country, settlement, and household were included as fixed effects in both models.

ACKNOWLEDGMENTS. In Cameroon, we thank R. Ngoufo, the team of field enumerators, and the generous participation of householders in the interview process. Research in Ghana was supported by the Ghana Wildlife Division of the Forestry Commission. We also thank G. Ogbango, M. Lartey, and M. Obedo for their considerable efforts in the field. Research in Tanzania was aided by Sokoine University of Agriculture and the assistance of R. Alfonso, M. Mohammed, and D. Ngoumu. Research in Madagascar would

not have been possible without assistance from B. J. R. Rasolofoniaina, Z. C. Donné, E. J. Gasta, Wildlife Conservation Society Madagascar, and the Malagasy Ministry of Water and Forests. For financial support, we acknowledge Conservation International Madagascar, the Margot Marsh Biodiversity Fund, the National Geographic Society Conservation Trust, the University of California Berkeley Center for African Studies, and National Science Foundation Grants 2006036191 and 0818185.

1. Milner-Gulland EJ, Bennett EL, Society for Conservation Biology 2002 Wild Meat Group (2003) Wild meat: The big picture. *Trends Ecol Evol* 18:351–357.
2. Robinson JG, Bennett EL (2000) *Hunting for Sustainability in Tropical Forests* (Colombia University Press, New York).
3. Redford KH (1992) The empty forest. *BioScience* 42:412–422.
4. Robinson JR, Redford KH, Bennett EL (1999) Wildlife harvest in logged tropical forest. *Science* 284:595–596.
5. Brashares JS, et al. (2004) Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science* 306:1180–1183.
6. de Merode E, Homewood K, Cowlishaw G (2004) The value of bushmeat and other wild foods to rural households living in extreme poverty in Democratic Republic of Congo. *Biol Conserv* 118:573–581.
7. Wilkie DS, et al. (2005) Role of prices and wealth in consumer demand for bushmeat in Gabon, Central Africa. *Conserv Biol* 19:268–274.
8. Fa JE, Albrechtsen L, Johnson PJ, Macdonald DW (2009) Linkages between household wealth, bushmeat and other animal protein consumption are not invariant: evidence from Rio Muni, Equatorial Guinea. *Anim Conserv* 12:599–610.
9. Godoy R, et al. (2010) The effect of wealth and real income on wildlife consumption among native Amazonians in Bolivia: estimates of annual trends with longitudinal household data. *Anim Conserv* 13:265–274.
10. Barrett, et al. (2010) On Biodiversity Conservation and Poverty Traps. *Proc Natl Acad Sci USA* 108:13907–13912.
11. East T, Kumpel NF, Milner-Gulland EJ, Rowcliffe JM (2005) Determinants of urban bushmeat consumption in Rio Muni, Equatorial Guinea. *Biol Conserv* 126:206–215.
12. Schenck M, et al. (2006) Why people eat bushmeat: Results from two-choice, taste tests in Gabon, Central Africa. *Hum Ecol* 34:433–445.
13. Njiforti HL (1996) Preferences and present demand for bushmeat in northern Cameroon: Some implications for wildlife conservation. *Environ Conserv* 23: 149–155.
14. Barrett CB, Arcese P (1998) Wildlife harvest in integrated conservation and development projects: Linking harvest to household demand, agricultural production and environmental shocks in the Serengeti. *Land Econ* 74:449–465.
15. Frees EW (2004) *Longitudinal and Panel Data: Analysis and Applications in the Social Sciences* (Cambridge University Press, Cambridge, UK).
16. Damania R, Milner-Gulland EJ, Crookes DJ (2005) A bioeconomic analysis of bushmeat hunting. *Proc Biol Sci* 272:259–266.
17. Wilkie DS, Carpenter JF (1999) Bushmeat hunting in the Congo Basin: An assessment of impacts and options for mitigation. *Biodivers Conserv* 8:927–955.
18. Nielsen MR (2006) Importance, cause and effect of bushmeat hunting in the Udzungwa Mountains, Tanzania: Implications for community based wildlife management. *Biol Conserv* 128:509–516.
19. Bennett EL, et al. (2007) Hunting for consensus: Reconciling bushmeat harvest, conservation, and development policy in West and Central Africa. *Conserv Biol* 21: 884–887.
20. Fa JE, Currie D, Meeuwig J (2003) Bushmeat and food security in the Congo Basin: Linkages between wildlife and people's future. *Environ Conserv* 30:71–78.
21. Golden CG (2009) Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: A conservation and livelihoods issue. *Oryx* 43:386–392.
22. Jones KE, et al. (2009) PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648.