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Assessing the Sustainability of Waiwai Subsistence Hunting In Guyana with Implications for Co-Management in Amazonian Indigenous Reserves

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Assessing the sustainability of Waiwai subsistence hunting in Guyana by comparison of static indices and spatially explicit, biodemographic models

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Abstract

While bushmeat hunting is critical to the livelihoods of millions of people throughout the tropical world, it is also a major threat to wildlife conservation. Assessing the sustainability of hunting has been a major goal in conservation biology but developing methods that accurately predict patterns of prey depletion has proven notoriously problematic. In this study, we sought to assess the sustainability of the hunting of indigenous Waiwai in Guyana by comparing results from the most commonly used static sustainability index, the production model, with results from spatially explicit biodemographic models for three indicator species; tapirs *Tapirus terrestris*, spider monkeys *Ateles paniscus*, and curassows *Crax alector*. Our goals were to (1) assess how conclusions about sustainability differ between the two methods and (2) to determine the suitability of biodemographic modeling for non-primate taxa. We used hunter-self monitoring data to calculate annual harvest and to estimate parameters for biodemographic models. The production model indicated that all three species were being overharvested, with *T. terrestris* harvested at six times the sustainable rate. In contrast, biodemographic models indicated that each species would persist in the Waiwai catchment area in 20 years (although *A. paniscus* would be close to extirpation), even if the Waiwai population increased by 64% and shifted to all shotgun hunting. Predicted densities for *A. paniscus* and *C. alector* were statistically indistinguishable from empirically derived encounter rates and those for *T. terrestris* were consistent with the locations of Waiwai kills, demonstrating the robustness of the model. While the weaknesses of static sustainability indices are well documented, they continue to be used and conclusions based on their results are still cited and influential in determining conservation policy. Our study demonstrates that biodemographic models perform far better than static indices and that the biodemographic approach is robust for a range of different prey species.

Introduction

Bushmeat hunting is critical to the food security and livelihoods of millions of people throughout the tropical world (Fa, Peres & Meeuwig, 2002; Nasi, Taber & Van Vliet, 2011). In Amazonia, an estimated 1.3 million tons of bushmeat is consumed annually, primarily by rural and indigenous populations (Nasi *et al.*, 2011). For many Amazonian indigenous groups, bushmeat is a major source of protein (Dufour, 1991; Murrieta *et al.*, 2008; Sirén & Machoa, 2008), fat (Sirén & Machoa, 2008), and micronutrients (Sarti *et al.*, 2015). In addition, subsistence hunting often plays an important role in indigenous symbolism, mythology, material culture, and group identity (Shepard, 2002; Cormier, 2003; Shaffer, Marawanaru & Yukuma, 2017*a*).

Unfortunately, unsustainable hunting is one of the greatest threats to wildlife conservation throughout the tropical world. Commercial hunting has led to large-scale depletion throughout central and West Africa and Asia (Fa *et al.*, 2002; Nasi *et al.*, 2011) and subsistence hunting has led to local extinction of several prey species, particularly primates and large ungulates, in many areas of Amazonia (Robinson & Bennett 2004; Bodmer, Eisenberg & Redford, 1997; Peres, 2000; de Thoisy, Renoux & Julliot, 2005; Franzen, 2006; de Thoisy, Richard-Hansen & Peres, 2009). Areas where subsistence hunting may have once been sustainable have suffered considerable prey population declines as a result of increased population densities, technology change, and increased market integration (Alvard *et al.*, 1997; Robinson & Bodmer 1999; Peres, 2000; de Souza-Mazurek *et al.*, 2000; Franzen, 2006;

Nasi *et al.*, 2008; Zapata-Ríos, Urgilés & Suárez, 2009). Therefore, determining and promoting the sustainability of subsistence hunting is critical for both conservation and livelihoods throughout the tropics.

However, assessing the sustainability of hunting has proven notoriously problematic (Weinbaum *et al.*, 2013). Tropical bushmeat hunting has been studied intensively for more than 30 years and various methods have been proposed to measure the extent to which hunters deplete prey populations (Weinbaum *et al.*, 2013; Van Vliet, Fa & Nasi, 2015). The most commonly used methods for determining sustainability are static indices that use relatively simple algorithms to predict the maximum sustainable harvest (MSH) for a given prey species (Weinbaum *et al.*, 2013). Unfortunately, these indices are beset with problems (Slade, Fomulkiewicz, & Alexander, 1998; Milner-Gulland & Akcakaya, 2001; Levi *et al.*, 2009; Weinbaum *et al.*, 2013; Van Vliet *et al.*, 2015) and perform poorly under realistic conditions in most bushmeat systems (Milner-Gulland & Akcakaya, 2001). At several study sites, hunting deemed unsustainable through the use of static indices has continued for decades with little to no evidence for prey depletion (Bodmer, 1994; Alvard *et al.*, 1997; Novaro, Redford & Bodmer, 2000; Hill, McMillan & Farina, 2003; Peres & Nascimento, 2006; Koster, 2008; Van Vliet & Nasi, 2008; Ohl-Schacherer *et al.*, 2007). This is particularly true in hunting zones adjacent to large areas of unhunted forest, where prey populations may be replenished through source-sink dynamics (Novaro *et al.*, 2000; Sirén, Hambäck & Machoa, 2004). Conservationists have often applied the precautionary principle when assessing hunting sustainability and errored on the side of concluding hunting is not sustainable (Milner-Gulland & Akcakaya, 2001; Van Vliet *et al.*, 2015). However, because many human populations depend on bushmeat for their livelihoods, overly conservative methods are also undesirable (Nasi *et al.*, 2011).

More recent approaches to assessing sustainability have sought to improve on static indices by incorporating spatial heterogeneity and predictive modeling (Salas & Kim, 2002; Sirén *et al.*, 2004; Levi *et al.*, 2009; Van Vliet *et al.*, 2010; Sirén & Parvinen, 2015). The biodemographic models developed by Levi *et al.* (2009), for example, incorporate patterns of hunter behavior and changes in human demographics to project future densities of prey species across a spatial landscape. While biodemographic modeling has been shown to accurately capture patterns of the depletion of primates at a few study sites (Levi *et al.*, 2009; Shepard *et al.*, 2012; Shaffer *et al.*, 2017b), and is argued to be highly effective for co-management (Shaffer *et al.*, 2017b), it remains underutilized in the hunting literature. It has only been applied at a few study sites, with a handful of species, and no studies have directly compared the results of biodemographic models with traditional static indices. Therefore, while this approach shows a great deal of promise for assessing depletion, its taxonomic flexibility and the comparability of biodemographic results with the more widely reported sustainability indices are poorly known.

In this paper, we present the first direct comparison of spatially explicit, biodemographic modeling with traditional sustainability indices to assess the sustainability of the subsistence hunting of indigenous Waiwai in Guyana. We compared results from the most commonly used index, the production model (Robinson & Redford, 1991), with results from biodemographic models for three indicator species; the lowland tapir *Tapirus terrestris*, the black curassow *Crax alector*, and the black spider monkey *Ateles paniscus*. Our goals in this study were to (1) assess how conclusions about the sustainability of subsistence hunting may differ between static, one-off indices and more robust biodemographic models and (2) determine the suitability of biodemographic modeling for nonprimate taxa.

Materials and methods

Study site

The data for this research were collected during a long-term study of the subsistence hunting of indigenous Waiwai forager-horticulturalists in the Konashen Community Owned Conservation Area (KCOCA), Guyana. Approximately 225 Waiwai live in the 625 000 HA KCOCA, almost all of whom live in the village of Masakenari (Fig. 1). Masakenari is the only permanent settlement in the KCOCA and the nearest village outside of the reserve is 80 km northwest of the KCOCA border. The Waiwai practice swidden cassava horticulture and rely heavily on fish and bushmeat as protein and fat sources. Waiwai hunting is exclusively for subsistence and no bushmeat is traded or sold outside of the reserve, with the exception of occasional long-distance trips to visit family in other villages throughout southern Guyana.

Sustainability modeling

We focused our analysis on tapirs, curassows, and spider monkeys for several reasons. First, they are among the five most important subsistence species for the Waiwai, both in terms of number of individuals harvested and by weight (Shaffer *et al.*, 2017b; results). Second, these species are highly vulnerable to overharvesting and are, therefore, excellent indicator species for the overall sustainability of the bushmeat system (Peres, 1990, 2000; Begazo & Bodmer, 1998; Peres *et al.*, 2016). Third, these species are critically important seed dispersers whose depletion can severely affect forest regeneration in Amazonian ecosystems (Begazo & Bodmer, 1998; Fragoso, Silvius & Correa, 2003; Peres & Palacios, 2007; Stevenson, 2011; Peres *et al.*, 2016). Finally, including a primate, a perissodactyl, and a galliforme bird in our sample allowed us to compare the results of sustainability models across a diverse range of taxa.

Unfortunately, we were unable to model depletion in two other important Waiwai prey species, the lowland paca *Cuniculus paca* and the white-lipped peccary *Tayassu pecari*. Density estimates are difficult to obtain for both species, as pacas are nocturnal and the large home ranges of white-lipped peccaries require high survey effort for accurate densities (Peres 1996; Fragoso 1998). In addition, neither species is well suited to modeling using the biodemographic
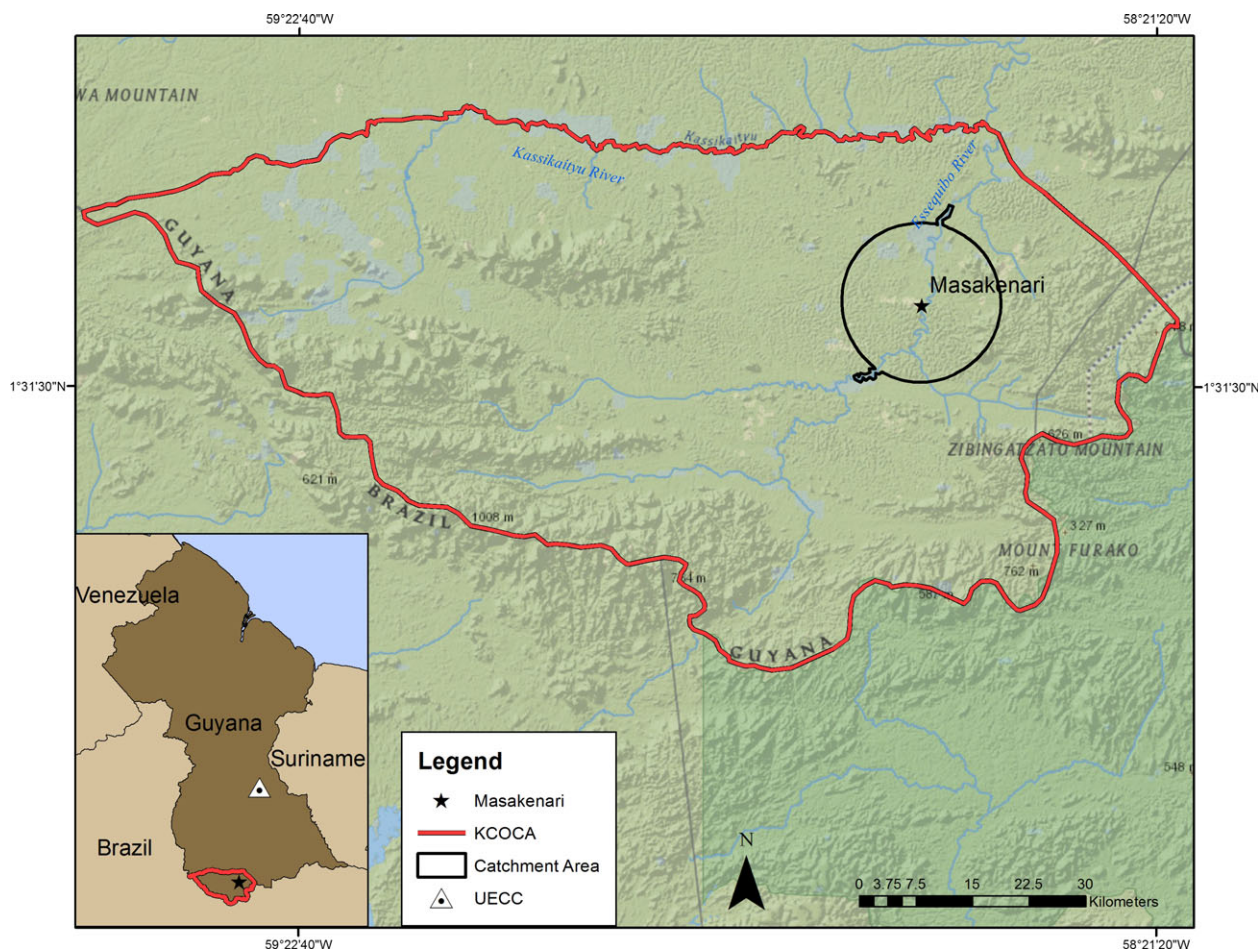
Figure 1 Location of the Konashen Community Owned Conservation Area (KCOCA) within Guyana. The inset map also shows the location of the Upper Essequibo Conservation Area (UECC), where density estimates were obtained for the three species. [Colour figure can be viewed at wileyonlinelibrary.com]

approach. Because the Waiwai hunt pacas almost exclusively on rivers, their hunting behavior of this species violates the assumption of central place foraging in the biodemographic models. The ranging behavior of peccaries, particularly their large and shifting home ranges that blur the distinction between source and sink, make their encounters with hunters and their diffusivity difficult to model (Levi *et al.*, 2009).

Collection of harvesting data

To estimate the extent of Waiwai harvesting of the three prey species and to obtain parameter values for biodemographic models, we established a participatory hunter self-monitoring program in July of 2014 (Shaffer *et al.*, 2017b). We provided a random sample of 15 Waiwai hunters (out of 44 in Masakenari) with two different self-monitoring forms that they completed after each hunt (Supporting Information). One monitoring form allowed us to calculate the total annual harvest for each species by the 15 hunters and estimate the total annual harvest for the village by multiplying our sample totals by three. The other form provided empirical

estimates of kill rates (number of prey individuals killed per group encounter) for shotgun hunting and bow hunting. More detailed information on the hunter self-monitoring program can be found in Shaffer *et al.* (2017b). The dataset used in this study consists of 1 year of hunter harvesting data, collected from August 1, 2014 to August 1, 2015.

To estimate the size of the Waiwai hunting catchment area for use in the production model, we created a buffer with a radius of 10 km around Masakenari. The Waiwai are central-place foragers, with most hunting trips consisting of day excursions radiating from Masakenari on various hunting trails or the Essequibo River (Shaffer *et al.*, 2017a,b). The maximum distance hunters travel from the village during these day trips was approximately 10 km when traveling on trails (mean = 6.3) and 13 km when traveling by river (Shaffer *et al.*, 2017b). We, therefore, extended the buffer along the north and south portions by adding two 3 × 1 km strips along the Essequibo River. This method provided a catchment size of 360 km². We then compared the georeferenced locations of kills from the hunter self-monitoring forms to determine the percentage of kills that occurred within this

area. 75% of kills for which accurate location data were obtained (230 of 306) took place within the catchment. Consequently, we excluded the other 25% of kills from our analysis of harvesting rates for the production model.

Density estimation

To obtain densities of each species at carrying capacity, we used data from line-transect surveys conducted at an unhunted site with similar forest composition to the KCOCA – The Upper Essequibo Conservation Concession (UECC) – 240 km north of Masakenari. While obtaining density estimates from the KCOCA itself would have been optimal, we chose to use estimates from the UECC to assure that densities were unaffected by hunting pressure. We established four, 6 km transects within the UECC in December of 2007 (Supporting Information). We conducted line-transect surveys during February–April, and September–November of 2008 using standard line-transect methodology (Peres, 1999; Buckland *et al.*, 2010). Density was calculated from survey data using the DISTANCE software (Buckland *et al.*, 1993). Because sighting rates were below the recommended minimum number of independent sightings for robust model fits (Buckland *et al.*, 1993; Peres, 1999), we used the effective strip-width (ESW) method (Whitesides *et al.*, 1988; Chiarello, 2000). This method involves calculating a species-specific ESW by determining the perpendicular distance where sighting frequency was equal to or <50% of the preceding level. Group density was then estimated using the formula:

$$D_g = \frac{\text{total encounters}}{2(\text{ESW})L},$$

where D_g is the density of groups/km^2 and L is total transect length. Group density was multiplied by mean group size to obtain population density estimates (K).

Traditional sustainability indices

The most commonly used methods for assessing the sustainability of hunting in tropical forests rely on simple algorithms to calculate a maximum sustainable yield and corresponding MSH given the prey species' reproductive output, density at carrying capacity, and the catchment area in which most hunting occurs (Milner-Gulland & Akcakaya, 2001). The empirically observed harvest (OH) of the hunter population is then compared to the model calculated MSH and, if OH exceeds MSH, hunting is determined to be unsustainable. The simplicity of these algorithms allows sustainability to be calculated relatively easily if accurate harvest data and density estimates are available and they have been used extensively in the literature (Weinbaum *et al.*, 2013). However, researchers have documented numerous problems with these methods (Milner-Gulland & Akcakaya, 2001; Levi *et al.*, 2009; Weinbaum *et al.*, 2013; Van Vliet *et al.*, 2015). For example, their results are highly dependent on the size of the catchment area (Levi *et al.*, 2009), they are highly susceptible to errors due to stochastic processes (Salas & Kim, 2002), they do not incorporate spatial

heterogeneity (Novaro *et al.*, 2000; Sirén *et al.*, 2004; Levi *et al.*, 2009), they cannot project future sustainability (Levi *et al.*, 2009), particularly if hunter technology or population size changes, and their results are very difficult to validate (Milner-Gulland & Akcakaya, 2001; Levi *et al.*, 2009; Van Vliet *et al.*, 2015). Nevertheless, the bushmeat hunting literature is replete with results from studies that assess sustainability using these indices (Weinbaum *et al.*, 2013).

We used the Robinson & Redford (1991) production model because it is the most commonly applied sustainability index in the literature (Weinbaum *et al.*, 2013). This model calculates MSH using an estimate of the annual production of a prey species under optimal conditions and an estimate of the proportion of that production that can be harvested. Production depends on the population size and the natural intrinsic rate of increase of that population. The proportion of production that can be sustainably harvested is set somewhat arbitrarily as 20% of production for long-lived species, 40% for short-lived species, and 60% for very-short lived species (Robinson & Redford, 1991). Therefore, MSH is calculated according to the following equation:

$$\text{MSH} = 0.6K(\lambda_{\max} - 1)F,$$

where K is the prey population density at carrying capacity, $\lambda_{\max}$ is the maximum finite rate of increase and F is the proportion of population production that can be sustainably harvest based on natural mortality. Sustainable production is then calculated per km^2 for a given catchment area and compared to annual harvest (per km^2) to determine if current harvest is unsustainable (i.e. OH exceeds MSH). We obtained values of $\lambda_{\max}$ for each species from the literature (Robinson & Redford, 1991; Begazo & Bodmer, 1998; Levi *et al.*, 2009) and used $F = 0.2$ for each species as suggested by Robinson & Redford (1991) for long-lived prey.

Biodemographic models

Several researchers have sought to address the weaknesses in static sustainability indices by implementing spatially explicit, predictive modeling approaches (Salas & Kim, 2002; Sirén *et al.*, 2004; Levi *et al.*, 2009; Van Vliet *et al.*, 2010; Iwamura *et al.*, 2014). For example, biodemographic models provide a number of advantages over static indices, including their incorporation of source/sink dynamics, the capacity to model densities into the future based on current or changing hunting pressure, their ability to assess the effect of hunting pressure on the density of prey across space rather than treating sustainability as a simple yes/no binary, and the capability to model the spatial spread of hunting effort rather than depending on an arbitrarily defined catchment area. Further, the predicted densities from these models can be compared to empirically derived data for model validation (Levi *et al.*, 2009, 2011). Biodemographic modeling has been used to assess the sustainability of the hunting of spider and wholly monkeys by indigenous Matsigenka in Manu National Park (Levi *et al.*, 2009, 2011), spider monkey hunting in the settlement of Sarayacu, Ecuador (Levi *et al.*,

2011), and by us for black spider and bearded saki monkey hunting by the Waiwai in Guyana (Shaffer *et al.*, 2017*b*). However, the method has only been applied to primates and no studies have directly compared results from biodemographic models with those from static indices.

The models we used in this study were a derivation of Levi *et al.*'s (2009) numerical model with source-sink dynamics. This model uses six parameters and the projected human population size for each year of the predicted period to produce a continuous spatial surface of prey animal densities (Levi *et al.*, 2009; Shaffer *et al.*, 2017*b*). The specific equations for this model are available in Levi *et al.* (2009, 2011) and the model is available as a Python script for ArcGIS (see Levi *et al.*, 2011). Model parameters included the carrying capacity for the species K, the maximum exponential population growth rate r ($\lambda_{max} = e^r$), the kill rate d, hunts per hunter per year *hphy*, spatial spread of hunting effort (mean distance from settlement center during hunts) σ, and a diffusivity parameter D (Table 1). The model uses K, *hphy*, and σ to calculate the probability that hunters will encounter the prey species in any 1-km^2 grid-cell around the settlement during a single year, and, based on d, the likelihood that encounters will lead to kills (Shepard *et al.*, 2012). The density of the prey species in the subsequent year depends on the reproductive rate (r) and migration from source areas (D). Densities can be predicted for any number of years into the future, under a variety of different population growth scenarios.

In our model, we obtained values for r from the literature and estimated K from line-transect surveys (Supporting Information). We estimated d, σ, and *hphy* from hunter self-monitoring form data. The models assume that hunters are central-place foragers, an assumption that is consistent with the hunting behavior of the Waiwai (Shaffer *et al.*, 2017*a*,*b*). However, because the Waiwai hunt opportunistically along the Essequibo and Kassikaityu Rivers during long distance travel, we also modeled a hunting pressure of 10 hunts per year at 2 km intervals along commonly traveled portions of these rivers within 16 km of Masakenari, and five hunts per year at 2 km intervals >16 km from Masakenari.

Model validation

We first produced a validation model for the three species for 2015 based on the past 10 years of demographic growth in Masakenari and the current population of 44 hunters. To validate our models for spider monkeys and black curassows, we compared predicted densities to empirically derived encounter rates from line-transect surveys conducted in the KCOCA in 2013 and 2015. We established two, 10 km transects radiating out from Masakenari and conducted surveys using standard line-transect survey methodology (Supporting Information). We produced a cumulative distribution function (CDF) of model-predicted densities from 0 to 10 km from Masakenari and compared it with the CDF of group encounter rates from transect surveys (Levi *et al.*, 2011; Shaffer *et al.*, 2017*b*). For the model data set, the CDF consisted of data points at 1-km intervals from 0 to 10 km, and each point represented the fraction of prey species density at carrying capacity before that distance from Masakenari (Shaffer *et al.*, 2017*b*). For the transect data set, each data point in the CDF represented the fraction of group observations from transects occurring before the specified distance from Masakenari (i.e. the number of group encounters before the distance from Masakenari divided by the total number of group encounters). We used a two-sample Kolmogorov–Smirnov test to determine if the distributions of the model predicted densities and the empirically derived encounter rates were statistically indistinguishable (P value approaching 1.000).

While we also calculated a CDF of model-predicted densities for tapirs, validation with transect data was not possible due to the low number of tapir encounters. Instead, we used a rough method of validation by comparing the extinction envelope around Masakenari (area where tapir density was predicted to be 0 in 2015) to the locations of tapir harvests from self-monitoring data.

Projected sustainability

We predicted densities of each species across the KCOCA in 20 years under a 'Status Quo' demographic scenario, where the village of Masakenari is projected to grow from 225 individuals to 350 during the 20 year period (with the same percentage of hunters). However, we conservatively estimated that the Waiwai would switch from a mix of 80% shotgun and 20% bow hunting to all shotgun hunting (Shaffer *et al.*, 2017*b*). For each prey species, we calculated the extinction envelope around Masakenari, the percentage of the core hunting catchment area where the species was

Table 1 Parameters for biodemographic models (see Results)

Parameter	Definition	Value *Ateles paniscus*	Value *Tapirus terrestris*	Value *Crax alector*	Data source
K	Carrying capacity	8.07	0.53	4.10	Line-transect surveys
r	Maximum intrinsic growth rate	0.07	0.20	0.38	Robinson & Redford (1991), Begazo & Bodmer (1998)
d	Individuals killed per group encounter	1.20	0.40	1.10	Self- monitoring forms, hunter follows
hphy	Hunts per person per year	24.00	40.00	40.00	Self-monitoring forms
σ	Mean distance from settlement center during hunts	6.00	6.00	6.00	Self-monitoring forms, hunter follows
D	Diffusivity of species or ¼ annual mean-square displacement	0.10	0.01	0.10	Begazo & Bodmer (1998), Fragoso *et al.* (2003), Noss *et al.* (2003), Levi *et al.* (2009)

predicted to be extirpated (densities ≤10% of carrying capacity), and the percentage of the total KCOCA area were the species was extirpated.

We conducted all statistical analysis in R and all spatial analysis in ArcGIS [Environmental Systems Research Institute (ESRI)]. All research was approved by the Environmental Protection Agency of Guyana and the Institutional Review Board and Institutional Animal Care and Use Committee of Grand Valley State University.

Results

Harvesting data

The 15 sampled Waiwai hunters harvested a total of 4313 kg of bushmeat during the study period, representing 358 individuals from at least 36 species. The total estimated annual harvest for Masakenari was 1074 individuals weighing a total of 12 940 kg. Average bushmeat consumption was 57.5 kg/person/year. The most frequently harvested species were paca (66 harvested, total village estimated harvest of 198), curassow (56 harvested, 168 estimated), and spider monkey (39 harvested, 117 estimated; Fig. 2). The most important species by weight were tapir (49% of total harvest), white-lipped peccary (12.1%), and paca (10.6%; Fig. 2).

Production model

The production model indicated that Waiwai hunting of spider monkeys, curassows, and tapirs was unsustainable, with each species being considerably overharvested (Table 2). The harvesting rate for curassows was approximately double the MSH, spider monkeys were even more extensively overharvested, and tapirs were harvested at a rate more than six times that deemed to be sustainable.

Biodemographic models

The CDFs of predicted densities for the 2015 model for both curassows ($D = 0.45$, $P = 0.988$) and spider monkeys ($D = 0.67$, $P = 0.759$) were statistically indistinguishable from empirically derived encounter rates (Fig. 3). Consistent with the results of the 2015 model for tapirs (Fig. 3), no individuals were observed during transect surveys, or harvested by hunters, within 4 km of Masakenari and they were very rarely observed or killed within 6 km of Masakenari. However, they were relatively commonly harvested within 8 km of Masakenari. The high degree of fit between model predictions and encounter rates (as well as observed offtake for tapirs), indicate that the model was robust for accurately capturing patterns of depletion in these species.

Biodemographic models indicated that each species was likely persist within at least a portion of the Waiwai catchment area in 20 years (Fig. 4). However, spider monkeys were considerably depleted, with a predicted extinction envelope of 7.6 km and predicted densities above 10% for only 19% of the catchment area. Curassows were predicted to persist (densities >10% of K) in approximately one quarter of the catchment area (72% extirpation, 6.7 km radius of extinction). Tapirs were the least vulnerable of the three species in biodemographic scenarios, persisting in 54% of the catchment area. They showed an extinction radius of 5.3 km, although tapir densities were slower to recover at the edge of the extinction radius than the other species due to their decreased diffusivity. On a broader scale, all three species were predicted to be found at carrying capacity over a vast majority (>90%) of the KCOCA.
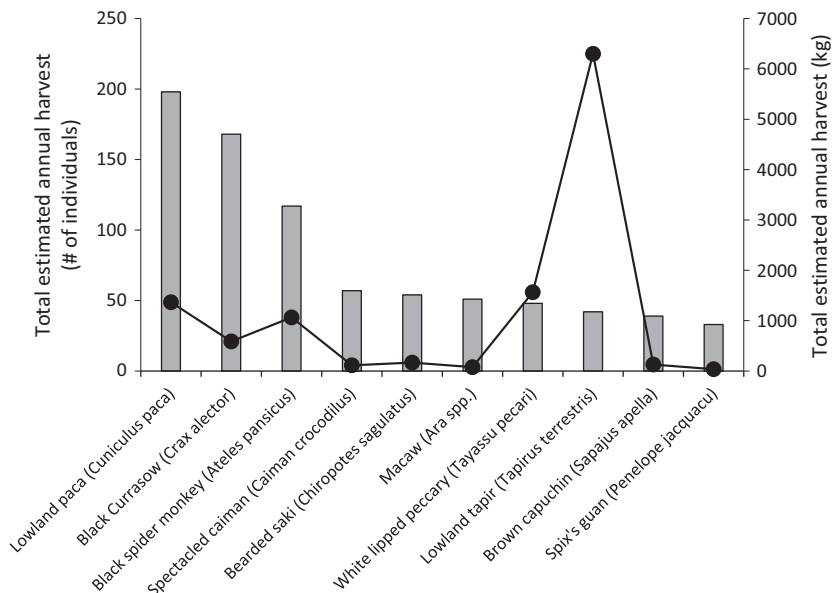
Figure 2 Estimated annual harvest totals for the ten most frequently targeted Waiwai prey species. Estimated total for all 44 hunters in Masakenari are based on a random sample of 15 hunters multiplied by three.

Table 2 Density estimates and comparison of results from production models and biodemographic models

Taxa	Density	Rate of increase[a]	MSH	OH[b]	OH/km²	%Harvested[c]	Sustainable?	Extinction radius (km)	% of Catchment extirpated	% of KCOCA extirpated
Ateles paniscus	8.07	1.07	0.07	92	0.26	377	No	7.6	80.6	6.9
Tapirus terrestris	0.53	1.22	0.01	32	0.09	635	No	5.3	46.1	2.8
Crax alector	4.10	1.46	0.19	126	0.35	187	No	6.7	71.9	5.7

MSH, maximum sustainable harvest; OH, observed harvest; KCOCA, Konashen Community Owned Conservation Area.
[a]Values obtained from Robinson & Redford (1986, 1991) and Begazo & Bodmer (1998).
[b]OH = number of individuals harvested by all Waiwai hunters from within the catchment area. Estimated by multiplying the total village harvest by 0.75 (as 75% of kills took place within the catchment area).
[c]The percentage of maximum total production that is being harvested. Values over 100% indicate overharvesting.

Discussion

Our study demonstrates considerable differences between the results of the production model and biodemographic modeling for three diverse prey species. The production model indicated that all three were being harvested unsustainably, consistent with many previous studies of Amazonian subsistence hunting using this method (Alvard *et al.*, 1997; Mena *et al.*, 2000; Peres & Nascimento, 2006; Zapata-Ríos *et al.*, 2009). However, biodemographic modeling results suggested that each species would persist in at least a portion of the Waiwai catchment area in 20 years, even with an increase in population density and a switch to all shotgun hunting. Further, while the production model showed that tapirs were the most vulnerable prey species (and were in fact being harvested at a rate more than six times higher than the predicted MSH), biodemographic models suggested spider monkeys were likely to suffer more extensive large scale depletion, largely because of their extremely low reproductive rates and the ability of hunters to kill them at high rates upon a group encounter.

The results of our biodemographic models are consistent with the fact that tapirs are still being harvested at high rates by the Waiwai and can be found relatively close to Masakenari. The Waiwai have inhabited the same catchment area for over 20 years, with a relatively stable population and consistent hunting technology. While we do not have detailed data on harvesting patterns over that time, interview data suggest that past tapir harvesting rates were similar to those observed currently. Unlike the production model, our 2015 biodemographic model predicts a relatively small radius of extinction around Masakenari, with tapir densities recovering relatively quickly at the edge of the extinction envelope (although less quickly than the two other species). Similar patterns of 'nonsustainable' harvesting of tapirs continuing for many years with little evidence of depletion have been reported for other study sites (Bodmer, 1994; Alvard *et al.*, 1997; Novaro *et al.*, 2000; Townsend, 2000; Peres & Nascimento, 2006). For example, Peres & Nascimento (2006) found that Kayapo hunters in Brazil were still harvesting tapirs at extremely high levels (14 times the MSH according to the production model) despite exploiting the same catchment area for 23 years. By incorporating source-sink

dynamics and the spatial spread of hunting effort, the biodemographic approach accurately projects such continually high offtakes.

Importantly, although our biodemographic model results show the persistence of all three species in the Waiwai catchment area and very little depletion relative to the overall size of the KCOCA, they also indicate cause for concern. They suggest considerably more depletion than currently exists in the KCOCA, particularly of spider monkeys. In addition to the negative effects on biodiversity conservation, this depletion would also threaten Waiwai food security, as hunter catch-per-unit-effort will go down considerably for these species. An increase in Waiwai hunting effort (more *hphy* and/or increased kill rates) could extirpate all three species from the catchment area. In addition, more extensive landscape degradation in source areas, and/or the establishment of settlements outside of the catchment area, will severely increase depletion across the KCOCA. Further, the large areas of depletion around Masakenari could have highly negative effects on forest structure. All three species are important seed dispersers (Peres *et al.*, 2016), including for highly valued Waiwai resources (e.g. *Oenocarpus bacaba*), and even a relatively small area of extirpation may cause considerable detrimental effects on forest regeneration. For these reasons, as well as the more general difficulty of operationalizing the concept of 'sustainability' (Weinbaum *et al.*, 2013; Sirén, 2015), we do not conclude that Waiwai hunting is sustainable. Instead, we join others in emphasizing a shift in focus to the extent to which prey populations are likely to be depleted and using these predicted patterns of depletion to inform long-term monitoring and active management (Levi *et al.*, 2011). By projecting densities across space, biodemographic modeling allows for the establishment of quantitatively informed no harvest zones and other conservation interventions in a way that static indices do not (Levi *et al.*, 2011; Shaffer *et al.*, 2017b).
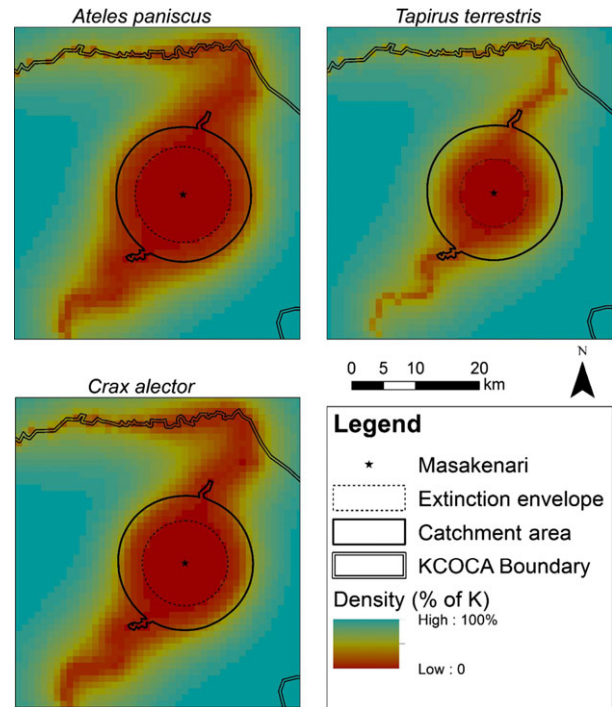
While the biodemographic approach has been shown to adequately model the effects of hunting in primate species (Levi *et al.*, 2011; Shepard *et al.*, 2012; Shaffer *et al.*, 2017b), our study is the first to validate these models with other taxa. Our results suggest that biodemographic models can be equally effective for assessing the sustainability of curassow hunting and they provide initial validation of the
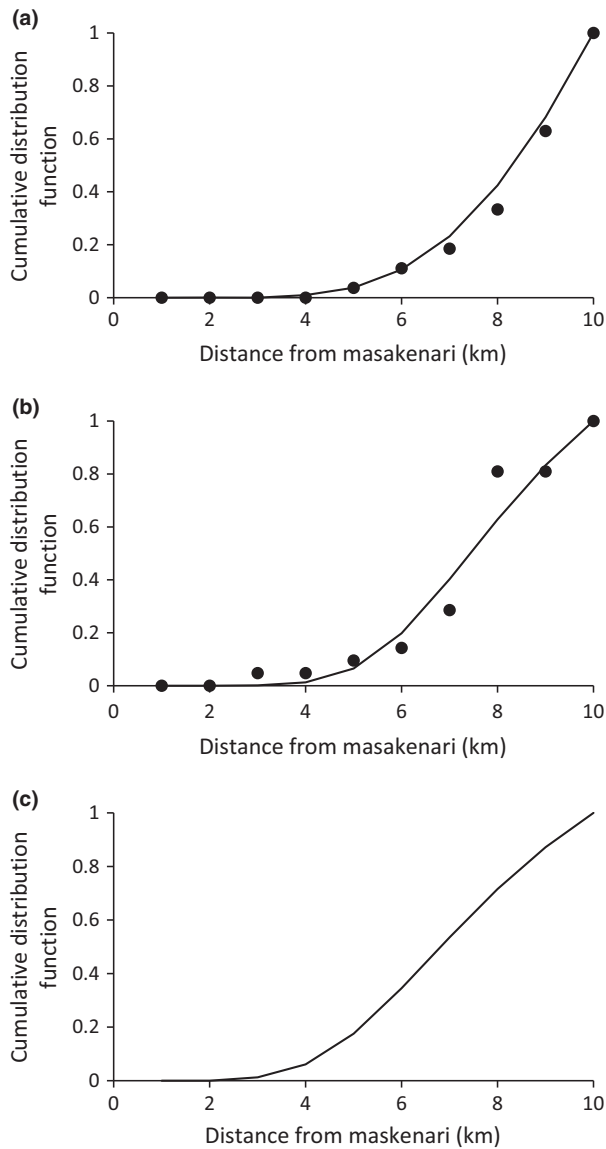
Figure 3 Cumulative distribution functions (CDFs) for the predicted densities from the 2015 model compared to CDFs from empirically derived encounter rates for (a) *Ateles paniscus* and (b) *Crax alector*. Because the number of encounters of *Tapirus terrestris* were too few for analysis, (c) shows the CDF of model predicted densities only for this species.

Figure 4 Projected densities from biodemographic models for black spider monkeys *Ateles paniscus*, lowland tapirs *Tapirus terrestris*, and black curassows *Crax alector*. Species densities are projected 20 years into the future and the population of Masakenari is predicted to grow from 225 to 350 individuals.

model for tapirs. However, biodemographic modeling does have limitations. The models used in this study are poorly suited to species that have very large and/or shifting home ranges (e.g. white-lipped peccaries) and they assume central-place foraging by hunters (Levi *et al.*, 2009). In addition, some of the parameters, particularly kill rate and *r*, are difficult to estimate. Further, the method remains relatively untested, particularly for nonprimate taxa. We therefore recommend more extensive testing of these models to validate results in other bushmeat systems and for other prey species.

Implications for hunting management

Although the weaknesses of static sustainability indices are well established (Milner-Gulland & Akcakaya, 2001; Levi *et al.*, 2009; Weinbaum *et al.*, 2013; Van Vliet *et al.*, 2015; they continue to be used in the literature (Zapata-Ríos *et al.*, 2009; Cuthbert, 2010; Weinbaum *et al.*, 2013), and conclusions based on their results are still cited and influential in determining conservation policy (Terborgh, 2000; Zimmerman *et al.*, 2001; Zapata-Ríos *et al.*, 2009; Weinbaum *et al.*, 2013). Our study demonstrates that static indices can lead to misleading results about the long-term sustainability of bushmeat systems, particularly in areas surrounded by large portions of unhunted forest. This is the situation for many areas throughout Amazonia, particularly the hundreds of millions of hectares of forest managed as indigenous reserves (Peres, 1993). While indigenous reserves present a number of conservation challenges, they also offer tremendous opportunities for conserving large areas of the Amazon (Zimmerman *et al.* 2001; Nepstad *et al.*, 2006; Peres & Nascimento, 2006; Shepard *et al.* 2010; Shepard *et al.*, 2012). In these reserves, conclusions about sustainability have enormous implications for indigenous food security, cultural identity, biodiversity conservation, and governance (Peres & Nascimento, 2006; Shepard *et al.*, 2012). Therefore, it is critical that conservationists employ more robust methods for assessing sustainability, like the biodemographic approach demonstrated here,

while simultaneously treating conclusions based on static indices with caution.

Finally, it is important to note that accurately assessing sustainability is only one aspect of actually achieving the goal of sustainable hunting (Sirén, 2015). Managing hunting for long-term sustainability is a complex task that also requires shared goals among all stakeholders, appropriate governance, and the commingling of sometimes disparate ontologies (Sirén, 2006; Nadasdy, 2007; Salo, Sirén & Kalliola, 2014; Shaffer *et al.*, 2017*b*). We have previously argued that the biodemographic modeling approach is particularly well suited for co-management because model parameters can be estimated by hunters, validating results is straightforward, and model outputs can be congruent with the hunting ontologies of Amazonian indigenous groups (Shaffer *et al.*, 2017*a,b*). The current study demonstrates that the biodemographic approach is also robust for a range of different prey species and that biodemographic models perform far better than static sustainability indices.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Population density estimates from the Upper Essequibo Conservation Area (UECC), based on a total effort of 310 km.
Data S1. Hunter self-monitoring protocol.
Data S2. Line transect survey methodology for density estimates.
Data S3. Biodemographic model parameters.
Data S4. Transect survey methodology for model validation.