# Wild meat: a shared resource amongst people and predators

R. J. Foster, B. J. Harmsen, D. W. Macdonald, J. Collins, Y. Urbina R. Garcia and C. P. Doncaster

**Abstract** Millions of people throughout the tropics consume wild meat. Overhunting reduces food security for people and large predators, yet little is known of the impact of hunting in systems where people and predators target the same prey species. We collate published data on predator diet in Belize with interview data about the consumption of wild and domestic meat by Belizeans, to compare the wild-meat diets of humans, jaguars *Panthera onca* and pumas *Puma concolor* and assess the sustainability of the combined offtake by humans and jaguars. Six wild mammal species (nine-banded armadillo *Dasypus novemcinctus*, paca *Cuniculus paca*, collared peccary *Pecari tajacu*, white-lipped peccary *Tayassu pecari*, red brocket deer *Mazama americana* and white-tailed deer *Odocoileus virginianus*) comprised 7% of the animal-protein meals eaten by Belizeans. Overall, 80% of these meals were eaten by 20% of interviewees, suggesting a necessary role of wild meat for the minority. The same species were found in 69 and 86% of jaguar and puma scats, respectively. We estimate a national annual harvest of c. 4,000 tonnes of these six wild mammals by humans and jaguars, of which 78% is hunted by people. Sustainability is difficult to evaluate because prey population data are lacking in Belize. However, simple models suggest that a sustainable harvest at this rate would require higher prey population densities than averages recorded in hunted Neotropical forests. We emphasize the need for robust regional estimates of game species densities, to improve assessments of sustainability and inform hunting regulations. We recommend that the requirements of predators as well as those of people be considered when assessing wild meat harvests.

**Keywords** Hunting, jaguar, Neotropical forest, prey, puma, sustainable, wild meat

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## Introduction

Wild meat provides protein and income for millions of people throughout the tropics. Overhunting, in combination with human population growth, development and deforestation, has intensified the decline of tropical terrestrial vertebrates (Fa et al., 2007). Defaunation of tropical forests has far-reaching social, economic and ecological implications. It threatens food security and livelihoods (Gordon et al., 2012) and alters forest regeneration and composition, with cascading effects on other taxa (Stoner et al., 2007; Reider et al., 2013). It also depletes wild prey hunted by carnivores and thereby encourages livestock predation, which can be unsustainable for the rural poor and can lead to retaliatory lethal control of carnivores (Loveridge et al., 2010).

From the perspectives of food security and biodiversity conservation, alleviating the bushmeat crisis (Nasi et al., 2008) requires a better understanding of interactions between people, non-human predators and prey. Assessments of wild meat harvest in the tropics have focused primarily on offtake by people in two systems, the Congo and Amazon Basins (e.g. Fa et al., 2002). In the Congo Basin, low livestock production means that both urban and rural people rely heavily on wild meat (Nasi et al., 2011). In the Amazonian countries the protein demands of urban populations are fulfilled by intense livestock production but wild meat often comprises a significant proportion of the protein consumed by forest-dwelling communities (Rushton et al., 2005; Nasi et al., 2011; World Bank, 2013a,b,c). The roles of non-human predators have been largely overlooked in studies of these systems. In particular there has been limited research on human–carnivore competition and on the viability of prey populations that are targeted both by people and carnivores. Two studies have detected overlap between predator diet and hunter harvest composition, indicating a negative correlation between

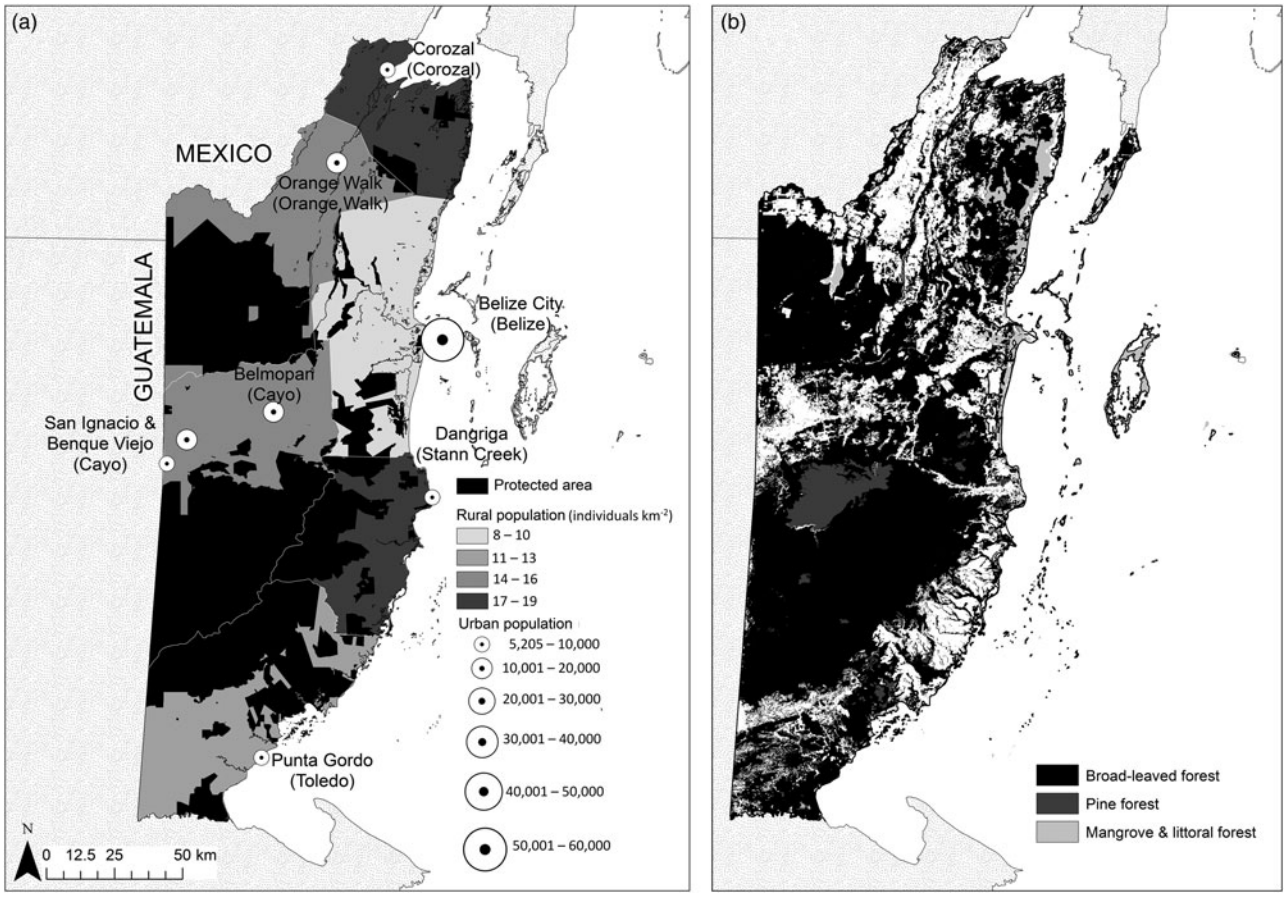


FIG. 1 (a) Map of Belize, showing the locations of protected areas, the rural population density outside protected areas, and the human population in urban centres, with districts in parentheses. (b) Forest cover in Belize (Cherrington et al., 2010; Meerman, 2011).

hunting intensity and predator density/occurrence (Brazil, Leite & Galvão, 2002; Gabon, Henschel et al., 2011). To our knowledge, however, no attempts have been made to explore the sustainability of the three-way interaction between human hunters, predators and prey. Here we report the first study to estimate harvest rates by both people and a predator, and to thereby assess the sustainability of hunting shared prey species.

The Central American country of Belize offers an opportunity to analyse human–predator–prey interactions in a simple system with only two potential wild competitors, the jaguar *Panthera onca* and puma *Puma concolor*, in a region that constitutes a critical link in the transcontinental corridor for jaguars (Rabinowitz & Zeller, 2010). We measured the importance of wild mammals in the Belizean diet on a national scale, and identified correlates of consumption rate. We tested for dietary overlap between people, jaguars and pumas, to assess whether they might be competing. We estimated national annual harvests of the six wild mammal species, both by people and jaguars, evaluated sustainability using simple species-specific models, and discussed the implications of wild-meat harvest for people, predators and prey species.

Hunting wild prey for human consumption is documented throughout Central America (Wilkie & Godoy, 2001; Jones & Young, 2004; Koster, 2008; Smith, 2008); however, unlike the well-studied regions of the Congo and Amazonia, little is known of the scale or importance of wild meat in the diet of Central Americans. To our knowledge this study represents the first national assessment of wild-meat consumption in Central America.

## Study area

Belize is the least densely populated country in Central America, with a mean of 14 people per km² across six districts: Corozal, Orange Walk, Cayo, Belize, Stann Creek and Toledo (Belize Statistics Office, 2010). Seven urban centres accommodate 43% of the population (Fig. 1); the remainder live in rural areas, where the population growth rate is 2.3% per year, the fastest in Central America (UN, 2013). Approximately 63% of the mainland is forested

(Cherrington et al., 2010; Meerman, 2011), principally secondary moist broadleaf forest regenerating following natural and anthropogenic disturbances, interspersed by patches of remnant primary forest (P. Cho, pers. comm.). On the mainland, 43% of the land area comprises national, private or candidate protected areas (Fig. 1), which are uninhabited. However, only 17% of the mainland is legally protected against wildlife extraction, and enforcement is limited. Outside these lands, game hunting and the sale of game meat are licensed within species-specific seasons (Belize Wildlife Protection Act, 2000, 2003). It is illegal to hunt or sell game meat without a licence, and to hunt outside the specified seasons. Few people apply for permits (RG, unpubl. data), however, and the government lacks the capacity to enforce these laws.

## Methods

### National survey

In 2010 we interviewed 806 people across Belize, at each of the district bus stations and in the market squares of the main urban centres (Fig. 1), to sample a wide cross-section of society using public transport and visiting the markets (although potentially under-sampling the wealthy elite and those from remote villages). We asked interviewees about their community and district of residence, weekly income bracket (USD 0–75, 76–150, 151–225, 226–300, 301+), and how often they ate different meats, citing local names for five types of domestic stock (chicken, pork, sheep/mutton/lamb, beef, buffalo), six species of wild terrestrial mammal (nine-banded armadillo *Dasypus novemcinctus*, paca *Cuniculus paca*, collared peccary *Pecari tajacu*, white-lipped peccary *Tayassu pecari*, red brocket deer *Mazama americana*, white-tailed deer *Odocoileus virginianus*) and three types of wild aquatic vertebrates (saltwater fish, freshwater fish and Central American river turtle *Dermatemys mawii*). Finally, we asked if they ate other meats. Only 10 of the interviewees reported eating wild mammals other than the six listed, which we henceforth refer to as the six common wild mammal species in the human diet. Because the interviews were conducted by university students, not government officials, and respondents were asked about meat consumption, not explicitly about hunting, it is unlikely that respondents under-reported their consumption of wild meat as a strategy to hide illegal hunting activities. We see no reason to suspect a bias of over-reporting of wild meat consumption. However, in case of under-reporting, our estimates of consumption and thus harvest should be considered conservative.

Of 806 responses 702 were given in a frequency format of *x* meals per week/month/year and were converted to meal servings per person per year. The remaining 104 respondents answered in terms of the quantity of meat consumed by the household over a specified period. These data were excluded from analyses requiring the meal frequency format.

### Diet composition and shared use with predators

We calculated the relative frequency of occurrence of each species in the diet as:

$$100 \times \sum(\text{servings of species } x \text{ per year}) \Big/ \sum(\text{servings per year over all species})$$

using data from interviewees who provided unambiguous numerical responses for each species (n = 647). We calculated dietary diversity of the wild mammal component (the six common species) in terms of food niche breadth, *B*, following Levins (1968) and standardized to $B_{sta}$ following Colwell & Futuyma (1971). Values of $B_{sta}$ range from zero to unity (low to high dietary diversity). We used the niche overlap index of Pianka (1973) to compare usage of the six common species between humans, jaguars and pumas, using published data on jaguar and puma diet from Belize (Foster et al., 2010b).

### Variation in consumption rate of wild mammals

We categorized consumption data by frequency: never, yearly (< twice per year), monthly (< twice per month), weekly (< twice per week) and daily (≥ twice per week). We used ordinal logistic regressions to test whether consumption-rate category differed (1) between the six common species of wild mammal, and (2) between districts and rural/urban areas.

We tested for Pearson product-moment correlations between the district mean annual consumption of wild mammal meals per person and (1) poverty, (2) indigence (extreme poverty) and (3) forest cover per person (calculated as area of district forest cover/district population). For forest cover the test was repeated excluding white-tailed deer, as they favour deciduous forest interspersed with grassland and are rare in mature evergreen forest (Reid, 2009).

### Harvest of wild mammals by humans

We asked people who prepared wild meat for consumption on a regular basis to estimate the number of servings (meals) they obtained from an average-sized individual of each of the six target species (Supplementary Table S1). These estimates captured species-specific variation in serving sizes but did not distinguish subsistence consumption from sale for profit, or cultural differences between the food preparers. We used these estimates to convert the number of meals

consumed by people to the number of animals removed from the wild:

$$\text{Individuals} = \frac{\text{Number of servings of species } x \text{ eaten per year}}{\text{Number of servings obtainable from one individual of species}}$$

These are conservative estimates, given our lack of knowledge of animals that were injured by hunters and subsequently died in the field. For each district we categorized the offtake estimates as rural or urban depending on where interviewees lived, calculated the mean for each category, and extrapolated to the national level by multiplying by the rural and urban populations for each district (Belize Statistics Office, 2010). We excluded children $< 5$ years old, assuming negligible serving size.

## Harvest of wild mammals by jaguars

To estimate the annual meat intake of adult jaguars we used mean masses of male and female jaguars in Belize (Rabinowitz & Nottingham, 1986; Foster, 2008) and assumed that males require 40 g of meat per day per kg of body mass (after Emmons, 1987; following Polisar et al., 2003; Novack et al., 2005; de Azevedo & Murray, 2007). For females we derived reproductive correction factors from Laundré (2005) to estimate the larger daily requirements during pregnancy (44 g), lactation (60 g) and dependency (cubs taking solid food; 128 g), adjusted by the mean lengths of pregnancy (96 days), lactation (74 days) and dependency (556 days; Kitchener, 1991; Sunquist & Sunquist, 2002) and combined to estimate the mean requirements of a reproductively active female jaguar.

We estimated the annual harvest of each wild mammal from estimates of the annual meat requirements of adult jaguars and published estimates of the relative biomass of prey consumed by jaguars from an area of c. 525 km² within and outside Cockscomb Basin Wildlife Sanctuary, a protected area in south-east Belize (Foster et al., 2010b). We assumed that diet in the Sanctuary was representative of all protected areas and diet outside was representative of all unprotected areas. However, we recommend further research on jaguar diet across Belize. Foster (2008) and Figueroa et al. (in press) estimated the size of the national jaguar population by extrapolating from 16 published and unpublished density estimates spanning the country. The population estimates are crude and have potential for refinement as more survey data become available from other areas of Belize, and more robust methods of density estimation are developed (e.g. Borchers et al., 2014). We used upper limits of 520 and 240 jaguars within and outside protected areas, respectively (Foster, 2008; Figueroa et al., in press), and assumed a 1 : 1 sex ratio. Separately for males and females, within and outside protected areas, we calculated the mass of each species consumed annually as:

$$\text{Mass} = (\text{relative biomass of species } X \text{ consumed}) \times (\text{annual intake of meat by adult jaguar})$$

For prey $> 15$ kg and for armadillos we assumed that 30% of the carcass was inedible (Emmons, 1987; Polisar et al., 2003; Novack et al., 2005). There is no evidence of jaguars preying preferentially on young prey in Belize (e.g. adults comprise 86% of the peccary biomass consumed by jaguars; Foster et al., 2010b), and therefore we used mean mass of adult prey species in our calculations. We estimated the number of individuals hunted annually per jaguar as:

$$\text{No. of individuals} = \text{mass of species } X \text{ consumed per year by adult jaguar} / \text{mean mass of species } X$$

National offtake was calculated by multiplying harvest per jaguar in each category (male/female, inside/outside protected areas) by our estimate of the number of jaguars in each category. To estimate harvests by district we multiplied national offtake in protected areas by the ratio of district protected area to national protected area, repeated for unprotected areas, and summed the two products.

We were unable to estimate the national offtake by pumas because only one abundance estimate exists for Belize, from a 110 km² site in protected forest (Kelly et al., 2008). Evidence suggests that pumas are less common than jaguars in Belize (Foster et al., 2010a; RJF & BJH, unpubl. data).

## Sustainability of wild-mammal exploitation

For each prey species we converted the offtake estimates (number of individuals harvested) to harvest densities (individuals harvested per km² of suitable habitat) by dividing by the species-specific habitat areas available for each prey species (Supplementary Table S2). We used broad habitat categories within which it is likely that habitat use varies on a finer scale. For example, species that use agricultural landscapes may only use certain crops, and this may vary seasonally. Estimates of species-specific habitat areas (Supplementary Table S2) could be improved by future research on fine-scale habitat use by prey species. We estimated harvest densities per district and overall at the national level. The district estimates assume no transfer of meat across district borders between harvest and consumption. The national estimate makes no assumption about the district of origin of the meat. We assessed the sustainable use of the six mammals, using simple models for production and harvest (Robinson & Redford, 1991; Robinson & Bodmer, 1999; Bodmer & Robinson, 2004).

### Production model

For each species we compared our estimates of annual harvest by people to the estimates of maximum sustainable harvest in Robinson & Redford (1991), which were derived from estimates of the finite rate of increase, carrying capacity and life span of the species. A harvest was considered unsustainable if it exceeded the maximum sustainable harvest. We excluded harvest by jaguars from these models because the estimates of Robinson & Redford (1991) derive from populations that are not hunted by people but are subject to non-anthropogenic pressures such as predation. The model of maximum sustainable harvest (Robinson & Redford, 1991) assumes that population growth is density-dependent such that maximum production occurs at 60% of the carrying capacity; it further assumes that the sustainably harvestable proportion of production varies with life span such that 20% of production can be harvested for long-lived (> 10 years), 40% for short-lived (5–10 years) and 60% for very short-lived species (< 5 years). Because prey densities in human-hunted areas are generally lower than the densities used by Robinson & Redford (1991) to estimate maximum sustainable harvest, we used this model only to identify unsustainable harvests, not to confirm sustainable harvests.

### Harvest model

For each species we estimated the threshold prey density ($D$) below which the observed harvest would be unsustainable, by rearranging the harvest model of Robinson & Bodmer (1999) such that $D = (2 \times P)/(R \times F)$, where $P$ is the observed annual harvest by people and jaguars, $R$ is the number of young produced per female-year, and $F$ is the correction factor for lifespan (explained above). Parameter estimates for the model were derived from the literature (Supplementary Table S3). We compared the threshold estimates to prey field density estimates reported in the literature from hunted field sites within the Neotropics to assess the sustainability of observed harvests, assuming that density estimates from the region are representative of prey densities in Belize. We chose to compare with hunted rather than pristine systems because hunting occurs across Belize.

The maximum sustainable harvests and field density estimates for these models are based on species inhabiting tropical forest. However, our estimates of species harvest densities assume that armadillos also use savannah and agricultural areas, collared peccaries also use savannah, and white-tailed deer are more associated with these open habitats than with deep swathes of wet forest (Supplementary Table S2). In the absence of non-forest field density estimates we assumed that density was the same across all habitat types, although the density and productivity of some species may be higher in open areas than in tropical forest (Robinson & Bennett, 2004).

White-lipped peccaries of Central America tend to be limited to large undisturbed tracts of forests (Reid, 2009). Our inclusion of all forest fragments probably overestimates the area of habitat available for this species and consequently underestimates both the harvest per km² of suitable habitat and threshold density necessary to sustain the observed harvest of white-lipped peccaries.

## Results

A mean of 134 ± SD 25.4 people (n = 806) were interviewed in each of the six districts. Approximately half of the interviewees were from the urban centres; the remainder were from 123 of the country's 349 rural communities (Supplementary Table S4). Representative samples of rural populations were interviewed in all districts except Stann Creek and Toledo, which were undersampled relative to their fraction of the total populations (Supplementary Table S4). Of the 806 interviewees 75% ate at least one of the six common wild mammal species. There was no association between income bracket and the proportion of people who consumed wild-mammal meat ($\chi^2_4 = 3.00$, $P > 0.56$). People reported eating other mammal species at low rates: tapir *Tapirus bairdii* (0.4% of people), puma and/or jaguarundi *Puma yagouaroundi* (0.1%), coati *Nasua narica* (0.1%), raccoon *Procyon lotor* (0.1%) and howler monkey *Alouatta pigra* (0.1%). Additionally, 7% of people reported eating iguana (Iguanidae) and 2.4% wild birds.

### Composition of diet and shared use with felid predators

Domestic mammals and poultry comprised 62.4% of reported animal-protein meals, with the remainder comprising fish (30%), wild mammals (7.3%) and wild reptiles (0.3%). Wild mammals comprised 10.4% of animal-protein meals in rural areas and 4.9% in urban areas. The standardized food niche breadth, $B_{sta}$, for the wild mammal component of the diet was 0.57 overall, and higher in the rural population (0.62) than in the urban population (0.48).

Paca was the most common wild mammal species in both human and puma diets, whereas armadillo was most frequent in the jaguar diet (Table 1). Relative use by humans of the six common wild mammal species was more similar to pumas than jaguars (Pianka index: human–puma = 84%, human–jaguar = 48%; Table 1). Relative occurrence of wild ungulates in the human diet was 3.0%, compared to 17.7 and 20.8% for jaguars and pumas, respectively. Paca comprised 2.9% of human diet, compared to 57.9% for pumas; armadillo comprised 1.4% of human diet, compared to 46.4% for jaguars (Table 1).

TABLE 1 Relative incidence of the six common wild mammals in people's animal-protein meals and in jaguar *Panthera onca* and puma *Puma concolor* scats, ordered by increasing body mass of prey (data in parentheses are percentages based only on these six species, which comprise 7, 69 and 86% of human, jaguar and puma diet, respectively), estimates of annual national harvest by humans and jaguars, and the total live biomass harvested.

| Species | Relative incidence (%) | | | National harvest (individuals per year) | | | Total live biomass harvested (t per year)[4] |
|---|---|---|---|---|---|---|---|
| | Human[1] | Jaguar[2] | Puma[3] | Human | Jaguar | Total | |
| Armadillo *Dasypus novemcinctus* | 1.4 (19.3) | 46.4 (67.7) | 7.1 (8.3) | 100,343 | 108,683 | 209,026 | 1,045 |
| Paca *Cuniculus paca* | 2.9 (40.0) | 4.5 (6.5) | 57.9 (67.5) | 130,574 | 4,452 | 135,026 | 1,148 |
| Collared peccary *Pecari tajacu* | 0.5 (6.7) | 5.0 (7.3) | 3.6 (4.2) | 14,129 | 4,262 | 18,391 | 350 |
| Red brocket deer *Mazama americana* | 0.5 (7.5) | 2.9 (4.2) | 8.6 (10.0) | 8,748 | 1,832 | 10,579 | 233 |
| White-lipped peccary *Tayassu pecari* | 0.3 (3.7) | 9.8 (14.2) | 7.9 (9.2) | 4,849 | 6,132 | 10,982 | 368 |
| White-tailed deer *Odocoileus virginianus* | 1.7 (22.9) | 0.0 (0.0) | 0.7 (0.8) | 28,064 | 0 | 28,064 | 954 |
| Other foods | 92.7 | 31.4 | 14.2 | | | | |
| *Total* | 100 (100) | 100 (100) | 100 (100) | 286,707 | 125,360 | 412,068 | 4,098 |

[1]n = 647 interviews, equivalent to 278,684 meals
[2]From Foster et al. (2010b); n = 322 scats, equivalent to 378 prey items
[3]From Foster et al. (2010b); n = 127 scats, equivalent to 140 prey items
[4]Calculated from mean live weight of adult prey, derived from Reid (2009)

## Variation in rate of consumption of wild mammals

People who ate wild mammals generally did so monthly to yearly (Fig. 2). Consumption rates differed for the six common wild-mammal species (logistic regression, $|z| > 6.00$, $P < 0.001$), except between red brocket deer and collared peccary, which were eaten at similar rates ($|z| = 0.54$, $P = 0.589$; Fig. 2). Mean meal frequencies per person per year varied from 12.6 for paca to 1.2 for white-lipped peccary; 60% of the interviewees ate paca whereas only 8% ate white-lipped peccary. Overall, 80% of wild-mammal meals were eaten by 20% of interviewees (n = 634), reflecting the representation of hunters in the national population (c. 20%; YU, unpubl. data). On a species-by-species basis the fraction of interviewees eating 80% of meals was 2% for white-lipped peccary, 6% for collared peccary and red brocket deer, 8% for armadillo and 17% for white-tailed deer and paca.

Paca, armadillo, collared peccary and white-tailed deer were eaten more often in rural than urban areas (all $\chi^2_1 > 30.8$, $P < 0.0001$); no such differences were detected for red brocket deer or white-lipped peccary. Consumption of wild mammals was higher in rural Toledo than elsewhere: 30% of interviewees there ate wild meat daily (≥ twice per week), compared with 5–13% in rural areas of the other five districts (Fig. 3). Toledo differed from each of the other districts pooled across urban–rural sample types (logistic regression $z \geq 2.73$, $P < 0.05$) and the rural Toledo sample differed from urban samples pooled across districts ($z = 4.17$, $P < 0.01$), as did the rural Orange Walk sample ($z = 3.11$, $P < 0.01$), with no other district or type effects or interactions, after Bonferroni correction for multiple pairwise comparisons. Overall, consumption was higher in rural Toledo than in other rural samples pooled across districts.

The mean district rate of consumption of wild mammals correlated positively with the district area of forest available per person, both including and excluding meals of white-tailed deer (Pearson coefficients > 0.9, $P < 0.05$, n = 6; Fig. 4), but not with the district levels of poverty or indigence (both $P > 0.07$). However, Toledo, where the level of indigence is more than twice as high as in the other districts, also had the highest consumption rate (Fig. 4) and significantly higher rates in rural areas (Fig. 3).

## Harvest of wild mammals by humans and jaguars

We estimated that humans and jaguars took similar quantities of armadillos annually, whereas humans took more than twice as many of the three ungulate species that, combined, comprise 18% of jaguar diet: collared peccary, white-lipped peccary and red brocket deer (Table 1). An estimated 4,000 t of biomass of the six common species was harvested each year by jaguars and people combined, with humans responsible for 78% of this (Table 1).

## Sustainability of wild-mammal exploitation by humans and jaguars

*Production model* Annual national harvests of paca and white-tailed deer exceeded the maximum sustainable harvest of rainforest populations at carrying capacity; harvests of armadillo and red brocket deer were borderline unsustainable (Table 2). Harvests of either peccary species did not exceed the maximum sustainable harvest but because low harvests may reflect current depletion we cannot conclude harvests are sustainable.

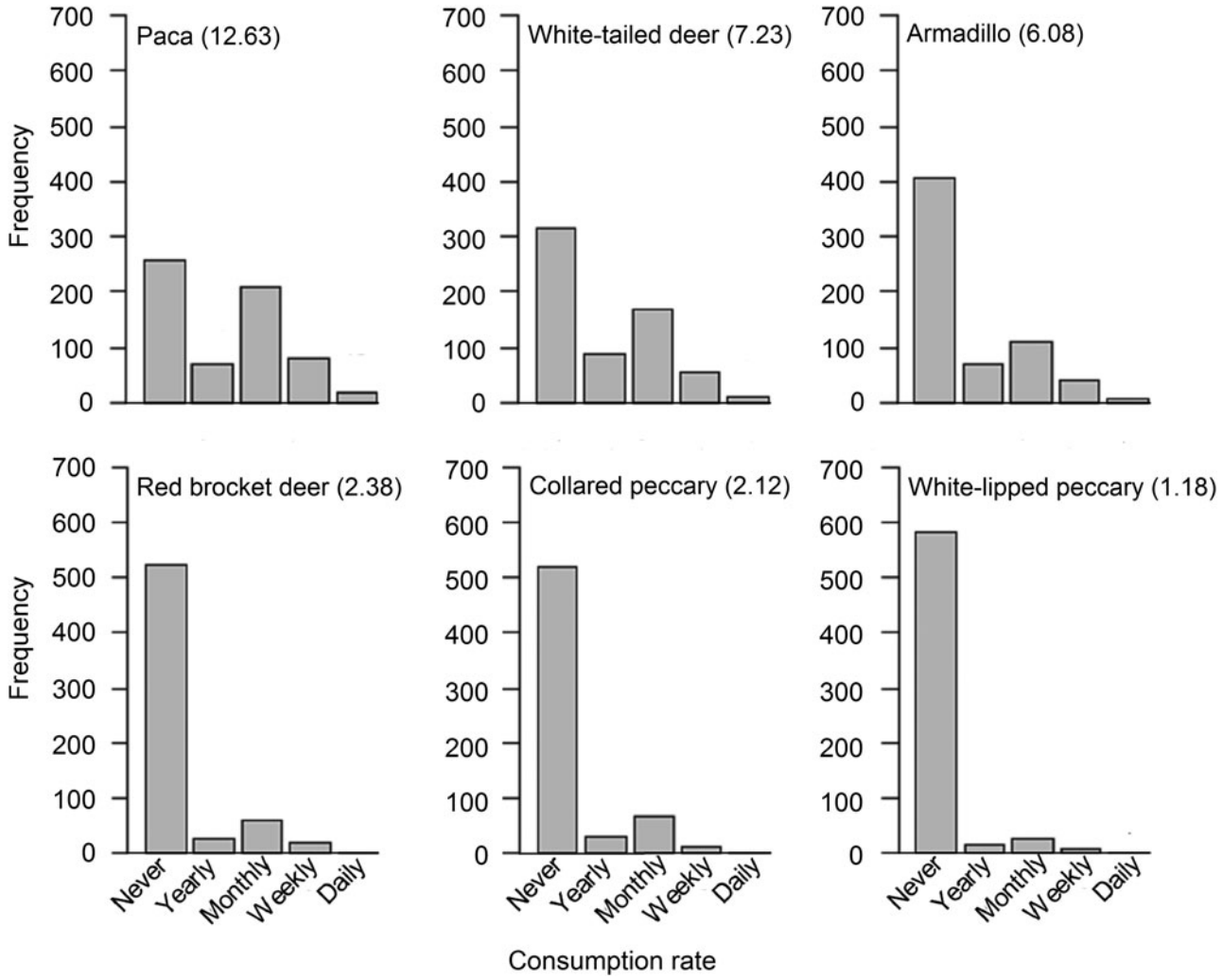


FIG. 2 Frequency distributions of consumption rates for the six wild mammal species common in the human diet in Belize, with the mean number of meals per person per year in parentheses. Data are based on the responses of 634 interviewees to the question 'How often do you eat species *x*?'.

*Harvest model* Minimum district-level densities of paca, white-tailed deer and red brocket deer necessary to sustain the observed offtake by humans and jaguars combined were higher than maximum field density estimates of these species at hunted sites across the Neotropics (Table 2). For armadillo and both peccaries the minimum district-level threshold densities exceeded the median field density estimates, and the national threshold densities exceeded the maximum field density estimates from hunted sites (Table 2). If the hunted field density estimates from across the region reflect true prey densities in Belize, and if the harvests that we have estimated are unbiased, then combined harvests by people and jaguars in Belize could not be considered sustainable for any of these species. Even in the absence of predation by jaguars the rates of offtake by people may not be sustainable.

## Discussion

Our survey revealed that consumption of wild meat is commonplace throughout Belize. At least 75% of the sampled human population consumed wild mammals irrespective of their income, which is consistent with dietary decisions based on culture rather than economics. Greater diversity of wild meat in the diet of rural vs urban people, and increased consumption rate with forest cover, may simply reflect greater availability of wild species in rural and forested areas. However, the higher consumption rate in the rural south, where extreme poverty is more than twice as prevalent as in the other districts, suggests that wild meat may comprise a necessary dietary component in this area. Further study could explore the interaction between culture, ethnicity, tradition and economics as drivers of wild meat harvest.

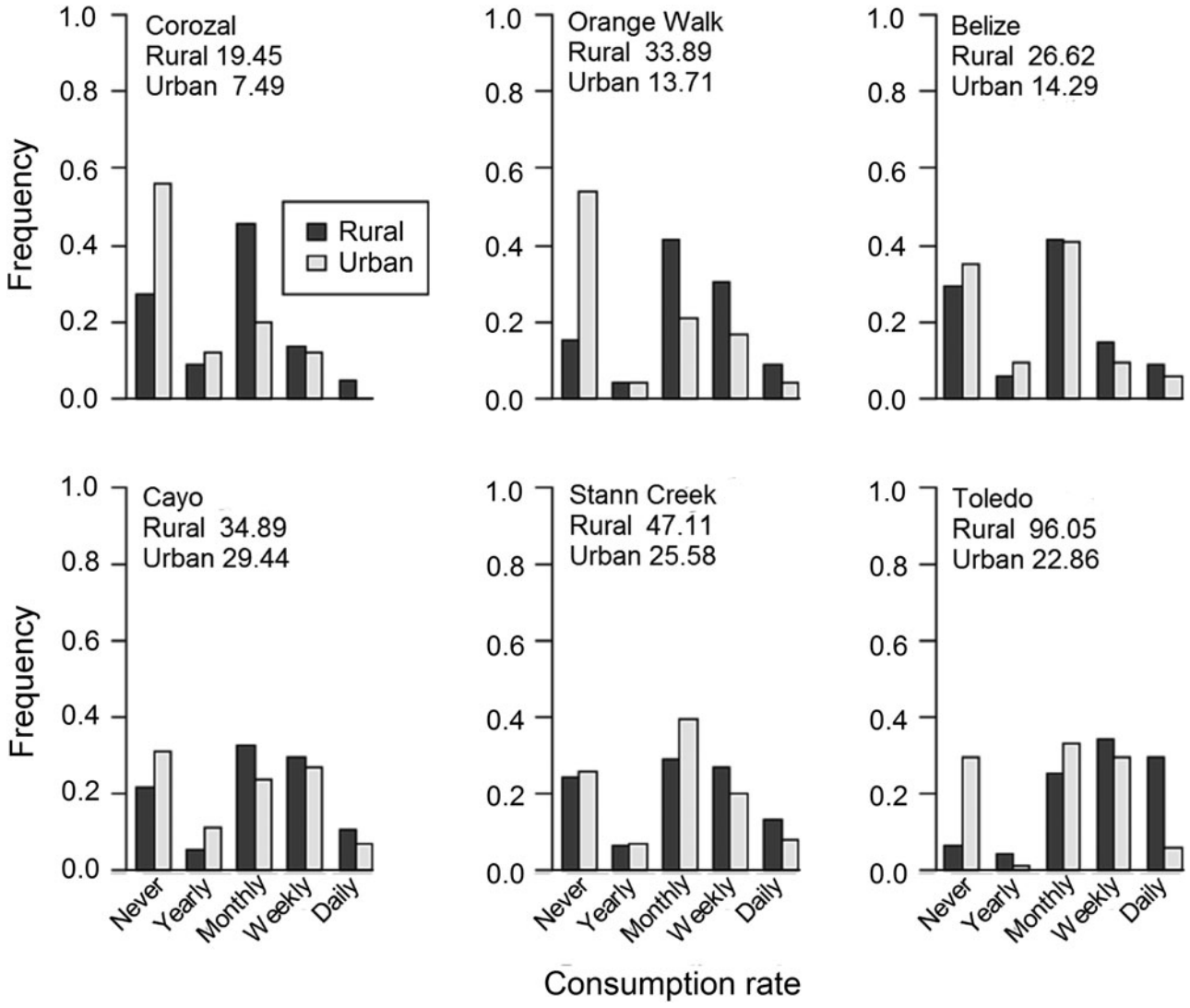


FIG. 3 Frequency distributions (scaled to a maximum of 1.0) of consumption rates of wild mammals in the six districts of Belize (Fig. 1), based on the responses of 344 and 290 interviewees in urban and rural areas, respectively, with the mean number of wild-mammal meals consumed per person per year in rural and urban areas given below each district name.

We found variation in the human consumption of the six common mammal species, with paca eaten by most people and most often. Paca is cited as the most commonly harvested or consumed wild mammal throughout southern Mexico and Central America (e.g. Escamilla et al., 2000; Altrichter, 2001; Smith, 2005; Koster, 2008), and in Belize was the wild mammal most commonly consumed by both people and pumas. White-tailed deer was the next most often consumed wild mammal among people but has been detected only at a low rate in the diet of pumas in Belize (Foster et al., 2010b; RJF & BJH, unpubl. data). Given that white-tailed deer is a significant component of puma diet in Jalisco, Mexico (Nùñez et al., 2000), the widespread and frequent consumption of white-tailed deer by people across Belize suggests an exploitable resource for pumas that was not detected in the scat data of Foster et al. (2010b). Possibly we underestimated the potential for competition between humans and pumas. Although pumas are opportunistic in their diet throughout their North American range and are highly adaptable to a variety of environmental conditions and prey species (Sunquist & Sunquist, 2002), competition with the larger, potentially dominant, jaguar and humans for space and food may limit the puma population in Belize (Harmsen et al., 2009; Foster et al., 2010b). Unlike pumas, jaguars are commonly detected throughout human-influenced landscapes in Belize and they have a broader diet than do pumas (Foster et al., 2010a,b; RJF & BJH, unpubl. data), overlapping less with the wild-meat diet of people. Armadillos and ungulates comprise 42% and 22%, respectively, of jaguar diet by biomass (Foster et al., 2010b). Although armadillos are less important in the diet of Belizeans, the estimated national harvest of armadillos by people is equivalent to the offtake by jaguars. Moreover, we estimate that Belizeans consume

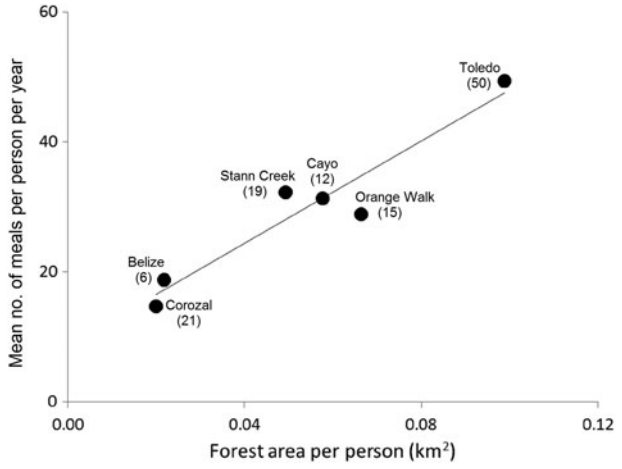


FIG. 4 Response of mean wild-mammal consumption (six common species) per person per year to forest area per person per district ($r^2 = 0.9$, n = 6, $P < 0.01$). The percentage of people living in extreme poverty in each district is shown in parentheses (UN, 2010).

almost three times as many peccaries and red brocket deer (combined) as does the jaguar population.

The shared resource of wild meat puts people and predators in direct conflict when supply is limited (c.f. Hockings & Sousa, 2012, for a counter-example of low-conflict sharing). Competition for peccaries and deer may be driving livestock predation in Belize. Both jaguars and pumas attack livestock, although jaguars do so more frequently (Brechin & Buff, 2005; Foster, 2008; RJF & YU, unpubl. data). Foster et al. (2010b) found that c. 30% of jaguar diet within a protected forest comprised wild ungulates, falling to 7% outside the protected forest, where it was supplemented by domestic ungulates. Prey-switching by jaguars has been documented in Brazil, associated with shifts in the relative abundances of peccaries and livestock (de Azevedo & Conforti, 2008; Cavalcanti & Gese, 2010). Where wildlife hunting occurs alongside livestock farming we may expect a tipping point at which predators become most vulnerable to the combined impacts of wild prey depletion (competition with humans) and lethal control associated with the protection of livestock (conflict with humans). In Belize, human and livestock densities are lower than in the rest of Central America (Wint & Robinson, 2007; World Bank, 2013a,b,c); however, wild meat harvests exceed levels that are considered sustainable in other hunted Neotropical forests (this study) and depredation is common (Foster, 2008; RJF & YU, unpubl. data). Harvests of wild meat have not been evaluated nationally elsewhere in Central America. Because other Central American countries have less forest cover per person and greater livestock production than Belize we may expect lower wild-meat consumption per capita, but this may be offset by the higher human densities.

Harvesting of wild prey and conversion of habitat for livestock rearing by a growing human population undoubtedly affect mammalian community structure. Notably, jaguars and white-lipped peccaries have been extirpated from El Salvador (Caso et al., 2008; Keuroghlian et al., 2013), which has the highest human density, lowest forest-area per rural person, and highest livestock density in Central America (World Bank, 2013a,b,c). In Belize, the proximity to forest of many livestock holdings exposes them to predation, and retaliatory lethal control has a significant impact on the jaguar population (Foster, 2008). Following Mexico's acceptance of Belize as an exporter of cattle, the expansion of the cattle industry in Belize for international export may have consequences for jaguars, depending on whether efforts to increase cattle production are complemented by improved management. Intensification of production may reduce opportunistic attacks. However, poorly managed expansion and large-scale forest clearance for poor-quality pastureland will destroy habitat for forest-dwelling species, potentially increasing hunting pressure by people and predators in the remaining forest patches and providing easy-to-catch domestic prey for predators.

Our estimate that jaguars take less than one-quarter of the wild mammals that are commonly consumed by both people and jaguars in Belize suggests that humans have greater impact on prey populations than do the felid predators with which they compete. We estimate that during 2010 at least 300,000 wild animals (c. 3,000 t) across the six mammal species were consumed by people, yet only three hunting licences were issued in Belize (RG, unpubl. data). Hunting is mostly illegal and unmonitored. The government is keen to set species-specific hunting limits but lacks basic information about the wild mammal populations. There is a need for robust estimates of density and productivity of wild-meat species and the carnivores that hunt them, to inform assessments of sustainability and hunting legislation. Our findings that 75% of Belizeans eat wild meat but 80% of the wild meat is consumed by just 20% of the people exemplify the Pareto Principle of the vital few (Juran, 1995) and suggest a distinction in motivation between the minority for whom wild meat forms a major portion of the diet and the majority whose consumption of wild meat is dietetically trivial. The 20% can be targeted for involvement in education on sustainable harvests, programmes to monitor offtake, development projects to reduce reliance on wild meat, and law awareness and enforcement activities. With 41% of the growing Belizean population living in poverty (UN, 2010), we may expect the impact on natural resources such as wild game to increase.

We used simple models of production and harvest to assess the sustainability of harvests of the six common wild mammal species. The harvest model raised concern for all six species, suggesting that the estimated national offtake rates could only be sustained if mean densities across Belize exceeded those recorded elsewhere in the

TABLE 2 Sustainability indicators for the six wild mammals common in the human diet in Belize, based on a production model and a harvest model and ordered by increasing body mass of prey. Production model: annual national harvest by humans (with minimum and maximum values and associated districts in parentheses) and estimates of maximum sustainable harvest. Harvest model: national threshold density required to sustain annual harvest by jaguars and humans (with minimum and maximum values and associated districts in parentheses), and median field density estimates from hunted sites throughout the Neotropics.

| Species | Production model | | Harvest model | |
|---|---|---|---|---|
| | Annual harvest, individuals $km^{-2}$ (range)[1] | MSH[2] (individuals $km^{-2}$) | Threshold density, individuals $km^{-2}$ (range)[1] | Median field density estimates[3], individuals $km^{-2}$ (range) |
| Armadillo | 5.1 ($2.9^{CY}$–$9.1^{TO}$)[4] | 5.19 | 19.8 ($14.4^{CO}$–$28.3^{TO}$)[5] | 13.5 (9.5–16.7) |
| Paca | 8.9 ($4.1^{OW}$–$13.4^{SC}$)[6] | 1.31 | 53.0 ($25.8^{OW}$–$79.0^{SC}$)[6] | 3.9 (0.5–6.2) |
| Collared peccary | 0.9 ($0.3^{BZ}$–$1.9^{CO}$) | 2.41 | 11.4 ($4.7^{BZ}$–$23.0^{CO}$)[5,7] | 2.0 (0.1–5.9) |
| Red brocket deer | 0.6 ($0.3^{OW}$–$1.1^{SC}$)[4] | 0.67 | 4.1 ($2.4^{OW}$–$6.9^{SC}$)[6] | 0.9 (0.2–1.8) |
| White-lipped peccary | 0.3 ($0.03^{BZ}$–$0.5^{SC}$) | 0.83 | 10.4 ($3.2^{BZ}$–$13.6^{SC}$)[5,7] | 1.9 (0.0–7.0) |
| White-tailed deer | 4.2 ($3.0^{OW}$–$6.0^{CO}$)[6] | 0.95 | 27.1 ($19.6^{OW}$–$39.3^{CO}$)[6] | 1.7 (1.3–1.8) |

[1]CO, Corozal; CY, Cayo; OW, Orange Walk; BZ, Belize; SC, Stann Creek; TO, Toledo
[2]Maximum sustainable harvest, from Robinson & Redford (1991) and Koster (2008)
[3]Field density estimates derived from published literature and unpublished data (Supplementary Material 1); means were calculated for studies which gave field density estimates from multiple sites within the same study area
[4]District maximum exceeds maximum sustainable harvest
[5]District minimum exceeds median field density estimate
[6]National estimate and district range exceed maximum sustainable harvest or maximum field density estimate
[7]National estimate exceeds maximum field density estimate

Neotropics or if there was immigration from outside Belize to replenish depleted populations. Heterogeneous hunting pressure can produce source–sink dynamics such that dispersal from unhunted areas replenishes otherwise overexploited hunting grounds (e.g. Novaro et al., 2000; Naranjo & Bodmer, 2007). Transboundary poaching in the protected forest of western Belize by hunters from Guatemala has been associated with a decline in prey species, particularly white-lipped peccaries (Bridgewater et al., 2006; Salas & Meerman, 2008; Perez et al., 2009), suggesting that local overexploitation is not compensated for by dispersal from unhunted areas. The production model suggested that the level of hunting of pacas and white-tailed deer in Belize exceeded the maximum sustainable harvests in tropical rainforests whereas those for white-lipped and collared peccaries were below the maximum sustainable harvests. Weaknesses of the harvest and production models as indicators of sustainability are well-known (Milner-Gulland & Akçakaya, 2001; Weinbaum et al., 2013) and we interpret the results cautiously. For example, our estimates of species reproductive output for use with the harvest model were derived from the literature and were not site-specific. The available data on the reproductive biology of Neotropical mammals are limited. We recommend that priority should be given to the collection of such data because inaccurate estimates of fecundity will have considerable influence on the interpretation of the harvest model. For a given harvest rate a twofold overestimation of reproductive output halves the estimated threshold density for a sustainable harvest. Ideally, location-specific data would be used; such data could be collected by requesting that hunters retain the reproductive organs of their quarry for analysis of pregnancy rates (e.g. Hurtado-Gonzales & Bodmer, 2004). Priority must also be given to estimating prey density in the area of interest. For comparison with the harvest model, we used field densities derived from the literature for hunted sites elsewhere in the Neotropics because there are no data available on prey densities in Belize. Despite the lack of site-specific input parameters for density and productivity, the models provide a useful first attempt at assessing the impact of hunting by people and non-human predators on wild prey, and help us to identify where more information is needed. Both models suggest that the paca population is hunted unsustainably; however, paca is still consumed widely and frequently, perhaps reflecting a need to account for spatial variation in density or productivity within forested landscapes (e.g. Peres & Palacios, 2007). For example, some mammals attain greater productivity and densities in secondary forests and in forest–fallow–farm mosaics, where crops supplement the diet, than in undisturbed forest (Camilo et al., 2004; Robinson & Bennett, 2004; Smith, 2005; Koster, 2008; Smith, 2008). In particular, Smith (2005) reported that the habitat mosaics created by shifting agriculture in Panama may be important for pacas during seasonal food shortages. This type of farming is common within the forested landscape of Belize, particularly in the south (Bridgewater, 2012). The heterogeneous landscape may support higher productivity and/or density of pacas than assumed in our models (e.g. Smith, 2005) and this warrants further investigation, particularly of the fine-scale

balance between refuge habitats acting as population sources amongst hunting sinks (Novaro et al., 2000). In contrast, the national harvests of collared and white-lipped peccaries were both estimated to be less than half of the maximum sustainable harvests for these species. We suspect that these low figures reflect populations that are already depressed below their maximum productivity, as suggested by the low occurrence of collared peccaries and the absence of white-lipped peccaries in jaguar diet outside protected forest compared to within, and lower photographic capture rates of white-lipped peccaries in unprotected lands than in protected forest (Foster et al., 2010b; RJF & BJH, unpubl. data). Anecdotal evidence suggests increasing rarity and local extirpation of white-lipped peccaries, reflecting the range-wide declines documented by Altrichter et al. (2012).

The sustainability of hunting is difficult to assess in the tropics. We have provided the first insight into the scale of mammal harvests by people and predators in Belize. Studying people–predator–prey interactions across multiple tropical systems will contribute to a more unified understanding of the relationships between carnivore dynamics, the availability and harvest of wild meat, and livestock predation, which has implications for human livelihoods, food security, forest regeneration and conservation of biodiversity.

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## References

Altrichter, M. (2001) The importance of wild mammals in the diet of the populations of Osa Peninsula, Costa Rica. *Revista Mexicana de Mastozoología*, 4, 99–107.

Altrichter, M., Taber, A., Beck, H., Reyna-Hurtado, R., Lizarraga, L., Keuroghlian, A. & Sanderson, E.W. (2012) Range-wide declines of a key Neotropical ecosystem architect, the Near Threatened white-lipped peccary *Tayassu pecari*. *Oryx*, 46, 87–98.

Belize Statistics Office (2010) *Population and Housing Census*. Belize Statistics Office, Belize City, Belize.

Belize Wildlife Protection Act (2000) Chapter 220. Revised Edition 2000.

Belize Wildlife Protection Act (2003) Chapter 220. Revised Edition 2003.

Bodmer, R.E. & Robinson, J.G. (2004) Evaluating the sustainability of hunting in the Neotropics. In *People in Nature: Wildlife Conservation in South and Central America* (eds K.M. Silvius, R.E. Bodmer & J.M.V. Fragoso), pp. 299–323. Columbia University Press, New York, USA.

Borchers, D., Distiller, G., Foster, R., Harmsen, B. & Milazzo, L. (2014) Continuous-time spatially explicit capture–recapture models, with an application to a jaguar camera-trap survey. *Methods in Ecology and Evolution*, 5, 656–665.

Brechin, S.R. & Buff, J. (2005) *Exploring Human–Jaguar Conflicts in Belize, Central America, Part II: A Nationwide Study*. Unpublished report. Wildlife Conservation Society, New York, USA.

Bridgewater, S. (2012) *A Natural History of Belize: Inside the Maya Forest*. University of Texas Press, Austin, USA.

Bridgewater, S.G.M., Pickles, P., Garwood, N.C., Penn, M., Bateman, R.M., Porter Morgan, H. et al. (2006) *Chamaedorea* (Xaté) in the Greater Maya Mountains and the Chiquibul Forest Reserve, Belize: an economic assessment of a non-timber forest product. *Economic Botany*, 60, 265–283.

Camilo, G., Gros, P.M. & Asasa, C. (2004) Indigenous land use and hunting sustainability in a Central American rain forest. *Ecological Society of America Annual Meeting, Abstracts*, 89, 80.

Caso, A., Lopez-Gonzalez, C., Payan, E., Eizirik, E., de Oliveira, T., Leite-Pitman, R. et al. (2008) *Panthera onca*. In *The IUCN Red List of Threatened Species v. 2013.1*. Http://www.iucnredlist.org [accessed 26 July 2013].

Cavalcanti, S.M.C. & Gese, E.M. (2010) Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, 91, 722–736.

Cherrington, E.A., Ek, E., Cho, P., Howell, B.F., Hernandez, B. E., Anderson, E.R. et al. (2010) *Forest Cover and Deforestation in Belize 1980–2010*. Technical report. Water Center for the Humid Tropics of Latin America and the Caribbean /NASA/Belize Ministry of Natural Resources and the Environment, Panama City, Panama.

Colwell, R.K. & Futuyma, D.J. (1971) On the measurement of niche breadth and overlap. *Ecology*, 52, 567–576.

de Azevedo, F.C.C. & Conforti, V.A. (2008) Decline of peccaries in a protected subtropical forest of Brazil: toward conservation issues. *Mammalia*, 72, 82–88.

de Azevedo, F.C.C. & Murray, D.L. (2007) Evaluation of potential factors predisposing livestock to predation by jaguars. *The Journal of Wildlife Management*, 71, 2379–2386.

Emmons, L.H. (1987) Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology*, 20, 271–283.

Escamilla, A., Sanvicente, M., Sosa, M. & Galindo-Leal, C. (2000) Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, Mexico. *Conservation Biology*, 14, 1592–1601.

Fa, J.E., Albrechtsen, L. & Brown, D. (2007) Bushmeat: the challenge of balancing human and wildlife needs in African moist tropical forests. In *Key Topics in Conservation Biology* (eds D. Macdonald & K. Service), pp. 206–221. Blackwell Publishing Ltd, Oxford, UK.

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

Figueroa, O.A., Foster, R.J., Wultsch, C., Mesa-Cruz, J.B., Kelly, M.J., Harmsen, B.J. et al. (in press) Estatus de Conservación del Jaguar en Belice. In *El Jaguar en el Nuevo Milenio: Perspectiva Continental* (eds R. Medellín, C. Chávez, A. de la Torre, H. Zarza & G. Ceballos). Fondo de Cultura Económica, Instituto de Ecología UNAM, Mexico City, Mexico.

Foster, R. (2008) *The ecology of jaguars in a human-influenced landscape*. PhD thesis. University of Southampton, Southhampton, UK.

Foster, R.J., Harmsen, B.J. & Doncaster, C.P. (2010a) Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica*, 42, 724–731.

Foster, R.J., Harmsen, B.J., Valdes, B., Pomilla, C. & Doncaster, C.P. (2010b) Food habits of sympatric jaguars and pumas across a gradient of human disturbance. *Journal of Zoology*, 280, 309–318.

Gordon, I.J., Acevedo-Whitehouse, K., Altwegg, R., Garner, T.W.J., Gompper, M.E., Katzner, T.E. et al. (2012) What the 'food security' agenda means for animal conservation in terrestrial ecosystems. *Animal Conservation*, 15, 115–116.

Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E.T. & Doncaster, C.P. (2009) Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a Neotropical forest. *Journal of Mammalogy*, 90, 612–620.

Henschel, P., Hunter, L.T.B., Coad, L., Abernethy, K.A. & Mühlenberg, M. (2011) Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. *Journal of Zoology*, 285, 11–20.

Hockings, K.J. & Sousa, C. (2012) Differential utilization of cashew—a low-conflict crop—by sympatric humans and chimpanzees. *Oryx*, 46, 375–381.

Hurtado-Gonzales, J.L. & Bodmer, R.E. (2004) Assessing the sustainability of brocket deer hunting in the Tamshiyacu-Tahuayo Communal Reserve, northeastern Peru. *Biological Conservation*, 116, 1–7.

Jones, C.B. & Young, J. (2004) Hunting restraint by Creoles at the Community Baboon Sanctuary, Belize: a preliminary survey. *Journal of Applied Animal Welfare Science*, 7, 127–141.

Juran, J.M. (1995) *Managerial Breakthrough*. McGraw Hill, New York, USA.

Kelly, M.J., Noss, A.J., Di Bitetti, M.S., Maffei, L., Arispe, R.L., Paviolo, A. et al. (2008) Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy*, 89, 408–418.

Keuroghlian, A., Desbiez, A., Reyna-Hurtado, R., Altrichter, M., Beck, H., Taber, A. & Fragoso, J.M.V. (2013) *Tayassu pecari*. In *The IUCN Red List of Threatened Species v. 2013.1*. Http://www.iucnredlist.org [accessed 26 July 2013].

Kitchener, A. (1991) *The Natural History of the Wild Cats*. A & C Black, London, UK.

Koster, J. (2008) The impact of hunting with dogs on wildlife harvests in the Bosawas Reserve, Nicaragua. *Environmental Conservation*, 35, 211–220.

Laundré, J.W. (2005) Puma energetics: a recalculation. *The Journal of Wildlife Management*, 69, 723–732.

Leite, R.M.P. & Galvão, F. (2002) El jaguar, el puma y el hombre en tres áreas protegidas del bosque atlántico costero de Paraná, Brasil. In *El Jaguar en el Nuevo Mileno* (eds R.A. Medellín, C. Equihua, C.L.B. Chetkiewicz, P.G. Crawshaw, A. Rabinowitz, K.H. Redford et al.), pp. 237–250. Fondo de Cultura Economica, Mexico City, Mexico, Universidad Nacional Autonoma de Mexico, Mexico City, Mexico & Wildlife Conservation Society, New York, USA.

Levins, R. (1968) *Evolution in Changing Environments*. Princeton University Press, Princeton, USA.

Loveridge, A., Wang, S.W., Frank, L.G. & Seidensticker, J. (2010) People and wild felids: conservation of cats and management of conflicts. In *Biology and Conservation of Wild Felids* (eds D. W. Macdonald & A.J. Loveridge), pp. 161–196. Oxford University Press, Oxford, UK.

Meerman, J. (2011) *Belize Ecosystems Shapefile 2011*. Http://www.biodiversity.bz/mapping/warehouse/profile.phtml?dcid=213957 [accessed 2 February 2012].

Milner-Gulland, E.J. & Akçakaya, H.R. (2001) Sustainability indices for exploited populations. *Trends in Ecology & Evolution*, 16, 686–692.

Naranjo, E.J. & Bodmer, R.E. (2007) Source–sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. *Biological Conservation*, 138, 412–420.

Nasi, R., Brown, D., Wilkie, D., Bennett, E., Tutin, C., van Tol, G. & Christophersen, T. (2008) *Conservation and Use of Wildlife-based Resources: the Bushmeat Crisis*. Secretariat of the Convention on Biological Diversity, Montreal, Canada, and CIFOR, Bogor, Indonesia.

Nasi, R., Taber, A. & van Vliet, N. (2011) Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. *International Forestry Review*, 13, 355–368.

Novack, A.J., Main, M.B., Sunquist, M.E. & Labisky, R.F. (2005) Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. *Journal of Zoology*, 267, 167–178.

Novaro, A.J., Redford, K.H. & Bodmer, R.E. (2000) Effect of hunting in source–sink systems in the Neotropics. *Conservation Biology*, 14, 713–721.

Núñez, R., Miller, B. & Lindzey, F. (2000) Food habits of jaguars and pumas in Jalisco, Mexico. *Journal of Zoology*, 252, 373–379.

Peres, C.A. & Palacios, E. (2007) Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica*, 39, 304–315.

Perez, A., Chin-Ta, C. & Afero, F. (2009) Belize–Guatemala territorial dispute and its implications for conservation. *Tropical Conservation Science*, 2, 11–24.

Pianka, E.R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4, 53–74.

Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M. E. & Eisenberg, J.F. (2003) Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biological Conservation*, 109, 297–310.

Rabinowitz, A. & Nottingham, Jr, B.G. (1986) Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology*, 210, 149–159.

Rabinowitz, A. & Zeller, K.A. (2010) A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation*, 143, 939–945.

Reid, F.A. (2009) *A Field Guide to the Mammals of Central America and Southeast Mexico*. Oxford University Press, New York, USA.

Reider, K.E., Carson, W.P. & Donelly, M.A. (2013) Effects of collared peccary (*Pecari tajacu*) exclusion on leaf litter amphibians and reptiles in a Neotropical wet forest, Costa Rica. *Biological Conservation*, 163, 90–98.

Robinson, J.G. & Bennett, E.L. (2004) Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems. *Animal Conservation*, 7, 397–408.

Robinson, J.G. & Bodmer, R.E. (1999) Towards wildlife management in tropical forests. *The Journal of Wildlife Management*, 63, 1–13.

Robinson, J.G. & Redford, K.H. (1991) Sustainable harvest of Neotropical forest mammals. In *Neotropical Wildlife Use and Conservation* (eds J.G. Robinson & K.H. Redford), pp. 415–429. University of Chicago Press, Chicago, USA.

Rushton, J., Viscarra, R., Viscarra, C., Basset, F., Baptista, R. & Brown, D. (2005) *How Important is Bushmeat Consumption in South America: Now and in the Future?* ODI Wildlife Policy Briefing, Number 11. The Overseas Development Institute, London, UK.

Salas, O. & Meerman, J. (2008) *Chiquibul National Park Management Plan 2008–2013*. Friends for Conservation and Development, Belize.

Smith, D.A. (2005) Garden game: shifting cultivation, indigenous hunting and wildlife ecology in western Panama. *Human Ecology*, 33, 505–537.
Smith, D.A. (2008) The spatial patterns of indigenous wildlife use in western Panama: implications for conservation management. *Biological Conservation*, 141, 925–937.
Stoner, K.E., Vulinec, K., Wright, S.J. & Peres, C.A. (2007) Hunting and plant community dynamics in tropical forests: a synthesis and future directions. *Biotropica*, 39, 385–392.
Sunquist, M. & Sunquist, F. (2002) *Wild Cats of the World*. The University of Chicago Press, Chicago, USA.
UN (2010) *Belize Scorecard and Outlook Report 2010*. United Nations Development Programme, Belmopan, Belize.
UN (2013) *World Statistics Pocket Book 2013 Edition*. United Nations, New York, USA.
Weinbaum, K., Brashares, J.S., Golden, C.D. & Getz, W.M. (2013) Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecology Letters*, 16, 99–111.
Wilke, D.S. & Godoy, R.A. (2001) Income and price elasticities of bushmeat demand in lowland Amerindian societies. *Conservation Biology*, 15, 761–769.
Wint, W. & Robinson, T. (2007) *Gridded Livestock of the World*. Food and Agriculture Organization of the United Nations, Rome, Italy.
World Bank (2013a) Http://data.worldbank.org/indicator/SP.RUR.TOTL [accessed 28 June 2013].
World Bank (2013b) Http://data.worldbank.org/indicator/AG.LND.FRST.K2/countries [accessed 28 June 2013].
World Bank (2013c) Http://data.worldbank.org/indicator/AG.LND.TOTL.K2/countries [accessed 3 July 2013].

## Biographical sketches

Rebecca Foster's research interests include ecological and social studies to understand the causes of human–wildlife conflict and find practical solutions. Bart Harmsen's research interests include carnivore ecology and interactions. David Macdonald is interested in the scientific underpinning of practical and policy solutions to problems in wildlife conservation. Josh Collins trained as a science teacher and has a background in zoology. Yahaira Urbina is a wildlife biologist whose work focuses on jaguar–human conflict. Rasheda Garcia is interested in understanding wildlife exploitation in Belize. Patrick Doncaster's interests include animal population dynamics, wildlife corridors and species conservation.