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Assessing the accuracy of distance- and interview-based measures of hunting pressure

Brian M. Griffiths[1] | **Joseph Kolowski**[2] | **Mark Bowler**[3,4] | **Michael P. Gilmore**[1] | **Elizabeth Benson**[5] | **Forrest Lewis**[5] | **Jared Stabach**[6]

[1]School of Integrative Studies, George Mason University, Fairfax, Virginia, USA
[2]Smithsonian Conservation Biology Institute, Smithsonian-Mason School of Conservation, Front Royal, Virginia, USA
[3]School of Science, Technology and Engineering, University of Suffolk, Ipswich, UK
[4]Suffolk Sustainability Institute, Ipswich, UK
[5]OnePlanet, Inc., Virginia Beach, Virginia, USA
[6]Smithsonian National Zoo and Conservation Biology Institute, Front Royal, Virginia, USA

Correspondence
Brian M. Griffiths, School of Integrative Studies, George Mason University, 4400 University Drive, Fairfax, VA 22030, USA.
Email: bgriffi7@gmu.edu

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Abstract

In the Amazon Rainforest, the sustainability of hunting is difficult to model. Accurate sustainability models for hunting of mammal populations require a spatially explicit measure of hunting pressure. Because field-based measures of hunting pressure are time and labor-intensive, distance-based proxies for hunting pressure are frequently used. In this study, we tested accuracy of distance-based parameters in predicting measured hunting pressure obtained through interviews for a riverine community in the Peruvian Amazon. We examined the spatial accuracy of the interviews and investigated the minimum requirements for spatial assessment of hunting pressure based on interviews. Results illustrate that hunter-reported animal kill locations were accurate to within a mean of 1 km. Interview effort results showed that approximately 4 months of interviews capturing at least 50% of hunts are necessary to obtain a complete measure of hunting pressure across the landscape. Generalized linear models identified a novel spatially explicit approach that explained 59% of the deviance in measured hunting pressure. Our model was based on distances from locations that are easily obtained through remotely sensed imagery, participatory mapping, and terrain characteristics, highlighting that biologically relevant and spatially explicit estimates of hunting pressure can be obtained without lengthy field-based methods. Hunting pressure across a landscape can be accurately predicted from remote sensing, participatory mapping, and terrain characteristics.

KEYWORDS

Amazon, bias, central place foraging, conservation, effort, hunt, management, model, wildlife

1 | INTRODUCTION

Overhunting is regarded as one of the greatest threats to biodiversity (Benítez-López et al., 2017; Redford, 1992; Schipper et al., 2008). In the tropics, as is the case globally, hunters generally target medium- and large-bodied game mammals to achieve a larger return on investment (Alvard et al., 1995; Barboza et al., 2016). Large-bodied mammals, however, often have very low reproductive rates and may not be able to sustain stable population sizes under heavy hunting pressure (Alvard, 1995; Salas & Kim, 2002). In addition, many of these same species (such as the Brazilian tapir [*Tapirus terrestris*] and red howler monkey [*Alouatta seniculus*]) are acknowledged as ecological keystones (Paine, 1995), the loss of which has been shown to have profound impacts on the forest itself, including altering the composition of local plant communities (e.g., see Beck et al., 2013; Brodie et al., 2009).

Quantifying the effects of hunting pressure on mammal populations is complex. Sustainability models, like the production model created by Robinson and Redford (1991), use a series of indices and ground-truthed data to extrapolate the effects of hunting on a large scale. The parameters that Robinson and Redford (1991) used include population density at carrying capacity and the intrinsic rate of population increase. Yet reliance on static parameters is known to overestimate sustainable harvest levels (Peres, 2000; Robinson, 2004). In addition, these models do not include a spatial component, which must be considered for a hunting model to be accurate (Novaro, 2004). In effect, these models assume a constant hunting pressure across the landscape, which has been shown to be a biased assumption (e.g., Benítez-López et al., 2017, 2019; Brodie & Fragoso, 2020; Ling & Milner-Gulland, 2008; Ohl-Schacherer et al., 2007; Sirén et al., 2013). Recently, spatially explicit models have been developed with a better ability to calculate the impacts of hunting on populations of specific species across a landscape. Levi et al. (2009, 2011), for example, created a robust biodemographic model to calculate depletion of primate populations caused by hunting. Salas and Kim (2002) created a similar model to calculate tapir depletion. Both models use a spatially explicit measure of hunting pressure as a parameter. This study evaluates the accuracy of several spatially explicit measures of hunting pressure and provides a new, less biased model for estimating pressure based on easily gathered data.

Several methods exist to calculate or estimate hunting pressure, also known as hunting effort, defined as the economic measure of resources invested by a hunter (Krebs & Davies, 1997). These measures usually include parameters associated with cost or resistance to a hunter moving across a landscape, including the need to spend more time to access a location (time-based parameters), travel further (distance-based parameters), or traverse more difficult terrain features (terrain-based parameters) (Benítez-López et al., 2019). Some physical features, such as rivers, may also act as barriers to movement (Brodie & Fragoso, 2020). Rist et al. (2008) evaluated time-based parameters of hunting pressure (such as number of hours spent hunting or number of days hunters were active) and found that they were prone to bias because of violation of inherent assumptions. For example, the number of hours spent hunting is a common metric used. But, since hunters are not always actively looking for prey while on a hunting trip, the metric is prone to overestimate hunting pressure (Rist et al., 2008).

Distance-based parameters are also commonly used to estimate hunting pressure, the simplest of which assumes that human hunters act as central-place foragers (Orians & Pearson, 1979), radiating outward from a central location such as a community. These measures are also prone to bias since heterogeneity of vegetation, soils, topography, and habitat quality can affect the distribution of both animals and hunters (Robinson & Bennett, 2000). Hunters may also utilize hunting camps in the forest as bases for single or multiday hunting trips, acting as pseudo-settlements and introducing high levels of hunting pressure at areas that are far from the community. Previous studies (see Levi et al., 2011) have applied central-place foraging theory to multiple community settlements but frequently ignore the use of hunting camps associated with individual settlements.

Another distance-based parameter used in hunting models is distance to major access points, such as navigable rivers (e.g., see Benítez-López et al., 2019; Bowler et al., 2016; Di Bitetti et al., 2008) or trails, adding a reticular component to hunting models rather than simply assuming central place foraging (Albert & Le Tourneau, 2007). While this parameter does not assume that hunters walk in a straight line from a community, it does assume that all rivers and trails are equally traveled. Models including parameters of effort, like distance to access points or the community can also include terrain-based parameters that can impede hunter movement (Sirén et al., 2013). These terrain-based parameters could also influence prey density, explaining variation in hunting pressure (Brodie & Fragoso, 2020).

Less-biased measures of hunting pressure include the use of hunter follows (Noss, 1998; Rist et al., 2008) or interviews to map hunters' actual travel routes or kill locations. In the hunter follow methodology, a trained observer follows the hunter with a GPS device during a hunt, marking locations and characteristics of animal kills. While this method greatly improves spatial accuracy of hunting pressure, it is expensive in terms of personnel hours required (Rist et al., 2010).

More detailed information can be collected using a series of surveys or interviews conducted with hunters on a regular basis. These interviews usually include a hand-drawn map of where the hunter went and where animals were killed. Interviews may be prone to error if the hunter has difficulty understanding provided maps. Previous work by Rist et al. (2010) showed that only 21% of hunters accurately reported their location to the level of defined hunting zones, with an average distance of

1.93 km between reported and actual locations. However, compared to hunter follows, it is possible to measure the activity of a much greater number of hunters with fewer personnel hours using registers or interviews. In both methodologies, resulting maps can be used to calculate direct measures of hunting pressure, such as distance walked by hunters in specific grid cells (e.g., see Sirén et al., 2004).

The objective of this study was to evaluate the accuracy of distance-based parameters for predicting hunting pressure. Here, we used weekly interviews with hunters to construct a map of measured hunting pressure that we then used to evaluate the extent to which measures including distance from the community, major access points, and hunting camps represent biologically relevant measures of hunting pressure. We also assessed the spatial accuracy of the more time-intensive and detailed hunter interviews using a sample of hunter follows and the point of diminishing returns for interview effort.

2 | MATERIALS AND METHODS

2.1 | Study site

Fieldwork was conducted in collaboration with the Maijuna (Orejón) indigenous group of the northeastern Peruvian Amazon. The Maijuna are a Western Tucanoan

FIGURE 1 Map of the Maijuna-Kichwa Regional Conservation Area (MKRCA) and the Sucusari community, where the study took place

people with a population of approximately 600 individuals (Gilmore, 2010). The Maijuna live in four riverine communities: Puerto Huamán and Nueva Vida along the Yanayacu River, Sucusari along the Sucusari River, and San Pablo de Totolla (Totoya) along the Algodón River. Each community has legal title to lands that directly border the Maijuna-Kichwa Regional Conservation Area (MKRCA), an area of 391,039.82 hectares that represents much of Maijuna ancestral lands (Figure 1). The MKRCA is made up of humid primary terra firme forest, floodplain forest, and a terraced habitat unique to this region (Gilmore et al., 2010). The region is characterized by a mean annual rainfall of 3100 mm and a mean annual temperature of 26°C (Marengo, 1998).

This study was conducted in a hunted region of the MKRCA, the Sucusari River basin, which is a tributary of the Napo River. The Sucusari community has legal title to 4771 hectares that adjoins the recently established MKRCA (Gilmore et al., 2010). The Sucusari community (72.92995 W, 3.24373 S) is approximately 126 km by river from Iquitos, the capital of the Region of Loreto. The community has 166 residents, divided into 32 monofamilial or plurifamilial houses (Roncal et al., 2018). Ethnicities of community members are split between Maijuna (59%), mestizo (35%), and Kichwa (6%) individuals.

2.2 | Measured hunting pressure

2.2.1 | Semistructured interviews

We conducted weekly semistructured interviews (Berg & Lune, 2014) with 19 active hunters (90.5% of all active hunters in the community) from September 2018 to June 2019 to document the frequency, success, and spatial distribution of hunting activity. The average age of hunters interviewed was 41.2 years, with a range of 22–68 years. All hunters in the Sucusari community were male. During each interview, hunters drew the routes of their recent hunting trips on a laminated map of the river basin, reported details of the hunt such as the date, time, and duration, and identified animal sightings and kill locations. The map included many familiar references, including tributaries, mineral licks, hunting camps, hunting trails, and line transect trails created during previous research to quantify mammal occupancy across the region (see Bowler et al., 2016).

For the purpose of the weekly interviews, we defined a hunt as any time a hunter left the community carrying a shotgun, the weapon used by all hunters in Sucusari. Hunts were only considered time that the hunter was actively searching for prey. For example, if a hunter searched for 3 hours, returned to the camp for 6 hours, then went out again for three more hours, two distinct hunts were recorded at 3 hours each. When a hunter reported a long hunt duration (10+ hours), the hunter was specifically asked if they were searching for prey the entire time to clarify. Opportunistic hunts, such as those that occurred when a hunter traveled to a neighboring community or went fishing while carrying a shotgun, were not considered during hunting pressure analyses since hunting for game was not the hunter's primary objective. We digitized interview maps using ArcGIS (v. 10.6, ESRI, 2018), then dissolved tracks from hunters into a raster data set of hunting pressure using the number of kilometers walked by hunters in each 1-km cell as a measure of hunting effort (following Levi et al., 2009; Sirén et al., 2004). We calculated the distance from the center of each cell to the community, the nearest major access point used for hunting and the nearest hunting camp or house. We determined major access points to be rivers and trails which were accessible year-round and experienced regular hunting by community members.

Since the river basin is only accessible by members of the community of Sucusari, we assumed that the only hunting occurring in this river basin is from the hunters of Sucusari. Since the hunters were all well known to the researchers and the overall number of hunters was only 19, we also assumed that all of the hunts undertaken by those 19 hunters were captured by interviews. Also, hunting is a legal activity throughout the river basin. Thus, hunters had no reason to withhold information during survey questionnaires.

2.2.2 | Hunter follows

Thirty hunts were followed during the study period with a GPS (Garmin GPSMap 64s), recording the hunter's route as well as the location of all species sighted and killed by the hunter, from January 2019 to May 2019. Hunter follows were not conducted during the first 4 months of the study in order to build rapport and trust with hunters before following them. These kill and sighting locations were used to assess the accuracy of hunter-reported kill and sighting locations identified on maps during interviews. Because hunters frequently hunted by canoe and hunters are able to recognize specific turns on the river, we used an information-theoretic approach (Burnham & Anderson, 2002) to test the hypothesis that hunters more accurately reported animal sighting and kill locations when hunting via canoe rather than on foot. Reporting error was calculated as the Euclidean distance between the location reported by the hunter and the location recorded by the observer with a

GPS. A mixed-effects linear model was created with reporting error as the response variable and hunt type (land vs. canoe), and number of days between the hunt and the interview as predictors, with the latter term aiming to account for potential reductions in spatial recall over time. Hunter was included as a random effect in the models to account for pseudoreplication and individual differences in reporting accuracy. All combinations of these covariates were compared to each other and to an intercept-only model using Akaike information criteria (AIC) corrected for small sizes to select the optimal model.

2.2.3 | Interviewing effort

We analyzed interview effort to determine the minimum number of months of interviewing needed to attain a reliable estimate of the spatial spread and magnitude of hunting pressure in Sucusari. We divided hunting pressure values in each grid cell by the total distance (km) walked by hunters to obtain the proportion of hunting pressure represented in each grid cell, a measure of hunting spread. We then subsampled interviews and recalculated values for each grid cell using only the interviews collected during the first month of our survey, the first 2 months, the first 3 months (and so on) to document the cumulative increase in spatial accuracy of hunting estimates that resulted with the concomitant increase in temporal sampling effort. The spatial accuracy of the resulting estimates were assessed based on the sum of squared error between the proportion of total hunting pressure across all cells from all 10 months and the proportions from the reduced cumulative interview effort as months of interviews were completed (i.e., residuals). We then determined when sampling effort achieved sufficient spatial accuracy, considered here as the point at which 90% of the possible variation in hunting pressure spread was captured by interviews. The full extent of possible error was calculated by the sum of squared error in not measuring any hunts at all. We conducted 100 iterations of random samples for 25, 50, and 75% of the total number of interviews to calculate mean residuals and 95% confidence intervals for each month.

2.2.4 | Distance-based parameter analysis

We used a generalized linear model framework to assess the relative utility of three indices of hunting pressure in predicting measured hunting pressure: distance from the community, distance from hunting camps, and distance to access points. Measured hunting pressure, represented as the distance (km) walked by hunters in each of 612 1-km grid cells, was our response variable. We included elevation and terrain roughness, calculated as the range in elevation between a cell and its eight surrounding neighbors (as in Stabach et al., 2017; Wilson et al., 2007) as terrain-based characteristics of a cost surface (Brodie & Fragoso, 2020). We filtered out zero values since the spatial extent of the hunting pressure layer was greater than the area that was hunted, leaving a sample size of 311 grid cells for analysis. We first created a full model with all individual predictor variables and inclusive of two-way interactions between each distance measure. We tested interactions in the model under the assumption that, for example, the influence of hunting camp proximity on hunting pressure varies with the distance from the community and/or major access points. We also included quadratic terms of elevation and surface roughness to account for potential nonlinear relationships between terrain-based variables and the response. All models were fitted with a gamma distribution since our response variable was restricted to values ranging from 0 to infinity. We used a backward-stepwise approach (Burnham & Anderson, 2002) to rank and evaluate competitive models based on AIC values and related metrics. We performed K-fold cross validation with 10 folds to validate model results. We ran 100 iterations of the K-fold cross validation and report the average root-mean-square-error (RMSE) scaled by dividing by the standard deviation of the response variable. K-fold cross validation was performed using the *cv.glm* function in the *boot* package (Canty & Ripley, 2020; Davison & Hinkley, 1997) in R (R Core Team, 2019).

3 | RESULTS

3.1 | Semistructured interviews

We recorded 671 hunts during the study period that comprised a total distance traveled of 8120.15 km. Overall, hunters traveled over land most frequently, but also frequently hunted by canoe or opportunistically from motorboats (Table S1). Hunters were active both day and night, but most hunts were conducted during the day (Table S1). On average, hunts were 6.85 h (median 6.00 h) in length, with a range of 10 min from a brief opportunistic encounter close to a house, to 27 h. Overall, 7.8% of the total game meat harvested, by mass, came from opportunistic hunts.

We followed 30 hunts with a GPS among 10 different hunters. On average, each of the 10 hunters was followed three times. Hunter follows spanned all three modes of travel and both day and nighttime periods (Figure S1). Hunter follows were mostly conducted in the southern half of the river basin, but several follows were completed in northern, remote reaches of the basin (Figure S2).

Measured hunting pressure values varied greatly across the river basin. Hunting pressure levels were almost five orders of magnitude (range = 0.032–254.52 km) higher at sites near the community in comparison to more remote areas of the river basin (Figure 2 (a)). Cells with notably high hunting pressure were located near the community, near hunting camps, and along major rivers (Figure 2(a)).

3.2 | Accuracy of hunter interviews

On average, hunters reported animal sightings within 953.78 m (*SD* = 691.69 m) from the actual location recorded by the observer. Half (50.0%) of these reports were within 600.00 m of the actual sighting location (Figure S3). Interestingly, hunters were generally more accurate in reporting animal locations during land-based hunts than river-based hunts, with average errors of 729.60 m (*SD* = 628.73 m) and 1193.38 m (*SD* = 1187.51 m), respectively. This was confirmed in regression models where only travel type (and not number of days between the hunt and interview) was identified in the highest ranked model, with a ΔAIC = 1.39 compared to the model with both number of days passed and travel type (ΔAIC = 1.43 compared to null model).

3.3 | Interview effort

Analysis of the point of diminishing returns of interview effort showed that the accuracy threshold (90% of total variation captured) was reached after about three and a half months of interviewing when all hunts were captured (Figure S3). After 4 months of interviewing, and including 100% of hunts, 94.69% of the variation in mean hunting pressure spread was captured. After 7 months of interviewing, 100% of hunts and 99.30% of the variation in mean hunting pressure spread was captured.

Analysis of the proportion of interviews showed that the number of months of interviewing needed to capture an accurate assessment of mean hunting pressure spread (>90% of variation captured) varied by proportion of interviews captured. Overall, the accuracy threshold for 50 and 75% of hunts captured was reached at about 4 months of interviews. Measuring 50% of hunts resulted in 89.83% of variation in mean hunting pressure spread captured after 4 months of interviews. Capturing 75% of hunts over a 4-month period resulted in 93.54% of the variation captured. If only 25% of hunts were measured, the accuracy threshold was reached after about 8 months, when 90.91% of the variation in mean hunting pressure spread was captured.

3.4 | Distance-based parameter analysis

The highest-ranking model was our optimal model, which included all three distance-based parameters

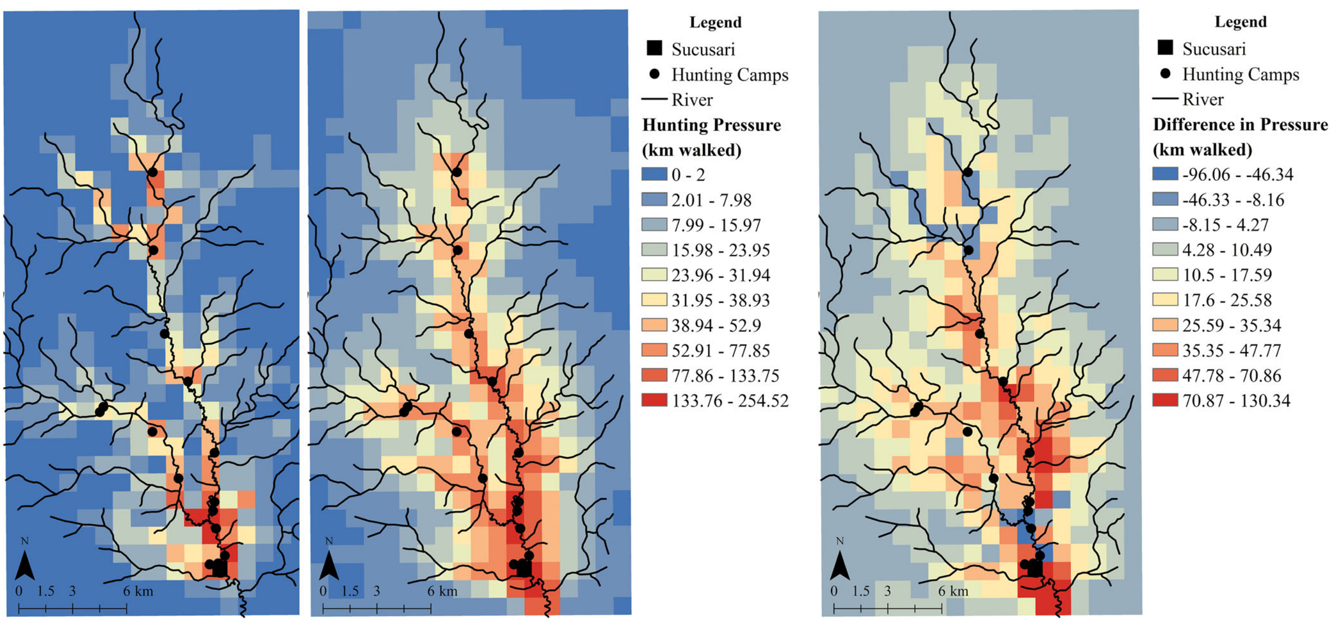

FIGURE 2 Hunting pressure (a) calculated from hunter interviews, (b) predicted by spatial model, and (c) model error (difference between a and b) in units of km walked by hunters in the Sucusari River basin, highlighting differences between results

(distance from the community, major access points, and hunting camps), an interaction between distance from access and hunting camps, the quadratic form of elevation, and surface roughness (Tables 1 and 2). The optimal model showed that there was a negative relationship between each respective distance measure and measured hunting pressure (Figure S5). Surface roughness and elevation had a negative impact on hunting pressure (Table 2). Response curves of the optimal model showed sharp increases in hunting pressure predicted nearby hunting camps and access points, in particular (Figure 2 (b) and 3). Visual depiction of model residuals showed some model underestimation of hunting pressure at some hunting hotspots, such as very close to the community and key hunting camps, and overestimation of hunting pressure in most areas farther from the community and from access points (Figure 2(c)). However, the model correctly captured the increase in hunting surrounding hunting camps and major rivers, particularly those closer to the community, with an explained deviance value of 0.597. After 100 iterations, K-fold cross validation results yielded an average RMSE of 19.935, which yielded a scaled average RMSE of 0.668.

Explained deviance values for distance from camps and access points, as individual covariates, were similar at 0.414 and 0.386, respectively. The distance from community parameter performed relatively poorly by itself in explaining variation in hunting pressure, with an explained deviance of 0.107 (Table 1).

4 | DISCUSSION

Spatially explicit, accurate measures of hunting pressure are key to modeling the impacts of hunting on animal populations and making land-use decisions (Levi et al., 2009, 2011; Novaro, 2004). When choosing a method to measure hunting pressure, researchers should consider the required resolution and spatial accuracy of the results and other practical considerations, such as availability of personnel hours and funding. In Sucusari, we showed that weekly interviews were an accurate method for collecting hunting pressure data, with an average reported error in kill locations of less than 1 km. An error of less than 1 km is much lower than the average reporting error (1.93 km) obtained by Rist et al. (2010). The difference in reporting may be because most of the hunters in Sucusari had previous experience doing participatory mapping exercises (Gilmore & Young, 2010, 2012; Young & Gilmore, 2013, 2014, 2017) and were effectively able to conceptualize a basemap of the landscape. The accuracy in reporting also demonstrates the need for researchers to use an accurate basemap with culturally and locally relevant reference points that hunters can use to pinpoint kill locations. While these methods can be used in areas where hunters are less familiar with participatory mapping, error should be assessed, and resolution of the analysis adjusted accordingly. Overall, our results show that for biological analyses that require a relatively high resolution

TABLE 1 Results of generalized linear models on accuracy of distance-based measures for predicting measured hunting pressure, showing all models up to cumulative Akaike weight >0.95 as well as individual distance-based parameters tested by themselves

Model	ΔAIC	Num. Par.	Weight	Expl. Dev.
Poly (elevation) + surface roughness + distance from access + distance from community + distance from camps + distance from access: distance from camps	0.00	9	0.453	0.597
Poly (elevation) + surface roughness + distance from access + distance from community + distance from camps + distance from access: distance from camps + distance from access: distance from community	0.58	10	0.339	0.599
Poly (elevation) + surface roughness + distance from access + distance from community + distance from camps + distance from access: distance from camps + distance from access: distance from community + distance from community: distance from camps	2.19	11	0.152	0.599
Distance from camps	123.84	3	0.000	0.414
Distance from access	141.14	3	0.000	0.386
Distance from community	285.52	3	0.000	0.107

Parameter	Estimate	SE	Lower CI	Upper CI
Elevation	**−6.679**	**2.866**	**−12.296**	**−1.062**
Elevation^2	**4.242**	**1.129**	**2.029**	**6.455**
Surface roughness	**−0.158**	**0.061**	**−0.277**	**−0.039**
Distance from access	**−0.866**	**0.087**	**−1.036**	**−0.695**
Distance from community	0.180	0.128	−0.071	0.432
Distance from camps	**−0.358**	**0.098**	**−0.549**	**−0.167**
Distance from access: distance from camps	**0.289**	**0.055**	**0.182**	**0.396**

TABLE 2 Coefficient estimates and 95% confidence intervals of optimal generalized linear model on accuracy of distance-based measures for predicting measured hunting pressure. Statistically significant coefficient estimates shown in bold

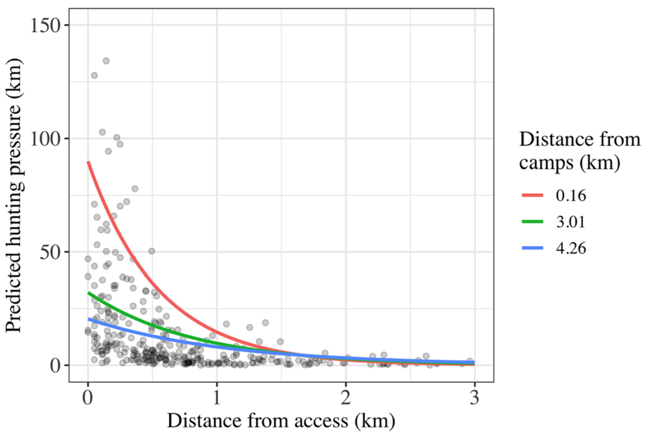

FIGURE 3 Generalized linear model results for predicting hunting pressure from interview data based on distance from hunting camps and access points (major rivers and trails). Displayed distance from camps values represent the minimum, mean, and third quartile of the data. Other covariates set to minimum (surface roughness), first quartile (elevation), and third quartile (distance from community). Raw data shown as points

(i.e., 1 km), interviews can be used in place of more demanding methods like hunter follows if a basemap with numerous familiar references is used.

Effort analyses revealed that measured hunting pressure, on a per month basis, was relatively constant after about 4 months of interviewing when 50–100% of hunts were captured. We found that if only 25% of hunts were captured using interviews, at least 8 months of interviews were needed to attain an accurate estimate of the spread of hunting pressure. Since our results showed that the number of months of interviews needed varies by the proportion of hunts captured, we suggest that future studies estimate the percentage of hunts captured when using interview-based methods. For studies using participatory mapping as a method to capture the spatial spread of hunting pressure, at least 50% of hunts should be captured for a period of 4 months. It should be noted that in areas where hunting pressure changes seasonally across the landscape, more than 4 months of interviews or 2 months in each season may be needed to capture the full extent of the spatial spread of hunting pressure. Although the overall number of hunters in Sucusari is small, we believe that these results are generalizable to other areas with more hunters since we considered the spread of hunting pressure, rather than magnitude.

The utility of participatory mapping and accuracy of hunter reporting of animal locations, with 50% of reports within 600 m of the actual location of the animal, demonstrates the importance of including and empowering local communities in the sustainable management of hunting and other forest resources (Becker & Ghimire, 2003; Berkes, 1999, 2004, 2007; Berkes et al., 2000; Gilmore et al., 2020; Roncal et al., 2018). In particular, the cultural practices and decision-making of individual hunters (Chaves et al., 2020; Hames, 2007; Hames & Vickers, 1982; Hill et al., 1987; Lemos et al., 2021) could add critical context to quantitative models on the sustainability of hunting and complement the methods presented here (Alvard, 1993). While this study aimed to create a quantitative tool that can be used with minimal fieldwork, community-based conservation based on interdisciplinary approaches can be particularly effective (Berkes et al., 2000; Charnley et al., 2007; Gadgil, 1998; Moller et al., 2009; Vieira et al., 2019), and we suggest that local ecological knowledge and traditional ecological knowledge (TEK) are included wherever possible. We would also like to note that participatory methods such as those described here are dependent upon building trust and respect with local communities. This study, for example, is built upon over 20 years of collaboration and mutual trust with the Maijuna (e.g., see Bowler et al., 2016; Gilmore, 2005; Gilmore et al., 2010, 2020; Griffiths et al., 2020, 2021). Regardless of their history with a community, we suggest that investigators and practitioners ask critical questions before engaging in community-based research, exploring the needs and wants of the community, and collaboratively developing methodologies. We also suggest that all results from studies are first shared with communities for transparency and approval, and that investigators critically think about the implications of their study for the community before publishing to ensure that research is empowering and not disenfranchising (Gilmore & Eshbaugh, 2011).

In instances where exact measured hunting pressure is not needed, a measure based on distance may be used instead. However, each of the commonly used distance-based measures for hunting pressure have underlying assumptions that can introduce bias. Overall, when extended to include access points and hunting camps, the central-place foraging theory provided a more accurate measure of hunting pressure for hunters in Sucusari. The central-place foraging theory (Orians & Pearson, 1979) states that at greater distances from the community, hunting pressure should be lower because those sites require more effort to access. Upon examining model results visually in Figure 2, sharp increases in hunting pressure are associated with areas that are nearby access points and hunting camps, particularly those that are also close to the community. The similar effect of distance from access points and distance from hunting camps on hunting pressure is likely due to correlation between the two measures, since hunting camps in Sucusari are frequently located alongside rivers to facilitate travel. Because our goal was to develop the most accurate predictive model, we allowed correlated predictors to be featured in the same model, yet we avoided any interpretation of standard errors of estimated coefficients in these models due to potential bias introduced by this collinearity (Dormann et al., 2013). These results indicate that studies using measures for hunting pressure to model hunting in riverine communities should include distance from access points, distance from the community, and the interaction between both parameters, at a minimum. The distance from hunting camps is not a commonly used measure (see Levi et al., 2011 for use of camps as microsettlements in models), likely because these camps cannot be reliably remotely sensed. The locations of hunting camps can sometimes be easily obtained through participatory mapping exercises with hunters, however, requiring only a small amount of fieldwork and personnel hours. In cases where it is not possible to gather locations of hunting camps (i.e., hunting is illegal and participatory mapping not possible), other parameters that could influence hunter movement should be used, such as distance from roads, human population density, protection status of the area, and distance to closest protected area (Benítez-López et al., 2019; Ziegler et al., 2016).

Even when the central-place foraging theory was extended to include access points and hunting camps, model deviations from observed hunting pressure were noted in several areas. As an example, some grid cells which were predicted to be hunted heavily were not entered by hunters during the study period. This may be due to a lack of trails or habitat heterogeneity which was not explained by our terrain-based parameters. For some systems, particularly those with large tracts of flooded forest or different soil types, the assumption that hunting pressure radiates from a central location may overestimate the smoothness and homogeneity of hunting across the landscape, as happened in our case. However, the heterogeneity of hunting pressure may have important ecological implications, as hunters rarely walk in straight lines, creating pockets of space that are relatively free of hunting pressure due to habitat and landscape features (Mockrin et al., 2011). This was seen in the map of measured hunting pressure, as cells with a value of almost zero were surrounded by heavily hunted cells. These pockets could be acting as source areas for nearby areas that are regularly traversed by hunters, influencing the movement of game species across the landscape. Assuming homogeneity in this landscape would lead observers to overlook these key refuges and therefore overestimate the effects of hunting.

Both elevation and surface roughness were significant covariates in the optimal model of predicting hunting pressure, indicating that terrain-based cost surfaces could have an impact on hunter movement and the accessibility of grid cells. Since surface roughness is neighborhood-based, influenced by neighboring cells, the measure mimics hunter movement as a hunter moves from a cell to a neighboring cell, and the resistance in that movement caused by terrain. Terrain-based covariates acting as a cost surface for hunter movement have been significant in other studies (e.g., Brodie & Fragoso, 2020). While it is unlikely that hunters recognize and respond to small changes in elevation or surface roughness while hunting, these parameters are likely indicators for some unmeasured resistance to movement, since higher elevation and surface roughness was associated with a decrease in hunting pressure. It is likely that for studies on much larger scales, where high resolution spatial data are not needed, spatial variation in hunting pressure is smoothed and the accuracy of model predictions would increase. However, additional covariates should be added to models as scale increases, which could include measures such as land cover (Brodie & Fragoso, 2020), population density, and demographic variables (Benítez-López et al., 2019).

Our study builds upon the body of literature that uses distance-based parameters to explain trends in hunting pressure and populations of prey species (e.g., Benítez-López et al., 2017, 2019; Brodie & Fragoso, 2020; Gill et al., 2012; Kümpel et al., 2010;

Ling & Milner-Gulland, 2008; Ohl-Schacherer et al., 2007; Sirén et al., 2013; Smith, 2008; Ziegler et al., 2016), but is the first to compare the spatial accuracy of these parameters to participatory mapping results. However, the accuracy of other parameters for hunting pressure has been assessed, including time-based parameters such as the number of hours spent hunting (Rist et al., 2008). Time-based parameters are similarly prone to bias due to sweeping assumptions, possibly limiting their utility in biological models (Rist et al., 2008). For example, time spent hunting may be problematic since hunters may be gone for several days and only hunt for a portion of that time. This distinction allowed us to filter out those hunts for our models and focus on the subset of hunts during which a hunter indicated he was actively hunting.

Measures of hunting pressure are commonly used to model animal distributions and hunting sustainability (Bowler et al., 2016; Zapata-Rios et al., 2009). Information about how animal populations respond to hunting pressure can provide useful context for making management decisions governing wildlife and land use. Our objective in this study was to provide a useful, straightforward, and accurate model for recent hunting pressure that can be applied to wildlife data.

4.1 | Conclusions

Distance-based measures provide accurate estimates of recent hunting pressure when combined into a single model. These measures are all easily recorded and can provide scientists and land-use managers a fast, efficient way to quantify hunting pressure across a landscape without using extensive field-based methods. Our results are widely applicable to riverine communities in the Amazon that depend on subsistence hunting and hunt in a manner similar to hunters in Sucusari, with shotguns, boats, and canoes. When precise estimates of hunting pressure at a fine resolution are needed, our results illustrate that participatory mapping-based interviews can be used instead of other more expensive and time-intensive methods. Further, interview-based methods can provide an accurate measure of the spatial spread of hunting pressure with only 4 months of surveying 50% of hunters in a community.

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CONFLICT OF INTEREST

The authors declare no potential conflicts of interest.

AUTHOR CONTRIBUTIONS

Brian M. Griffiths: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, validation, visualization, writing – original draft, writing – review and editing. Joseph Kolowski: Conceptualization, formal analysis, validation, writing – review and editing. Mark Bowler: Conceptualization, methodology, project administration, supervision, writing – review and editing. Michael P. Gilmore: Conceptualization, methodology, project administration, supervision, writing – review and editing, funding acquisition. Elizabeth Benson: Conceptualization, investigation, methodology. Forrest Lewis: Conceptualization, investigation, methodology. Jared Stabach: Conceptualization, formal analysis, validation, writing – review and editing, supervision, visualization.

DATA AVAILABILITY STATEMENT

Spatial data on hunting pressure used in this study is available upon reasonable request from the authors. Qualitative interview data are unavailable to be shared because individual hunters are identifiable from their responses.

ETHICS STATEMENT

All aspects of this study were approved by George Mason University's Institutional Review Board, project #1288488-1.

ORCID

Brian M. Griffiths https://orcid.org/0000-0001-9522-7731

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SUPPORTING INFORMATION

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