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Original Contribution

Eating Bushmeat Improves Food Security in a Biodiversity and Infectious Disease "Hotspot"

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Abstract: Hunting and consumption of wild animals, colloquially known as "bushmeat," is associated with health trade-offs. Contact with wildlife increases exposure to wildlife-origin zoonotic diseases yet bushmeat is an important nutritional resource in many rural communities. In this study, we test the hypothesis that bushmeat improves food security in communities that hunt and trade bushmeat regularly. We conducted 478 interviews with men and women in six communities near Cross River National Park in Nigeria. We used interview responses to relate prevalence and diversity of bushmeat consumption to household food security status. Animal-based foods were the most commonly obtained items from the forest, and 48 types of wild vertebrate animals were consumed within the past 30 days. Seventy-five percent of households experienced some degree of food insecurity related to food access. Bushmeat consumption was significantly associated with relatively higher household food security status. Rodents were more important predictors of food security than other animal taxa. Despite increased bushmeat consumption in food-secure households, food-insecure households consumed a higher diversity of bushmeat species. Results show that consumption of bushmeat, especially rodents, is uniquely related to improved food security. Reliance on a wider diversity of species in food-insecure households may in turn affect their nutrition, exposures to reservoirs of zoonotic infections, and impact on wildlife conservation. Our results indicate that food security should be addressed in conservation and public health strategies aimed at reducing human–wildlife contact, and that improved wildlife protection, when combined with alternative animal-based foods, would positively affect food security in the long term.

Keywords: Bushmeat, Food security, Nutrition, Ecosystem services, Nigeria, Zoonoses

Introduction

"Bushmeat"—a colloquial term for meat from wild animals in Africa—is widely consumed and traded, con-

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tributing to biodiversity loss and emergence of infectious diseases (Wolfe et al. 2005; Swift et al. 2007; Keesing et al. 2010; Kilonzo et al. 2013; Greatorex et al. 2016; Ripple et al. 2016). Increasingly, bushmeat consumption is considered an important component of local diets because it provides poor and marginalized hunting communities improved access to diverse and nutritious animal source foods (Brashares 2004; Brashares et al. 2011; Myers et al. 2013; Cawthorn and Hoffman 2015; Ripple et al. 2016; Brashares and Gaynor 2017). While biodiverse diets are often promoted as an effective way to improve health and food security within agronomic production systems (Burlingame 2000; Johns and Eyzaguirre 2006; Toledo and Burlingame 2006; Bharucha and Pretty 2010), we know very little about the nutritional contribution of animal biodiversity to individual diets or the consequent links to food security.

Compared to plant source foods, animal-based foods are particularly valuable as they offer increased bioavailability of micro- and macronutrients that can be difficult to obtain from plants alone (Murphy and Allen 2003). In general, intake of animal foods is positively associated with growth, cognitive development, and physical activity (Neumann et al. 2003). Negative health outcomes that are associated with deficiencies in micronutrients derived from meat (e.g., vitamin A, vitamin B-12, riboflavin, calcium, iron and zinc) include anemia, poor growth, rickets, impaired cognitive performance, blindness, neuromuscular deficits, and death (Murphy and Allen 2003). Indeed, studies have identified bushmeat as an important source of protein (Fa et al. 2003a), fat (Sirén and Machoa 2008), and iron (Golden et al. 2011), and have demonstrated links to improved nutritional status (Golden et al. 2011; Sarti et al. 2015; Fa et al. 2015).

Food-secure people "have at all times, physical, social and economic access to sufficient, safe and nutritious food which meets their dietary needs and food preferences for an active and healthy life" (USDA 1996). Food security is thereby determined not only by individual nutrients, but by availability, access, biological utilization, and stability of critical food resources (USAID 1992). The role of bushmeat in maintenance of food security is dependent on complex interactions within socioecological systems that can influence dietary patterns and food security. For example, *availability* of bushmeat depends on local ecologies, patterns of habitat disturbance, and resulting effects on animal biomass and/or biodiversity (Fa et al. 2003a). Socioeconomic factors also influence reliance on bushmeat in many regions (Brashares et al. 2011), which may in turn alter *access* to sufficient quantities of animal foods as well as the types of animals consumed. Cultural preferences and hunting practices can further influence how bushmeat is *utilized* as a food resource (Njiforti 1996; Fa et al. 2002; Friant et al. 2015). Where food security depends on bushmeat, *stability* may be threatened by unsustainable hunting and trade in bushmeat (Fa et al. 2003a, 2015). As such, food security may simultaneously depend on and drive the loss of biodiversity and bushmeat (Poppy et al. 2014). Additionally, emerging infectious disease risks are elevated in biodiverse tropical forest regions experiencing land-use changes, introducing multiple health trade-offs associated with bushmeat consumption (Allen et al. 2017; Pruvot et al. 2019). Disentangling the trade-offs between health benefits, health risks, and biodiversity conservation is a necessary step toward evidence-based decision making and policy formation (Pruvot et al. 2019).

In this study, we tested the hypothesis that bushmeat improves household-level food security through improved food access. We conducted this study in a cross section of 323 households within a biodiversity and emerging disease hotspot in West Africa (Nigeria) (Myers et al. 2000; WWF 2016), where bushmeat is economically and culturally significant (Fa et al. 2006; Friant et al. 2015) leading to multiple potential trade-offs between conservation and health. We compared the role of bushmeat consumption, relative to other food items, in predicting household-level food insecurity. We also tested the hypothesis that animal biodiversity was associated with food security by measuring differences in dietary composition of bushmeat in households that varied in their food security status. We consider our results in the context of the multiple dimensions of food security, and the interacting ecological, socioeconomic, and cultural factors that shape local diets.

Materials and Methods

Study Site and Respondents

Our study included six out of an estimated 105 communities within the support zone of Cross River National Park (CRNP) Nigeria (Fig. 1). The park is divided into two divisions, the northern Okwangwo division ($\sim$ 640 km^2) and the southern Oban ($\sim$ 3000 km^2) and forms the largest track of closed canopy rainforest in Nigeria. To capture the variability in our study area, we selected communities that represented the three predominate cultural groups

(Boki, Ejagham, and Ayo), were situated in both divisions of the park, were located in marginal rainforest zones (i.e., outside of the protected area) and deep rainforest zones (i.e., enclaves within Cross River National Park), and varied in dietary diversity, food security, and consumption of bushmeat (Friant et al. 2019). Cross River National park is part of the Cross-Sanaga-Bioko Faunal region—a biodiversity "hotspot" (Myers et al. 2000; WWF 2016). Diverse faunal assemblages within CRNP provide bushmeat to rural communities and urban markets throughout Southeastern Nigeria and into Cameroon (Fa et al. 2014). Due to high biodiversity, ongoing deforestation, dense and growing human population, and high rates of human—wildlife contact in the region, this area is also considered a "hotspot" for emerging zoonotic diseases (Allen et al. 2017).

Data Collection and Ethics Statement

Between June and August 2017, we administered 478 questionnaires to individuals from 323 households near

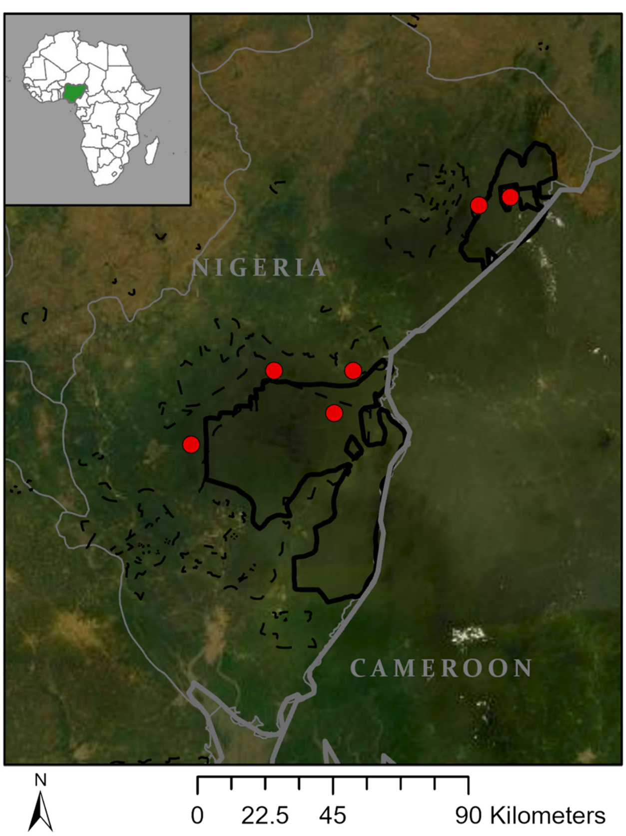

Figure 1. Map of study sites. Location of study communities (red) shown in relation to Cross River National Park (black outlines) and forest reserves (dotted outlines) within Cross River State, Nigeria (Color figure online).

Cross River National Park in South South Nigeria (*SI text*). We obtained basic demographic, livelihood, and socioeconomic information, including household participation in the bushmeat trade, alongside information on individual dietary diversity and household food security status.

Approximately 50 households were randomly selected from each community, representing on average 48% of households per village (range 14–84%). From each household, we interviewed the person responsible for food preparation to understand household-level food access (Coates et al. 2007) and individual-level dietary diversity (Kennedy et al. 2011). Because this person was typically a woman (n = 318), we randomly re-selected roughly half of households and interviewed men (n = 160) in addition to women to examine gender-based differences in dietary diversity within households. Informed consent was obtained from all individual respondents included in the study. Nigeria National Parks Service, Nigeria Health Research Ethics Committee (#NHREC/01/01/2007-18/05/2017), the City University of New York Integrated Institutional Review Board (#2016-0352), and Penn State Institutional Review Board (#00011190) approved all research activities. The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Variable Descriptions

Household and Demographic Information

We collected information to identify sociodemographic and livelihood factors that may influence food security status or bushmeat consumption. These data included: age (*years*); marital status (*yes*/*no*); living children within the household (*number*); education (0 *years—primary school*/*beyond primary school*); primary occupations (*top* 3; *open*); percentage of meat kept versus sold (*percentage*), identification of meat buyers (*from inside community*/*from outside community*). Proportions were recorded as none (0%), less than half (< 40%), half (40–60%), most (> 60%), or all (100%). For approximated estimates of proportions, categories were converted from ordinal indices to average percentages: none (0%), less than half (25%), half (50%), most (75%), and all (100%). We created a wealth index by scoring household assets, including: house ownership, material of roof and walls, number of rooms, type of toilet, household items, and hired farm laborer (Malleson et al. 2008). Households were categorized as relatively wealthy

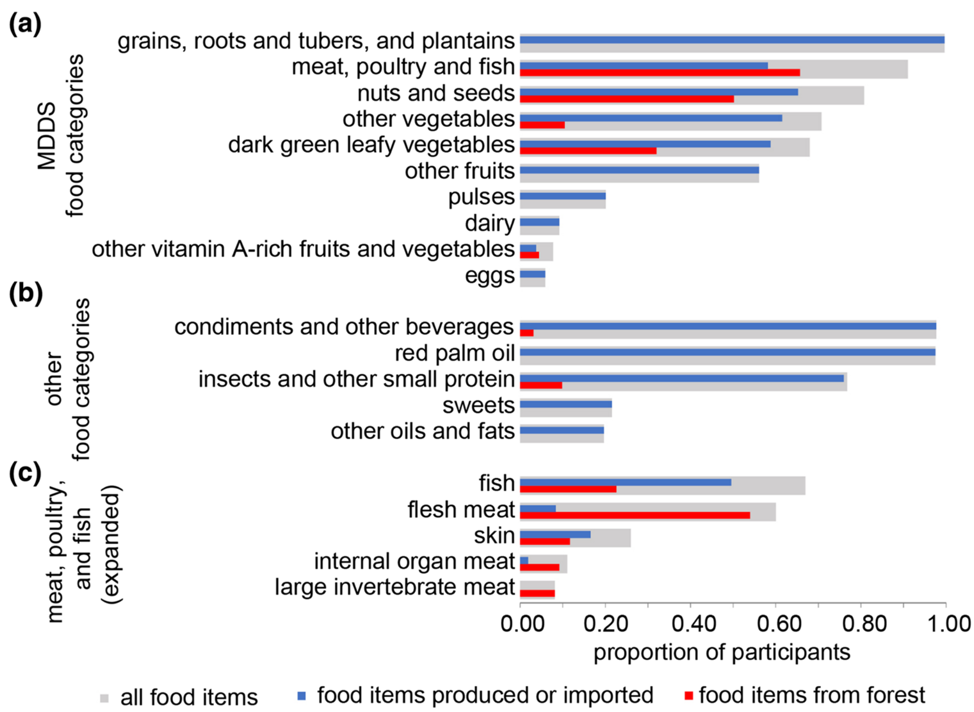

Figure 2. Individual dietary diversity. Foods reported by respondents during 24-h dietary recalls, including the source of food items consumed. Light gray bars indicate the proportion of respondents who reported consuming foods from Minimum Dietary Diversity Score (MDDS) food categories (**a**), and an expanded meat, poultry, and fish category (**b**). Different color bars represent percentages of respondents who consumed food items in each category sourced from the forest (red) versus produced or imported from outside of communities (blue) (Color figure online).

(score $\geq$ 8) and as relatively poor (score $<$ 8) out of 18 (Malleson et al. 2008).

Individual Dietary Diversity

We collected Individual Dietary Diversity Score (IDDS) data for all 478 respondents using 24-h recalls (Kennedy et al. 2011). We categorized food items into 15 food categories—10 main food categories and 5 other categories (FAO and FHI 360 2016). Within each category, we further categorized plant and animal-based food sources as either imported (sourced from markets outside of the community, either self-transported or obtained via trade), produced (cultivated foods grown within community owned lands, either self-produced or obtained via trade), or collected (wild foods sourced from forests or community owned lands, either self-collected or obtained via trade) (Table S1). We added an expanded 30-day recall for meat, poultry, fish, and large invertebrates [e.g., African giant snail (*Achatina achatina*) and crab (e.g., *Potamonemus sp.*)]. We calculated dietary diversity scores for all individuals (FAO and FHI 360 2016). In addition, we categorized women of reproductive age (15–49; n = 232) based on whether they met minimum dietary diversity scores (MDDS-W) (FAO and FHI 360 2016). We compared scores of women and men within the same households using paired t tests. Mid-upper arm circumference (MUAC), an indicator of short-term nutritional status, was measured to the nearest millimeter (mm) using MUAC tape (Frisancho 2008); however, pregnancy status was not known for females. MUAC measurements were used to evaluate physical consequences associated with insufficient intake (HFIAS) and dietary diversity (MDDS).

Food Security

We ranked 323 households on a Household Food Insecurity Access Scale (HFIAS) based on the prevalence and frequency of experiences of food insecurity related to food access (Coates et al. 2007). In each household, we interviewed the individual most involved in food preparation and meals and asked them to respond on behalf of the household. This was always the same person who was interviewed for the 24-h dietary recall. From interview responses, we calculated prevalence of households having experiences of nine household food insecurity access-related conditions within three domains (i.e., anxiety, insufficient quality, and insufficient quantity and physical consequences) to provide disaggregated information about behaviors and perceptions of households. We ranked households on the food insecurity access scale by combining prevalence and frequency-of-occurrence to create a score ranging from 0 (secure) to 27 (insecure) (Coates et al. 2007). Prevalence of household food insecurity was calculated using a standardized categorization scheme based on affirmative responses to more severe conditions and/or frequent experience of food insecurity conditions (Coates et al. 2007). We examined the relationship between dietary diversity and food insecurity under the hypothesis that lower dietary diversity would be associated with relative food insecurity.

Multivariate Regression Models Predicting Food Security Status

To identify food categories and items significantly associated with food security, we constructed three mixed-effects linear regression models built from different datasets (i.e., different levels of expansion of our MDDS food categories) to predict household placement on the food insecurity access scale. In the first model, we incorporated the 15 MDDS categories constructed from 24-h dietary recalls as covariates. In the second model, we expanded the meat, poultry, and seafood category to include the sources of foods within this category (e.g., domestic animal meat/ bushmeat, stream caught fish/imported fish, collected large invertebrates). In the final model, we expanded the bushmeat category to include the taxonomic groups of animals consumed as bushmeat (e.g., rodents, carnivores, ungulates, primates, birds, reptiles, and other small mammals).

We then examined the effect of village location (i.e., marginal vs. deep forest zone) on the relationship between food security and bushmeat consumption by incorporating village location as a main effect potentially interacting with the relationship between bushmeat consumption and household food insecurity. Finally, we constructed a set of mixed-effects logistic and linear regression models examining the relationship between sociodemographic variables on bushmeat consumption and household placement on the food insecurity access scale. Household-level models incorporated household engagement in bushmeat hunting, wealth, and number of children as variables potentially relating to bushmeat consumption and food security. For hunting households alone, we investigated whether the proportion of meat kept (vs. sold) related to bushmeat consumption or food security. At the individual level, our models included age, gender, education, and marital status as covariates potentially relating to individual bushmeat consumption.

We incorporated village as a random effect in all mixed models predicting food security status from dietary diversity categories and in household sociodemographic models. For our individual sociodemographic model, which included men and women from the same household, we incorporated household as a nested random effect within village. For all models, we initially included village and interviewer as crossed random effects, since interviewers (n = 4) appeared in more than one village (n = 6). We then fit null models including only the intercept and random effects. Interviewer explained zero variance and was thus removed from subsequent models. We included all predictor variables in full models; however, we retained only significant variables (at the alpha < 0.05 level) in final reduced models. We used backward elimination of predictor variables and AIC criterion for model comparisons and report the difference between full and reduced models. We performed all regression analyses with lmer and glmer functions in RGui 3.4.4 using the lme4 package.

Multivariate Analysis of Bushmeat Community Composition

We examined the multivariate composition of bushmeat communities consumed in food-secure and food-insecure households via non-metric multidimensional scaling analysis (NMDS) with Jaccard dissimilarity matrices. We tested for differences in compositional dissimilarity (position of the group centroid) and of homogeneity of dispersion using Permutational Multivariate Analysis of Variance (PERMANOVA) and analysis of multivariate homogeneity of group dispersion (PERMDISP) with 999 permutations, respectively. We performed analyses using the metaMDS, adonis2, and betadisp functions within the *vegan* package in RGui 3.4.4.

Results

Food Security and Dietary Diversity

During 24-h dietary recall surveys (n = 478), respondents reported consuming a minimum of 111 unique food items, including 30 recognized types of bushmeat and eight other

Figure 3. Household food insecurity. Proportion of households experiencing conditions related to food insecurity across three access-related domains.

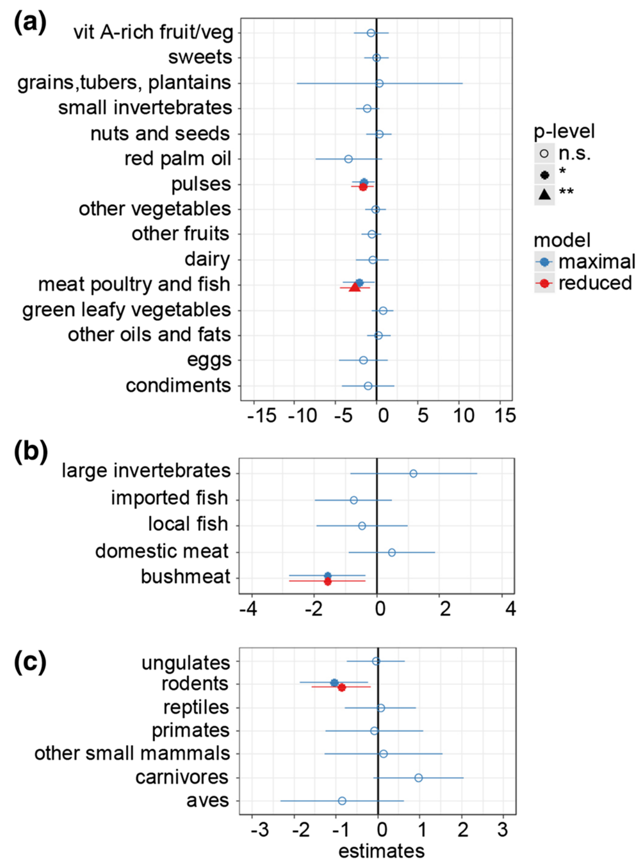

Figure 4. Food categories associated with food insecurity. Results of three mixed-effects linear models predicting household placement on the food insecurity access scale, incorporating: food categories (**a**), meat categories (**b**), and animal taxonomic groups (**c**) as predictor variables. Coefficient estimates from full models are shown in blue, and coefficients from reduced models retaining only significant predictors are shown in red. Village was included as a random effect in all models (Color figure online).

animals categorized as meat, poultry, fish, or other small proteins (SI text; Table S1). Meat, poultry, and fish, and to a lesser extent, vitamin A-rich fruits and vegetables (i.e., bush mango), were the only food groups where consumed food items were harvested from the forest more frequently than produced or imported (Fig. 2, Table S2). Food items categorized as meat, poultry, and fish were consumed by 91% of respondents. Among these items, fish (consumed by 67% of respondents) and animal skins (26%) were primarily imported from outside of communities, whereas flesh meat (consumed by 60% of respondents), internal organ meat (11%), and large invertebrates (8%) were mostly harvested from the forest (Fig. 2, Table S2).Within households, we found no significant difference in dietary diversity scores between women ($\mu = 4.97$) and men ($\mu = 5.11$) ($t = -88$, $df = 113$, $p = 0.37$). Seventy percent of reproductive women ($n = 161$) achieved minimum dietary diversity scores ($\mu \pm \mathrm{SD} = 5.04 \pm 1.24$; range 1–8). Ability to achieve minimum dietary diversity was not associated with higher MUAC ($t = 1.09$, $df = 228$, $p = 0.27$). Household food insecurity prevalence was 75%. Sixty-five percent of households reported anxiety or uncertainty about food, 87% reported perceptions of insufficient quality, and 87% reported insufficient intake and physical consequences of low food intake (Fig. 3). However, reported insufficient intake and physical consequences of low food intake was not significantly associated with mid-upper arm circumference ($t = 0.95$, $df = 320$, $p = 0.17$). Food insecurity scores ranged from 0 (secure) to 26 (insecure) out of a total of 27 possible points ($\mu \pm \mathrm{SD} = 10.33 \pm 6.18$). Households that had relatively high food security (i.e., low food insecurity access score) were more likely to have higher dietary diversity scores ($r_s = -0.21$, $df = 321$, $p < 0.001$).

Relative household food security was significantly primarily associated with the consumption of meat, poultry, and fish ($\beta \pm \mathrm{SE} = -2.67 \pm 0.92$; $p < 0.001$), and to a lesser extent, legumes ($\beta \pm \mathrm{SE} = -1.70 \pm 0.70$; $p < 0.05$) (Δ AIC = 13) (Fig. 4a, Table S3). Under an expanded meat, poultry, and fish model, relative household security was associated with increased consumption of

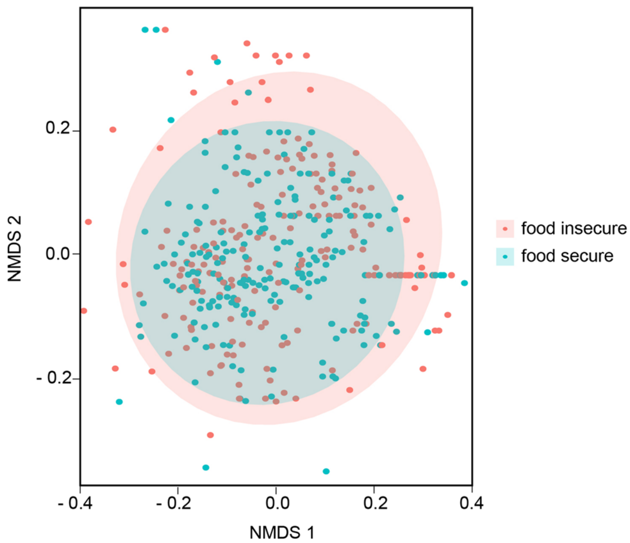

Figure 5. Bushmeat community composition. Non-metric multidimensional scaling (NMDS) plot of the first two axes of Jaccard distance matrix describing bushmeat community composition in food-secure (blue) and food-insecure (red) households (stress = 0.12; $k = 4$). The composition of bushmeat consumed by each respondent is represented by a point. Shaded area indicates 95% confidence interval ellipses (Color figure online).

bushmeat specifically ($\beta \pm$ SE $= -1.59 \pm 0.62$; $p < 0.05$; Δ AIC = 10) (Fig. 4b; Table S4). Under an expanded bushmeat model, relative household food security was related to increased consumption of rodents ($\beta \pm$ SE $= -0.88 \pm 0.36$; $p < 0.05$; Δ AIC = 8) (Fig. 4c; Table S5). Rodents reported as consumed by respondents included brush-tailed porcupine (*Atherurus africanus*; 21%), giant pouched rat (*Cricetomys emini*; 3%), marsh cane rat (*Thryonomys swinderianus*; 2%), and squirrel (Sciuridae spp.; 1%).

Community-Level Bushmeat Consumption

Ninety-four percent of respondents reported consuming bushmeat (48 reported types) during 30-day recalls (SI text; Table S6). Comparison of Jaccard dissimilarity matrices, built from bushmeat reported during 30-day dietary recalls, showed that individuals from food-secure and food-insecure households consumed different compositions of bushmeat (PERMANOVA: $F = 3.22$, $df = 1$, $p < 0.01$). Multivariate dispersion also differed between food-secure and food-insecure households (PERMDISP: $F = 15.06$, $df = 1$, $p = < 0.001$). Non-metric multidimensional scaling plot showed the composition of bushmeat consumed by food-secure households to be nested within the composition of bushmeat consumed by food-insecure households, with the latter showing higher dispersion (Fig. 5). Together, these results show that despite food-insecure households being less likely to consume bushmeat, they were more likely to consume a higher diversity of bushmeat species.

Socioecological Variables

Fifty-one percent of households reported involvement in bushmeat-related activities, either through hunting, trapping, or trading (*S1 text*). Eighty-four percent of households involved in bushmeat-related activities reported selling meat, and a majority of sellers (69%) reported selling to people outside of the community (on average 70% of meat obtained).

Several potentially confounding sociodemographic household variables were significantly associated with food insecurity. Household food security increased with wealth [$\beta = -0.42$ (95% CI -0.66, -0.18); $p < 0.001$] and decreased with the number of children [$\beta = 0.28$ (95% CI 0.05, 0.53); $p < 0.05$] (Δ AIC = 2). There was no relationship between household sociodemographic variables and individual bushmeat consumption nor any association between the amount of meat kept (vs. sold) by hunting households and bushmeat consumption or food security. However, there was a significant effect of individual-level variables on bushmeat consumption, with younger age [$\beta = -0.01$ (95% CI -0.03, -0.001); $p < 0.05$] and being male [$\beta = 1.25$ (95% CI 0.79, 1.78); $p < 0.001$] (Δ AIC = 3) significantly related to increased bushmeat consumption.

There was no interactive effect between bushmeat consumption and village location on food security; however, bushmeat consumers in marginal communities had higher food security compared to consumers in deep forest communities) [$\beta = 4.92$ (95% CI 0, 9.77); $p < 0.05$; Δ AIC = 1] (Fig. 6).

Discussion

Our study demonstrates that within Cross River National Park, a region identified as a biodiversity and emerging infectious disease "hotspot," bushmeat is an ecosystem service that helps protect households from relative food insecurity through improved access to animal-based food. Despite being less likely to consume bushmeat, individuals

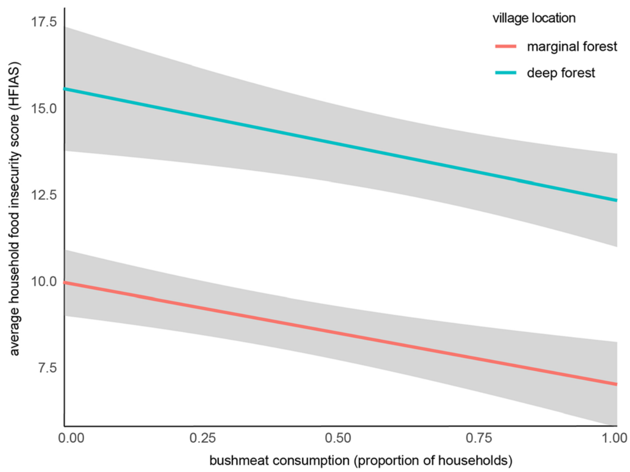

Figure 6. Community-level bushmeat consumption and food insecurity. Graph shows the relationship between food insecurity score (*y*-axis) and bushmeat consumption during 24-h dietary recalls (*x*-axis) comparing marginal and deep forest communities.

from relatively food-insecure households relied on a wider diversity of species, which may in turn alter the nutritional benefits they derive from meat as well as their exposures to reservoirs of zoonotic disease. Our results also reveal additional economic incentives of bushmeat trade that further alter the distribution of economic and nutritional benefits as well as exposures to potential reservoirs of zoonotic infections. Finally, our results help disentangle the dynamics between bushmeat and food security through observations that link bushmeat to the multiple dimensions of food security—availability, access, utilization, and stability.

Availability

Sufficient quantities of quality food must be available through wild harvest, domestic productions, or imports for maintenance of food security. Consumption of meat, seafood, and fish, and to a lesser extent, beans, was significant predictors of relatively high food security within communities. Respondents reported sourcing the highest proportion of "meat, poultry, and fish" food items from the forest, compared to items from other food categories, demonstrating the importance of bushmeat as an ecosystem service.

Although bushmeat is widely available via hunting and in rural markets across our study region (Fa et al. 2006; Friant et al. 2015, 2019), availability of bushmeat varies geographically, with consequences for livelihoods and food security on a local scale (Fa et al. 2015). Indeed, deep rainforest communities consumed more bushmeat relative to their food security status, indicating differences in availability and/or access to bushmeat across communities. Contrary to higher levels of biodiversity in deep rainforest areas, mammalian biomass may actually be lower in deep compared to marginal rainforest zones, as seen in the Congo (Fa et al. 2015). The presence of roads and increased access to markets may also reduce the availability of bushmeat locally when large-bodied prey are overharvested for market sale (Espinosa et al. 2014). Restricted access to trade routes and alternative animal-based foods, rather than simple differences in available bushmeat, may explain higher levels of food insecurity relative to bushmeat consumption in deep forest communities (Friant et al. 2019).

Bushmeat flesh and imported fish were the most commonly consumed food items classified as meat, poultry, and seafood (Fig. 2c; Table S2). These two food resources are found interchangeably in local dishes, and the availability of imported fish may in turn influence reliance on bushmeat. Nigeria relies heavily on imported fish to fill the demand gap (estimated 2.2 million metric tons) (FCWC 2016). Imported fish, more so than fish produced in inland fisheries, provides an alternative to bushmeat in forest-dwelling communities. In comparable West African systems, bushmeat consumption buffers communities against fluctuations in supplies from foreign marine fisheries (Brashares 2004). Locally sourced fish can provide an added buffer to fluctuations in availability of imported fish; however, stream caught fish are not abundant in our study communities, due in part to a long history of unsustainable fishing practices, including poisoning of streams. More recently, people describe the near-complete drying up of streams during the dry season and report draining deep water refugia of fish, which can kill all life stages of the fish and further alter the availability of alternatives.

Access

Food security requires adequate resources for access to available foods. In our study region, food insecurity was primarily related to eating small meals and an inability to eat preferred foods (Fig. 3). Variation in household access to adequate food was best explained by access to bushmeat, which was highly preferred (73% of respondents) over domestic meat and fish. Food security was also associated with higher dietary diversity, increased household wealth, and having fewer children. However, these same factors were not predictive of bushmeat consumption, such that, the relationship between bushmeat and food security appears to be independent of wealth. These results contrast with reported negative relationships between wealth and wildlife consumption in other parts of sub-Saharan Africa (Brashares et al. 2011), and positive relationships in Gabon regardless of rural or urban locale (Wilkie et al. 2004). Household wealth may, however, influence aspects of bushmeat consumption that were not measured in this study; for example, means of obtaining meat (purchased vs. hunted), portion size, consumption frequency and/or quality or type of meat. Nevertheless, bushmeat consumption was ubiquitous across households. However, we found that individual characteristics (e.g., age and sex) were related to consumption, which corresponds to the typology of hunters in this region (Friant et al. 2015). Interestingly, bushmeat consumption was not related to household hunting activities. Nor was it related to individual education or number of children. This finding directly contrasts with bushmeat hunting in the same region, which was associated with lower education and having more children (Friant et al. 2015). Differences between bushmeat hunting and bushmeat consumption may reflect contrasting values attached to consumption and hunting of bushmeat. Although bushmeat hunting is generally considered an undesirable livelihood, bushmeat itself is a highly preferred food item with additional cultural values (Friant et al. 2015). Disassociations between hunting and consuming bushmeat are not surprising given heavy involvement in bushmeat trade.

Food-secure and food-insecure households not only varied in likelihood of bushmeat consumption, but also in the diversity of bushmeat species they consumed. The average community composition of bushmeat consumed differed significantly between food-secure and food-insecure households, and this difference was heavily influenced by within group differences in bushmeat community composition (i.e., high beta diversity). Respondents consumed a core group of species, but those from food-insecure households consumed additional and different species. The differentiating species appear to be random (e.g., outliers evenly surround the core group as opposed to heavily weighted in the direction of any unique portion of species space; Fig. 5). However, food-secure households were more likely to consume rodents than were food-insecure households (Fig. 4c). Thus, increased access to animal biomass, particularly rodents, appears to be more important than animal biodiversity for improved food security status.

Utilization

In addition to availability and access to meat, food security necessitates utilization of various nutrients in food items, for example, via dietary diversity, proper food preparation and hygiene practices, and appropriate intra-household distribution of food (Hwalla et al. 2016). Overall, a quarter of the women in our study reported diets that did not meet minimum dietary diversity requirements indicating micronutrient inadequacy, and individual dietary diversity was lower in food-insecure households. We found no difference in dietary diversity between men and women from the same household. However, there was a gender-based difference in bushmeat consumption within households, indicating unequal distribution of bushmeat with consequences for individual food security, which directly contrasts to results from other regions (Golden et al. 2016).

Meat, poultry, and fish had the highest diversity of food items within a single food category [38 out of 111 total foods reported during 24-h recalls (Table S1)]; however, the nutritional significance of this diversity is not well understood, given the paucity of data on nutritional quality of wild meat (Cawthorn and Hoffman 2015). Bushmeat is routinely referred to in terms of its contribution to dietary protein in rural communities, and our results are supportive of this claim (Albrechtsen et al. 2005; Alves Fonseca et al. 2013; Vega et al. 2013). However, bushmeat and fish are also an important source of fat in some hunting communities (Sirén and Machoa 2008). Given the putative low fat content of wild meat, compared to domestic meat, skin, and fish (Sirén and Machoa 2008), and the high consumption of domestic animal skins and high palm oil (97% of respondent; Table S2), the importance of wildlife in contributing to dietary fat in our study communities is questionable. Conversely, internal organs were most commonly sourced from bushmeat and may offer added nutritional benefits that are not typically considered when measuring nutritional contributions of bushmeat to diets (e.g., micronutrients such as vitamins)(Neumann et al. 2003; Sarti et al. 2015).

Our results suggest potential interactions between food security and zoonotic disease exposure through dietary differences that influence differential patterns of human–wildlife contact in food-secure and food-insecure households. We found that relatively higher food security status was associated with consumption of rodents, which are known to be important hosts of re-emerging zoonotic diseases in Nigeria (e.g., monkeypox and Lassa Fever; Morand et al. 2015; Roberts 2018; Yinka-Ogunleye et al. 2018). However, we also found that food insecurity was associated with exploitation of a wider diversity of bushmeat species, which might increase exposure to a wider diversity of novel pathogens. Exposure risks are likely to be further exacerbated by the lack of safe handling practices identified in these same study communities (Friant et al. 2015). Furthermore, food insecurity can influence susceptibility to infections via known effects of poor nutrition on immune function and infection risk (Scrimshaw and SanGiovanni 1997). Such relationships may increase risk in our study area, where food insecurity is highly prevalent and is a driver of risky human–wildlife contact.

Stability

Long-term food security requires stable access to food. Conservative estimates of wildlife offtake in our study region as a whole show 900,000 mammals, birds, and reptiles being sold between Nigeria and Cameroon every year (approx. 12,000 tons of terrestrial vertebrates), with the majority in Nigeria (est. 600 kg harvested per kilometer squared every year) (Fa et al. 2006). In a sustainable bushmeat scenario in neighboring Cameroon, where population density is considerably lower, bushmeat protein would contribute 3–5% to local diets, which is far below current empirical estimates (Fa et al. 2003b). Indeed, we found high levels of bushmeat consumption, with over 90% of respondents reporting eating bushmeat in the previous 30 days.

Our study demonstrates additional economic benefits derived from bushmeat that also drive hunting. For example, half the households reported involvement in the bushmeat trade and a majority of hunters reported selling the bulk of meat that they hunt to people outside of the community. The proportion of bushmeat kept versus sold had no effect on bushmeat consumption or household food security, suggesting that hunters harvest amounts that exceed the needs of the household, and that trade of excess does not significantly affect household food security. Overall, communities with a higher proportion of households consuming bushmeat had on-average higher food security. Interestingly, marginal zone communities had higher food security compared to enclave communities, despite less consumption of bushmeat, possibly due to increased market vicinity and availability of alternatives (Friant et al. 2019). However, we did not look at differences in quantities consumed, which would lend further insight. Bushmeat trade can also affect food security of neighboring households, when traders sell meat to people outside of the communities at larger profit margins. Given the magnitude of commercial trade combined with importance of bushmeat for food security, declines in wildlife biomass are likely to adversely affect ecosystems and their services, including food security. Ecosystem health for the benefit of humans, animals, and the environment, will require improved wildlife protection and horizontal approaches that target root drivers of unsustainable bushmeat hunting, including improved access to nutritional and economic alternatives to assuage wildlife offtake locally, as well as rural and urban campaigns designed to shift preferences away from bushmeat and curb market demand.

Conclusion

A large number of wild species are used for food worldwide, especially in low- and middle-income countries; however, their contributions to food security are routinely overlooked and not well understood (Godfray et al. 2010). Our study highlights the importance of bushmeat in maintaining food security despite substantial participation in the bushmeat trade. Unsustainable hunting in this region threatens food security in the long term, especially when considering the positive feedbacks that could arise from interactions between over hunting and food insecurity. Effects would be especially great in regions across Africa where global hunger continues to rise and bushmeat is nutritionally important (FAO 2011; Golden et al. 2011).

Given the deep relationship between hunting and consumption of bushmeat and people's livelihoods, diets, and food preferences, interventions should combine improved forest protection with efforts that: (1) increase community recognition of long-term problems, (2) develop community-informed interventions, and (3) engage communities in research, implementation, and governance. Community-driven solutions will be necessary to identify and implement interventions that would help break the strong ties to hunting and consumption of bushmeat. While unsustainable hunting is not a widely recognized problem, communities readily acknowledge low household supply of meat. In an enclave community with limited access to markets, people demonstrated motivation to improve local fisheries and abandon unsustainable fishing practices, and interventions based on this approach would likely receive strong community backing. Although bushmeat is highly preferred over meat from domestic animals, our data show that people will incorporate domestic animals into their diets and food preferences as they become increasingly accessible (Friant et al. 2019). Nutritional alternatives to bushmeat could be offered in the form of animal husbandry programs [e.g., low-input backyard chickens (Wilkie et al. 2016; ACGG 2014)], and improved management of inland fisheries (Welcomme et al. 2010; Lo et al. 2019).

Our study communities lack the cultural traditions of raising livestock, and when introduced, many report the decimation of entire stocks due to disease and predation from animals and humans. Introducing animal husbandry into remote forest communities that lack these cultural traditions will require significant expertise and resources. One promising local solution is the development of roadside butcheries that have started to pop-up throughout the region. Indeed, domestic meat appears to be most readily available in remote communities with road or boat access to junctions with small butcheries providing cow and goat meat (Friant et al. 2019); however, road access also opens up increased opportunities for habitat destruction and bushmeat trade (Wilkie et al. 2000). Programs based on developing bushmeat alternatives offer promising opportunities for supplementing need-based consumption of bushmeat and mitigating food insecurity in response to declines in bushmeat availability (i.e., from overhunting or improved park protections). However, co-benefits for conservation and public health are likely to be low when hunters shift to economic-based hunting (Friant et al. 2019).

Economic alternatives to trade are also necessary to prevent unsustainable offtake and food insecurity in the long term. Though bushmeat is highly valued, hunting is considered a low-merit livelihood that people say they would give up if they had another opportunity (Friant et al. 2015). Farming of cocoa has provided this opportunity for many, but contributes heavily to deforestation (Oluyole and Sanusi 2009; Ruf et al. 2015). In our experience, construction opportunities that engaged youths for $4.20/day was enough to prevent them from entering the forest to hunt for a 3-month period, albeit unintentional (pers obs.). Thus, offering co-benefits for human, animal, and environmental health requires multi-faceted community-driven approaches that target multiple drivers of bushmeat hunting. This includes efforts that target nutritional, economic, and cultural drivers of human–wildlife contact, enhance community governance over natural resources, and improve wildlife and habitat protection.

Our results also help disentangle the multiple trade-offs of hunting and consuming bushmeat, and how they relate to conservation and health policies. For example, protecting endangered species is central to biodiversity conservation and this is often considered to conflict with food security in areas where people rely heavily on wild foods. Our results highlight the importance of animal biomass over species diversity in improving household food security, although we also note the importance of a broader range of species to food-insecure households which requires further attention. The trade-offs for local people will therefore be different across different groups of animals. For example, primate conservation initiatives that successfully prohibit primate hunting would be less likely to negatively impact food security and protecting primates would have high value for biodiversity conservation and disease prevention. In comparison, public health initiatives that advise against hunting and consumption of small prolific animals (e.g., rodents) as a means of blocking transmission pathways for zoonotic disease may have more adverse effects on food security. Indeed, rodents are relatively robust taxa (fast reproducers) offering sustainable alternatives to hunting vulnerable species (slow reproducers) (Cowlishaw et al. 2005; Ripple et al. 2016), thereby leading to additional trade-offs between conservation and health. Overall, interventions and policies centered on managing the human–wildlife interface in biodiversity and infectious disease hotspots should explicitly consider these trade-offs and strive to maximize co-benefits and minimize risks for environmental, food, and global health security.

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