Spatial tools for modeling the sustainability of subsistence hunting in tropical forests

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Abstract. Subsistence hunting provides a crucial food source for rural populations in tropical forests, but it is often practiced unsustainably. We use the empirical observation that subsistence hunters are central-place foragers to develop three "bio-demographic" hunting models of increasing complexity and realism for assessing the sustainability of hunting of an indicator species. In all our models, we calculate the spatial pattern of depletion of an indicator species (here, a large-bodied primate) across a landscape. Specifically, we show how to identify the area surrounding a human settlement that is expected to suffer local extinction. Our approach is an improvement over well-known sustainability indices of hunting, which are prone to error and do not provide clear links to policy prescriptions. Our first approach models the long-term effect of a single settlement and (1) can be parameterized with easily obtainable field data (such as settlement maps and knowledge of the major weapon used), (2) is simple enough to be used without requiring technical skill, and (3) reveals the asymptotic relationship between local human density and the level of game depletion. Our second model allows multiple settlements with overlapping hunting zones over large spatial scales. Our third model additionally allows temporal changes in human population size and distribution and source–sink dynamics in game populations. Using transect and hunting data from two Amazonian sites, we show that the models accurately predict the spatial distribution of primate depletion. To make these methods accessible, we provide software-based tools, including a toolbox for ArcGIS, to assist in managing and mapping the spatial extent of hunting. The proposed application of our models is to allow the quantitative assessment of settlement stabilization approaches to managing hunting in Amazonia.

Key words: Ateles *spp.; Brazilian Amazon; bushmeat; community-based conservation; human-inhabited protected areas;* Lagothrix *spp.; protected-area management; source–sink dynamics; spider monkey; sustainable hunting; wild meat; woolly monkey.*

Introduction

Hunting is widely acknowledged to be unsustainable throughout the world's tropical forests (Milner-Gulland et al. 2003). Large primates, keystone seed dispersers upon which much plant diversity depends (Peres and van Roosmalen 2002, Nuñez-Iturri and Howe 2007, Terborgh et al. 2008), are especially threatened by hunting (Peres 1990, Peres and Palacios 2007). On the other hand, game species are important sources of protein and income for millions of forest dwellers. In the Brazilian Amazon alone, the wild-meat harvest has been estimated to exceed 89 000 Mg (metric tons) annually (Peres 2000). Therefore, as with fisheries, the conserva-

tion challenge with wild-meat hunting is not to prevent exploitation outright but to prevent overhunting from depleting forests of their wildlife and species diversity, ultimately costing forest dwellers their food supply, and, potentially, ecotourism revenue and the political will to maintain defaunated forests in the face of alternative land use options. This challenge is both biological and political in nature, in that we require both a robust knowledge of the amount of offtake that can be sustained by a given target species and reliable governance mechanisms that can prevent exploitation from exceeding sustainable levels.

Within the hunting literature, sustainability has been defined and assessed most commonly via the use of "sustainability indices" (Milner-Gulland and Akçakaya 2001, Stephens et al. 2002), which are static algorithms that calculate a sustainable level of harvest within an arbitrarily defined catchment area. One of the most commonly used such indices, the Robinson and Redford

(1991) production model, uses literature values of a target species' carrying capacity and intrinsic population growth rate to calculate a maximum annual production, a fraction of which is then taken to be the species' MSY, or maximum sustainable yield, where the fraction is dependent on the life span of a typical individual (see Alvard et al. 1997, Slade et al. 1998, Ohl-Schacherer et al. 2007). The MSY is then compared to observed offtakes from the catchment area to assess whether offtake is sustainable. A similar approach is the harvest model of Robinson and Bodmer (1999), which uses empirical estimates of local game species densities and calculates a sustainable offtake from the expected annual fecundity.

Such sustainability indices have proven inadequate for measuring the impact of hunting because sustainability is treated as a static, binary "Yes or No" question, with the result being sensitive to the arbitrary choice of the size of the catchment area (Levi et al. 2009). Sustainability indices are also well known to overestimate the true MSY (Milner-Gulland and Akçakaya 2001) and can misinterpret low harvest rates as under-harvest rather than as evidence for previous depletion (Ling and Milner-Gulland 2006). Moreover, sustainability indices require extensive fieldwork that must be repeated for each new study site to obtain quantitative measures of game offtake or animal density (Robinson and Bodmer 1999, Sirén et al. 2004, Ohl-Schacherer et al. 2007, Smith 2008). Even ignoring these drawbacks, sustainability indices cannot be used to project the impact of hunting into the future, nor to visualize or quantify the distribution of hunting impact over space.

What is needed, therefore, are mechanistic models of hunting that can be parameterized with easily obtainable field data and that can be used to compare management options over long time frames, as is the case with population viability analysis approaches (Morris and Doak 2002).

To improve upon sustainability indices, which only model some of the biology of game species, recent work has used a bioeconomic approach to incorporate the behavior of hunters. An excellent example is given by Damania et al. (2005), who explore the effects of changes in market prices and different governance regimes (e.g., forest patrols vs. fines on the sale of wild meat) on the population dynamics of game species. Among other results, they find that penalties imposed on the market sale of game species discourage shotgun use, promote consumption of game meat at home, and, ultimately, allow game populations to increase, even in the absence of forest patrols.

The methods of Damania et al. (2005), however, are less applicable to systems where subsistence hunting is the norm and wild-meat markets are small or nonexistent, such as over much of the Neotropics (Fa et al. 2002). Examples include the larger indigenous and sustainable development reserves of the Brazilian Amazon (Nepstad et al. 2006, Peres and Nascimento 2006), as well as most strictly protected forest reserves in tropical South America, which typically contain human populations. In these situations, because human populations are more isolated, state enforcement of hunting laws, even if they exist, is largely nonexistent (Terborgh 1999). Thus, governance options such as forest patrols or market fines are not applicable throughout much of the Amazon Basin.

On the other hand, these less-populated areas have the advantage of containing often extensive unhunted areas that safeguard viable, high-density game species populations (Joshi and Gadgil 1991) that can serve as source populations for hunting sinks. However, arrayed against the long-term viability of these game populations is the rapid growth of indigenous and rural human populations (McSweeney 2005) and the general and increasing accessibility to hunters of much of the rest of lowland Amazonia (Peres and Terborgh 1995, Peres and Lake 2003).

To aid the assessment and management of subsistence hunting, we present a series of biodemographic hunting models, building on an approximate-form model introduced by Levi et al. (2009). The biodemographic approach combines a spatial model of game species population dynamics with human demographic data or a demographic model. This contrasts with the bioeconomic approach, which allows human behavior to change but holds human demography constant (Yu 2010).

A major advantage of a biodemographic approach is its use of relatively easy to collect data. We use human population size, which can be obtained from official census data or demographic interviews, settlement locations, which can be obtained from maps, remote sensing data, or a GPS unit, and some parameter values that can be obtained from the literature (Table 1; see also Alvard and Kaplan 1991).

We first present an *analytical, single-settlement model* that finds a solution for the steady-state (long-term) density of a hunted game species as a function of distance from a single human settlement. The result is a three-dimensional $(x, y,$ game density) surface of game population density that can be used to identify the circular area around a settlement within which hunting is not sustainable, which we call the "extinction envelope." Our approach redefines sustainability as a spatial and temporal concept rather than as a "Yes or No" question. Wild meat is an important protein source for subsistence hunters, and access to meat is reduced as the catch per unit effort declines. Thus, we also find an analytical solution for the catch per unit effort at the steady-state density. This model is implemented in a downloadable spreadsheet.

We then extend the single-settlement model to an *analytical, multiple-settlement model* in which hunting zones are allowed to overlap. This model is used to calculate the fraction of total landscape in which the focal game species is expected to be extirpated, under the assumption that the number and distribution of settlements remain stable.

TABLE 1. Parameter values, their interpretation, and references.

Parameter	Definition	Value	References
K	game species carrying capacity	25	Janson and Emmons (1991)
g	maximum intrinsic population growth rate	*Ateles*, 0.07; *Lagothrix*, 0.12	Robinson and Redford (1991)
d	monkeys killed per group encounter	bow, 0.1; gun, 0.9	Alvard and Kaplan (1991), Levi et al. (2009)
e	encounter rate constant to convert game species density to group encounters per kilometer walked	0.02	Endo et al. (2010), Levi et al. (2009)
hphy	hunts per hunter per year	40–80	Levi et al. (2009)
σ	spatial spread of hunting effort	Manu, 5; Sarayacu, 7	Ohl-Schacherer et al. (2007), Sirén et al. (2004)
D	diffusivity of monkeys	0.1	Levi et al. (2009)

Notes: When applying this model, the parameter σ is best estimated by noting that the mean of the Rayleigh distribution (mean hunt distance from settlement center) equals $(\sqrt{\pi/2})\sigma$. The diffusivity parameter D is one-fourth of the annual mean-square displacement of monkeys, which can be estimated by considering biologically reasonable movements.

However, this assumption can be violated in two ways. Population growth and spread can increase the number of settlements, and, conversely, some Amazonian indigenous groups are interested in creating no-take areas within their territories to ensure long-term persistence of game species vulnerable to hunting (G. H. Shepard, *personal observation*). For both cases, we present a *numerical, multiple-settlement model with source–sink dynamics*. Although not as tractable as the analytical models, the numerical model allows one to calculate levels of depletion or recovery around settlements after any number of years and in any order of settlement establishment or removal, respectively. We also use the numerical model for validation. To facilitate the use of both the analytical and the numerical models by managers and indigenous organizations, we have included a Python script (Supplement) for the software package ArcGIS (ESRI, Redlands, California, USA).

All our models gauge the effect of hunting in space and time, both on game populations and on humans via decreased access to game resources. Game populations are depleted around human settlements, with the intensity and extent of that depletion dependent on three inputs: (1) human population size and spatial distribution, (2) the weapon technology used (e.g., bow and arrow, shotgun), and (3) the average number of hunts per hunter per year. Thus, a map of human settlements in the area of interest, plus estimates of the above three inputs (from direct observation or literature values), together generate maps of present and future depletion that can be used to guide management.

METHODS

The key observation underlying our biodemographic approach is that subsistence hunters are central-place foragers who concentrate their effort near human settlements (Lu and Winterhalder 1997, Sirén et al. 2004, Ohl-Schacherer et al. 2007, Smith 2008). Given a certain amount of effort, the number of kills of a particular species will be a function of the desirability, vulnerability, and local abundance of that species.

For our focal species, we chose large primates, particularly spider monkeys (*Ateles* spp.) and woolly monkeys (*Lagothrix* spp.) because (1) they are highly prized and are thus pursued by many indigenous groups whenever encountered (Shepard 2002, da Silva et al. 2005); (2) their relatively stable home ranges (Symington 1988, Peres 1996) allow for predictable mean spatial encounter rates for a given density, and allow their migration to be viewed as a wavefront diffusing into the depleted hunting zone as previously occupied home ranges are recolonized; (3) they have very low reproductive rates and long life spans (Peres 1990), which, when coupled with the ease of detecting a large-bodied (6–9 kg) and large-group-living (up to 70 individuals) monkey moving through the forest canopy, makes them vulnerable to overhunting. This sensitivity to hunting means that large primates serve as an indicator species, such that when they are present, other game species will be as well. See Peres (2000) for a survey of Amazonian forest sites over 10 years (see also Alvard et al. 1997, Bodmer and Lozano 2001, Ohl-Schacherer et al. 2007, Smith 2008). Because many other game species are pursued by subsistence hunters, and because gun-hunters do not walk farther than do bow-hunters, even when primate populations are depleted (Alvard et al. 1997, Peres and Lake 2003, Ohl-Schacherer et al. 2007, Smith 2008; but see Sirén et al. 2004), we assume elasticity in demand for monkey meat. Alternative prey species are substituted as large primates are depleted, allowing us to assume that the spatial distribution of hunting effort is constant over the time period when large primates are depleted (Jerozolimski and Peres 2003).

To parameterize the models, we use estimates obtained through a three-year field study in Manu National Park, Peru (Ohl-Schacherer et al. 2007). More details are available in Levi et al. (2009) and Alvard and Kaplan (1991). A summary of parameter values used is in Table 1.

Analytical, single-settlement model

We start with a spatially explicit model for a single human settlement hunting for large primates, but the

approach generalizes to other territorial game species. The landscape is represented by a two-dimensional array (grid) of 1-km^2 bins, where each $N_{x,y,t}$ represents the density of the focal game species in bin (x, y) at time t.

Given a human population of size p, the population of the focal species in year $t + 1$ is a function of population growth $R(N_{x,y,t})$, offtake $O(N_{x,y,t}, p)$, which is a function of game species density $N_{x,y,t}$, and human population size p:

$$N_{x,y,t+1} = N_{x,y,t} + R(N_{x,y,t}) - O(N_{x,y,t}, p). \qquad (1)$$

In each bin, the total population production is:

$$R(N_{x,y,t}) = gN_{x,y,t}\left[1 - \left(\frac{N_{x,y,t}}{K}\right)^{\Theta}\right] \qquad (2)$$

where g is the maximum intrinsic growth rate, K is the population ceiling, and Θ is a parameter that controls the shape, or degree of onset, of density dependence.

Setting offtake in each bin to the product of the rate at which monkeys are encountered during human hunting forays, $E_{x,y,t}$, the mean number of monkeys killed per group encounter, d, and the level of hunting effort in that bin, $h_{x,y,t}$, we obtain

$$
\begin{aligned}
O(N_{x,y,t}, p_t) &= O_{x,y,t} \\
&= \frac{\text{encounters}}{\text{km walked}} \times \frac{\text{kills}}{\text{encounter}} \\
&\quad \times \text{km walked through } (x, y) \\
&= \text{encounter rate} \times \text{kill rate} \times \text{effort} \\
&= E_{x,y,t} d h_{x,y,t}. \qquad (3)
\end{aligned}
$$

The kill rate, d, is a constant, dependent on the hunting technology employed, and the encounter rate, $E_{x,y,t}$, is linearly dependent on the density of monkeys at (x, y) by $E_{x,y,t} = e \times N_{x,y,t}$. The encounter rate constant, e, has been determined empirically by distance sampling (Buckland et al. 1993, Endo et al. 2010) (Appendix A).

Spatial distribution of hunting effort.—The remaining term is the hunting effort in each bin and year, $h_{x,y,t}$, which is measured as the cumulative distance walked in each bin (x, y). This is the most difficult to derive. We operate on a square grid in polar coordinates with $r_{max}(\theta)$ and $r_{min}(\theta)$ defined as the distance to the far and near edges of a bin following the trajectory defined by the angle θ. θ_{min} and θ_{max} define the minimum and maximum angles that subtend bin (x, y) (Fig. 1a). Formulas for $r_{max}(\theta)$, $r_{min}(\theta)$, θ_{max}, and θ_{min} are derived with basic trigonometry (Appendix B).

The contribution to hunting effort by a single trajectory $H(\theta)$ can be calculated with two terms. The probability that a hunt goes beyond the far edge of the focal bin, $\Pr\{r(\theta) > r_{max}(\theta)\}$, contributes a distance walked of $(r_{max}(\theta) - r_{min}(\theta))$; the probability that a hunt ends in a bin, $\Pr\{r_{min}(\theta) \le r(\theta) \le r_{max}(\theta)\}$, contributes the expected distance walked in the bin $E[r(\theta) \mid r_{min}(\theta) \le r(\theta) \le r_{max}(\theta)]$. In sum, the contribution to hunting effort for each trajectory is

$$
\begin{aligned}
H(\theta) &= \Pr\{r(\theta) > r_{max}(\theta)\} \times \Big(r_{max}(\theta) - r_{min}(\theta)\Big) \\
&\quad + \Pr\{r_{min}(\theta) \le r(\theta) \le r_{max}(\theta)\} \\
&\quad \times E[r(\theta) \mid r_{min}(\theta) \le r(\theta) \le r_{max}(\theta)]. \qquad (4)
\end{aligned}
$$

The distribution of hunting effort measured in kilometers walked has been found empirically to approximate normality (Sirén et al. 2004, Ohl-Schacherer et al. 2007, Smith 2008). Thus, we model the distribution of hunting distances with the bivariate normal distribution converted to polar coordinates with standard deviation σ. To clarify previous confusion about the spatial distribution of hunting, note that integrating out θ over the polar coordinate form of the bivariate normal (equivalent to multiplying by 2π), gives the related Rayleigh distribution, which unlike the normal distribution is restricted to be nonnegative (as are distances from a human settlement). Thus the distribution of distances walked when hunting effort is isotropic is actually the Rayleigh distribution. The distribution of effort vs. distance has been informally called "normal" (Sirén et al. 2004) because it declines with distance as e^{-r^2}, giving it half of a normal-like shape. This effort vs. distance relationship can be derived from the distribution of distances walked by noting that all hunts that have walked past a particular location contribute effort to that location. In probability terms, this is simply 1 minus the cumulative distribution function of the Rayleigh distribution, or $e^{-r^2/2\sigma^2}$, which provides the observed normal-like decline in hunting effort, and since it is a CDF it need not integrate to 1. When applying this model, the parameter σ is best estimated by noting that the mean of the Rayleigh distribution (mean hunt distance from settlement center) equals $(\sqrt{\pi/2})\sigma$.

The first probability term requires summing over all the hunts that cross the borders of the focal bin by integrating radially outward from $r_{max}(\theta)$ to ∞, and the second requires summing over the hunts ending in the bin by integrating from $r_{min}(\theta)$ to $r_{max}(\theta)$. To sum the contribution of all trajectories that intersect the bin, we integrate $H(\theta)$ over the angles that subtend each bin (from θ_{min} to θ_{max}):

$$
\begin{aligned}
\int_{\theta_{min}}^{\theta_{max}} H(\theta)\, d\theta &= \int_{\theta_{min}}^{\theta_{max}} \int_{r_{max}(\theta)}^{\infty} \frac{r}{2\pi\sigma^2} \exp\left(\frac{-1}{2\sigma^2} r^2\right) \\
&\qquad \times \Big(r_{max}(\theta) - r_{min}(\theta)\Big)\, dr\, d\theta \\
&\quad + \int_{\theta_{min}}^{\theta_{max}} \int_{r_{min}(\theta)}^{r_{max}(\theta)} \frac{r}{2\pi\sigma^2} \exp\left(\frac{-1}{2\sigma^2} r^2\right) dr\, d\theta \\
&\quad \times \int_{0}^{2\pi} \int_{r_{min}(\theta)}^{r_{max}(\theta)} \frac{r^2}{2\pi\sigma^2} \exp\left(\frac{-1}{2\sigma^2} r^2\right) dr\, d\theta.
\end{aligned}
$$
$$(5)$$

This integral cannot be solved in closed form; thus, we derive an approximation for a bin centered s

distance units away as the fraction of hunts that walk at least distance s and fall within a wedge that is a fraction of the total circumference of a circle of radius s. The idea is that the circumference + 1 approximates the number of bins over which it is necessary to distribute the hunting effort. The addition of 1 both normalizes the function so that all hunts pass through the settlement (because $1/(2\pi s + 1) = 1$ when $s = 0$) and avoids division by zero at the settlement center. We derive our approximation to be

$$\int_{\theta_{\min}}^{\theta_{\max}} H(\theta) \, d\theta \approx \frac{1}{2\pi s + 1} \int_0^{2\pi} \int_s^\infty \frac{r}{2\pi\sigma^2} \exp\left(-\frac{r^2}{2\sigma^2}\right) dr \, d\theta$$

$$= \frac{1}{2\pi s + 1} \exp\left(\frac{-1}{2\sigma^2} s^2\right). \qquad (6)$$

Note that the exponential term in Eq. 6 is simply 1 minus the cumulative distribution function of the Rayleigh distribution as described previously, and is also equivalent to the empirically derived effort vs. distance relationship. Using p, the number of hunters, and hphy, the mean number of outgoing hunts per hunter per year, the total hunting effort $h_{x,y,t}$ can be written as

$$h_{x,y,t} = \text{hphy} \times p \times \exp\left(\frac{-1}{2\sigma^2} s^2\right) \frac{1}{2\pi s + 1}.$$

It can be written in Cartesian coordinates with $s = \sqrt{(x_0 - x)^2 + (y_0 - y)^2}$:

$$h_{x,y,t} = \text{hphy} \times p \times \exp\left(\frac{-1}{2\sigma^2}[(x_0 - x)^2 + (y_0 - y)^2]\right)$$

$$\times \frac{1}{2\pi\sqrt{(x_0 - x)^2 + (y_0 - y)^2} + 1} \qquad (7)$$

where (x_0, y_0) are the coordinates of the human settlement. Additionally, we must augment, rather than double, hphy to account for kills made on the return legs of hunting trips. Return legs should result in fewer kills than the outgoing legs because (1) game might already have been captured, thereby reducing motivation to pursue additional prey; (2) the afternoon encounter rate is lower than the morning encounter rate due to a reduction in prey foraging activity (Endo et al. 2010); and (3) given a failed outgoing hunt, the returning hunt is more likely to fail, because the hunter trajectories are correlated in space and time. To effectively capture the appropriate range of hphy, we perform our analyses for both lower and upper values of hphy, which represent the number of outgoing hunts per hunter per year, and double this quantity with the understanding that the true value is intermediate.

Accuracy of the approximation.—We compare the approximation to the results from numerically integrating $H(\theta)$ with the ratio

$$\frac{1}{2\pi s + 1} \exp\left(\frac{-1}{2\sigma^2} s^2\right) : \int_{\theta_{\min}}^{\theta_{\max}} H(\theta) \, d\theta.$$

We see that the error of the approximation is within $\pm 10\%$ for bins up to a distance of about 2.5 standard deviations of hunting effort. For example, if we assume $\sigma = 5$ km, the approximation holds to within 12–13 km, which is beyond the distance where hunting has a substantial impact (Fig. 1b). Additionally, for long distances, the approximation errs on the conservative side by apportioning more hunting effort than would be apportioned by the true value of the integral.

Analytical solution.—Using this approximation, we derive an analytical solution for the equilibrium or steady-state primate population size in bin (x, y) as a function of distance from a human settlement with a constant population size of hunters p. To do so, we set $N_{x,y,t+1} = N_{x,y,t} = N_{x,y}$, which is equivalent to setting production, R, equal to offtake, O, given by

$$R(N_{x,y}) = O(N_{x,y}, p)$$

or, more explicitly

$$gN_{x,y}\left[1 - \left(\frac{N_{x,y}}{K}\right)^\Theta\right] = \text{encounter rate} \times \text{kill rate} \times \text{effort}$$

$$gN_{x,y}\left[1 - \left(\frac{N_{x,y}}{K}\right)^\Theta\right] = E_{x,y,t} \times d \times h_{x,y,t}$$

$$gN_{x,y}\left[1 - \left(\frac{N_{x,y}}{K}\right)^\Theta\right] = e \times N_{x,y} \times d \times \text{hphy} \times p$$

$$\times \exp\left(\frac{-1}{2\sigma^2} s^2\right) \frac{1}{2\pi s + 1}. \qquad (8)$$

Solving for $N_{x,y}$ and noting that population size cannot be negative, we derive

$$N_{x,y}$$

$$= \max\left[0, K^\Theta\left(1 - \frac{e \times d \times \text{hphy} \times p \times \exp\left(\frac{-1}{2\sigma^2} s^2\right)}{g(2\pi s + 1)}\right)\right]^{1/\Theta}. \qquad (9)$$

Eq. 9 gives the steady-state game population density as a function of the distance from a settlement, s. Note that population (p), hunts per hunter per year (hphy), and kill rate (d) are all equally important parameters, meaning that an increase in kill rate, for example by allowing access to firearms, has the same impact as an increase in human population.

Hunting is, by definition, not locally sustainable in a region where the only steady state is zero. Alternatively, we can set a pseudoextinction threshold below the density needed to retain ecological functions (e.g., seed dispersal services). Setting $N_{x,y} = u$ in Eq. 9, where u is a
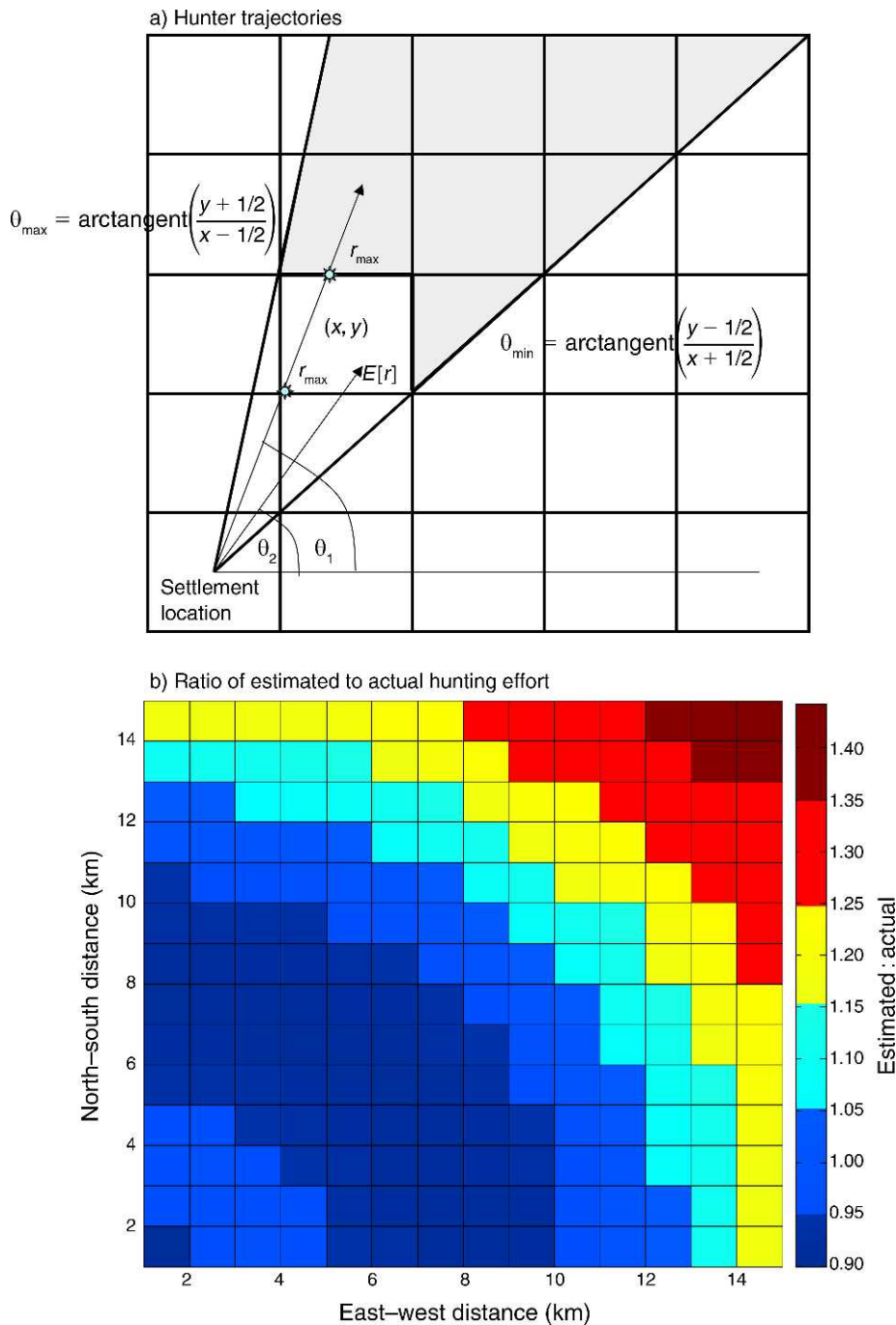
Fig. 1. Computation of hunting effort in each 1-km^2 grid cell (i.e., bin; small square). (a) The challenge is that grid cells are square, but hunter trajectories are described using polar coordinates. Our focal bin is indicated by (x, y). Note that grid vertices are located at the centers of each 1-km^2 bin. In each grid cell, hunters traveling on trajectories defined by $\theta_{min} \leq \theta \leq \theta_{max}$ can contribute to effort by walking past the bin and traveling $[r_{max}(\theta) - r_{min}(\theta)]$ through the bin [where $r_{max}(\theta)$ and $r_{min}(\theta)$, respectively, are distances to the far and near edges of a bin following the trajectory of angle θ], or by landing in the bin, in which case we assume a distance given by the expectation, $E[r(\theta) \mid r_{min}(\theta) \leq r(\theta) \leq r_{max}(\theta)]$. The gray-shading indicates the area past the far boundary of the focal bin. (b) Ratio of hunting effort approximation to actual effort obtained by numerical integration for a standard deviation of walking distance $\sigma = 5$ km.

pseudoextinction value, we can solve for the distance, s, which is the radius at which we expect the game population to be driven to pseudoextinction (or extinction, if $u = 0$ is chosen). The value of s can be calculated graphically or numerically (see our attached Microsoft Excel spreadsheet in Appendix C, Supplement) and can be used by managers to find the distance within which (pseudo-)extinction occurs. Parameter estimates (Table 1) can be taken from the literature or by direct observation (e.g., Levi et al. 2009).

Steady-state catch per unit effort (CPUE).— Although no hunters depend exclusively on spider and woolly monkeys for food, these species are important for many indigenous Amazonian populations (Shepard 2002, Cormier 2007) because they are reliably encountered due to their abundance, territoriality, and social behavior (Symington 1988, Endo et al. 2010). Thus, we use our result for the steady-state monkey population in each 1-km^2 bin (Eq. 9) to derive the steady-state CPUE, which is the number of monkeys killed per kilometer walked by a given human population size after the monkey population reaches steady state.

For simplicity, we place the focal settlement at the origin. The total annual offtake divided by the total effort defines the catch per unit effort as

$$
\text{CPUE} = \left[\sum_{\forall x} \sum_{\forall y} e \times N_{x,y} \times d \times \exp\left(\frac{-1}{2\sigma^2}(x^2 + y^2)\right) \right.
$$
$$
\left. \times \frac{1}{2\pi\sqrt{x^2 + y^2 + 1}} \right]
$$
$$
\div \left[\sum_{\forall x} \sum_{\forall y} \exp\left(\frac{-1}{2\sigma^2}(x^2 + y^2)\right) \right.
$$
$$
\left. \times \frac{1}{2\pi\sqrt{x^2 + y^2 + 1}} \right]. \tag{10}
$$

The denominator of this expression for CPUE is constant, so setting the denominator equal to $1/c$, we get a final expression for the steady-state CPUE:

$$
\text{CPUE} = ced \sum_{\forall x} \sum_{\forall y} N_{x,y} \times \exp\left(\frac{-1}{2\sigma^2}(x^2 + y^2)\right)
$$
$$
\times \frac{1}{2\pi\sqrt{x^2 + y^2 + 1}}. \tag{11}
$$

Note that the human population size (p) and hphy influence CPUE via the game population density $N_{x,y}$. Because gun-hunting populations can push CPUE below that which would have been obtained if everyone had continued to be a bow-hunter instead (see also Levi et al. 2009), this equality allows us to infer the human population size threshold at which gun-hunting becomes less profitable than bow-hunting in the long run (with human population size incorporated through $N_{x,y}$, which is given by Eq. 9). We thus have a method to calculate the effect of hunting on the viability of game

species both in terms of population persistence and as a food source for humans, allowing us to explore how different management options will affect the balance between conservation and livelihoods.

Analytical, multiple-settlement model

The advantage of the single-settlement model is that it is very easy to implement, and the extinction envelope is an obvious way to assess and quantify sustainability. However, we can also solve for the steady-state distribution of a game species exposed to hunting by multiple settlements with potentially overlapping hunting zones, which has not been possible with any previous measure of sustainability. To incorporate multiple settlements, the hunting effort term must now sum the effort contribution of each settlement i located at $(x_{0,i}, y_{0,i})$ and the population of each settlement, p_i:

$$
h_{x,y,t} = \text{hphy} \sum_{i=1}^{\text{settlements}} p_i \times \exp\left(\frac{-1}{2\sigma^2}[(x_{0,i} - x)^2 + (y_{0,i} - y)^2]\right)
$$
$$
\times \frac{1}{2\pi\sqrt{(x_{0,i} - x)^2 + (y_{0,i} - y)^2 + 1}}. \tag{12}
$$

Solving for the steady state as in Eqs. 8 and 9, but using the new hunting effort term,

$$
gN_{x,y}\left[1 - \left(\frac{N_{x,y}}{K}\right)^\Theta\right]
$$
$$
= e \times N_{x,y} \times d \times \text{hphy} \sum_{i=1}^{\text{settlements}} p_i
$$
$$
\times \exp\left(\frac{-1}{2\sigma^2}[(x_{0,i} - x)^2 + (y_{0,i} - y)^2]\right)
$$
$$
\times \frac{1}{2\pi\sqrt{(x_{0,i} - x)^2 + (y_{0,i} - y)^2 + 1}}
$$

and solving for $N_{x,y}$, the steady-state game population density in bin (x, y), we obtain

$$
N_{x,y} = \max\left[0, K^\Theta \left(1 - \frac{e \times d \times \text{hphy}}{g} \right.\right.
$$
$$
\left.\left. \times \sum_{i=1}^{\text{settlements}} \frac{p_i \exp\left(\frac{-1}{2\sigma^2}[(x_{0,i} - x)^2 + (y_{0,i} - y)^2]\right)}{2\pi\sqrt{(x_{0,i} - x)^2 + (y_{0,i} - y)^2 + 1}}\right)^{1/\Theta}\right].
$$
$$
\tag{13}
$$

There is no extinction envelope when multiple settlements are involved, but we can calculate a matrix of steady-state population density values if we specify the location and population of each settlement. Here, we generate two spatial distributions of 25 settlements each on a 200 × 100 km landscape, one dispersed and one clumped (i.e., including a large area where settlements

are prohibited), and we assess the resulting depletion caused by gun- and bow-hunters. The results can be summarized with cumulative distribution functions (CDFs), which summarize the distribution of spider monkey depletion across the landscape. Although the concept of an extinction envelope around a settlement does not exist here, a useful metric for comparing the sustainability of various landscape configurations is the fraction of the landscape in which the focal game species is extirpated under each configuration.

The steady-state CPUE when multiple settlements are included can be considered both as the local CPUE for some subset of the total number of settlements, or as the global CPUE, which is the total catch divided by the total effort. The multiple-settlement CPUE is a straightforward extension of the single-settlement CPUE. By summing the contribution to catch and effort over the desired settlements, the steady-state CPUE becomes

$$
\left[ed \sum_{\forall x} \sum_{\forall y} N_{x,y} \sum_{i=1}^{\text{settlements}} p_i \times \exp\left(\frac{-1}{2\sigma^2}[(x_{0,i}-x)^2 + (y_{0,i}-y)^2]\right) \right.
$$
$$
\times \left. \frac{1}{2\pi\sqrt{(x_{0,i}-x)^2 + (y_{0,i}-y)^2 + 1}} \right]
$$
$$
\div \left[\sum_{\forall x} \sum_{\forall y} \sum_{i=1}^{\text{settlements}} p_i \times \exp\left(\frac{-1}{2\sigma^2}[(x_{0,i}-x)^2 + (y_{0,i}-y)^2]\right) \right.
$$
$$
\times \left. \frac{1}{2\pi\sqrt{(x_{0,i}-x)^2 + (y_{0,i}-y)^2 + 1}} \right]. \qquad (14)
$$

We use this formula to find the global CPUE for the spatial arrangements of settlements. The CPUE, CDFs, and the steady-state distribution of game species can be calculated using the Matlab code in Appendix D and the Supplement). The generated hunter population and settlement coordinate data for the clumped and dispersed settlements that we used for this work are also provided. This model can also be implemented with a provided Python script to produce depletion maps in ArcGIS (Appendix E, Supplement).

Numerical, multiple-settlement model with source–sink dynamics

We now extend the model to add source–sink dynamics in the primate population. Because this numerical approach is not a steady-state solution, it can be used to model populations at any point in a time series, which also makes it a useful validation tool because we can compare the predicted and observed primate populations in any year after the establishment or removal of settlements and/or after an increase or decrease in human population size. For the same reason, this method is useful for gauging transient dynamics after a management intervention or external shock, such

as the introduction of new weapons, or the establishment of no-take zones.

We modify Eq. 1 to include a migration term and a hunter population at each time step:

$$
N_{t+1} = N_t + R(N_t) - O(N_t, p_t) + M(N_t). \qquad
$$

Following Levi et al. (2009), migration is taken to be a diffusion process, meaning that individuals move from higher density (less hunted) bins into lower density, neighboring bins and that the rate of diffusion becomes faster when the density difference between bins is higher. Thus, migration is given by

$$
M(N) = D \times \nabla^2 N \qquad (15)
$$

where D is the diffusivity constant (distance^2/time), which must be estimated, and ∇^2 is the Laplace operator, which is used to model heat flow or wave propagation; in two dimensions it is

$$
\nabla^2 N = \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}. \qquad (16)
$$

To discretize the Laplacian so that it can be applied on our array, we use the "five-point stencil" technique to write the finite difference approximation in two dimensions. The five-point stencil uses the values of the four nearest neighbors (up, down, left, right) to approximate derivatives on a grid. For bins 1-km across, and for a one-year time step, the stencil approximates the Laplacian as

$$
D \times \nabla^2 N \approx D \times (N_{x+1,y,t} + N_{x-1,y,t} + N_{x,y+1,t} + N_{x,y-1,t}
$$
$$
- 4N_{x,y,t}). \qquad (17)
$$

At the boundaries of our array, we hold the perimeter bins equal to K.

Solving this model numerically requires more technical skill than assessing sustainability using the previously derived analytical solutions, but we have provided a Python script for ArcGIS to make maps based on user-defined inputs. This script can be used to incorporate dynamics in order to quantify and visualize game depletion in space and time caused by a growing and spreading human population (Appendix E, Supplement). In this paper, we additionally use this model to compare the predicted spatial distribution of spider monkeys to empirical data, which is necessary for validation because data come from a particular year rather than at steady state.

Validating the model: predicting game depletion

Approach.—From published transect data we can validate the model's predictions against two variables: (1) the radius of local extinction ("extinction envelope"), which is determined by the radial distance beyond which individuals of the focal species can be found, and (2) the cumulative distribution function of the game population, which is a measure of the shape of game density
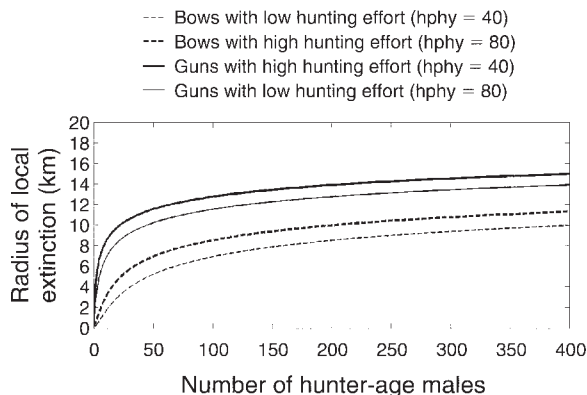
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FIG. 2. The increase in the radius of the extinction envelope increases nonlinearly with human population size and weapon choice. Gun-hunting, even by very small human populations, causes larger-scale local extirpation than does bow-hunting. As human population size increases, the radius of local extinction is ultimately limited by the distance that hunters can walk in a day, which is governed by σ. Hunting effort (low vs. high) is measured as hunts per hunter per year (hphy).

recovery at increasing distance from a human settlement. Because the numerical model can be solved for any time step, it can be directly compared to empirical data when we know the demographic history of the human settlement.

With empirical and modeled cumulative distribution functions, we use the two-sample Kolmogorov-Smirnov to test whether the empirical data and model output come from the same distribution. We compare two samples and look for a P value near unity to validate the modeled output as statistically indistinguishable from the empirical data.

Data sets for validation.—We first compare the model output to two vertebrate line-transect data sets (distance sampling) conducted at the same site, Yomybato, but at different times. Our earliest data set is a gray literature report conducted by Mitchell and Raéz-Luna (1991). One 8-km transect was conducted radially outward from the Matsigenka native community of Yomybato (Ohl et al. 2007, Ohl-Schacherer et al. 2007, Levi et al. 2009), at which time there were ~100 residents hunting almost exclusively with bow and arrow (Shepard et al. 2010). From 1976 to 1991, the number of hunters grew from 19 to 22, with a maximum of 24 in 1982 (G. H. Shepard, unpublished data). Because Yomybato had a stable population, we expect the steady-state results to show only slightly more depletion than that given from the numerical results or that is observed empirically, because there was time for the system to approach steady state.

Complementing the 1991 transects are data from a series of 4.5-km line transects conducted in 2006 and also radiating from Yomybato (Endo et al. 2010). Comparing the transect data from 1991 and 2006 provides evidence of how the spatial distribution of ateline monkeys has changed as the human population

has grown over time. In order to use a spatial scale that is consistent with the 1991 data, transects of 8 km long would have been ideal, but were not conducted.

To generate model expectations for the Manu transect data, we use a demographic data set that gives us the number of hunters (males aged 14–49) as an input into the model at each time step (for details, see Levi et al. 2009).

To analyze the spatial depletion from a second site and data set, we use published data from Sirén et al. (2004) to illustrate the effects of a large gun-hunting settlement on wildlife and to demonstrate the robustness of the model in predicting such impacts. In Sirén et al. (2004), hunters in the Ecuadorian Amazon recorded the distance of kills made from five clustered, gun-hunting hamlets with a total population of 960, collectively called Sarayacu. However, there are no accompanying transect or demographic data. Without demographic data, we cannot use the numerical method, but this site can reasonably be compared with the steady-state solution (Eq. 9), because the effect of additional increases in human population size in an already large human population have little effect on the extinction envelope, especially when guns are used. This is due to the asymptotic relationship between number of hunters and the extinction envelope (which we will discuss). Because Sarayacu is a ring of hamlets that are treated as one settlement, hunters walk farther from the "settlement center." Based on the published data on hunting effort vs. distance data, we thus use a greater spatial spread of hunting effort, σ = 7.

RESULTS

Analytical, single-settlement model

We first apply our model to the simplest case of one human settlement in an otherwise pristine environment. The circular area with radius s where the steady-state spider monkey population is zero (the extinction envelope) grows asymptotically with human population size. At small human population sizes, an increase in the gun-using population increases the extinction envelope much more than does the same increase in a bow-hunting population. This nonlinearity means that even small gun-hunting communities, or the adoption of guns by a fraction of hunters in a larger community, will result in the local extirpation of the ateline population in a large area. Observation of small gun-hunting populations entering an otherwise unhunted region are rare, but this result is consistent with Peres' (1990) observations from the Riozinho River of western Brazilian Amazonia that just three gun hunters in a newly exploited hunting zone were able to kill more than 200 woolly monkeys, 100 spider monkeys, and 80 howler monkeys between early 1985 and late 1986, rapidly driving populations of the two larger-bodied atelines to local extinction. Eventually, the effect of adding more hunters on the size of the extinction envelope diminishes

FIG. 3. Catch per unit effort (CPUE) at the steady-state spider monkey (*Ateles* spp.) population size for bow-hunters (dashed line) and gun-hunters (solid line). Gun-hunting has a higher CPUE in the long term only for unrealistically small human population sizes. For long-term access to primate meat, gun-hunting performs worse than bow-hunting. CPUE is defined as the number of monkeys killed per kilometer walked by a given human population size after the monkey population reaches steady state.
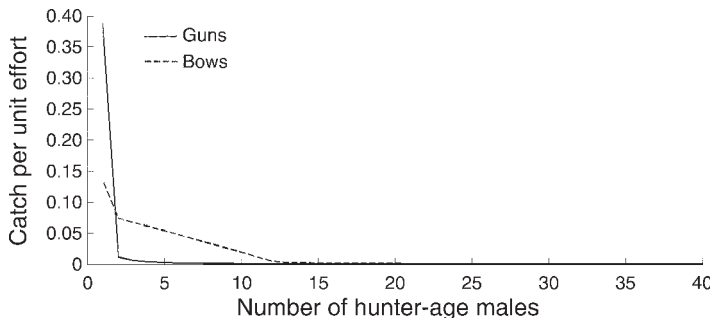
(Fig. 2), as even a large hunter population does not increase the distance that individuals can walk in a day. A useful aspect of this result is that estimates of the size of an extinction envelope are robust to errors in estimates of hunter numbers, the fraction of hunters using shotguns, and hunter effort level (except of course for the smallest settlements).

The killing efficiency of bow-hunters is much lower than those using guns, which results in a smaller radius of local extinction. The fact that bow-hunting is less efficient means that ateline primates remain extant within a large portion of the hunting zone, resulting in easier access to monkey meat. As a result, bow-hunters maintain a higher catch per unit effort than do gun-hunters over the long term, with the trivial exception of when there is only a single gun-hunter (Fig. 3).

Note that when the pseudoextinction threshold is zero (complete local extinction), the extinction envelope does not depend on the spider monkey carrying capacity K or the logistic theta parameter Θ, which is useful, because these are notoriously difficult to estimate. Also, multiplicative changes in the kill rate, human population, or

number of hunts per hunter per year all influence the extinction envelope equally. In other words, if switching from bow- to gun-hunting changes d by approximately one order of magnitude (Levi et al. 2009), this is mathematically the same as having 10 times the human bow-hunting population or each hunter hunting 10 times as often.

We can also visualize how spider and woolly monkey populations increase with distance from the human settlement (Fig. 4). The spider monkey's lower population growth rate causes it to exhibit depletion at greater distances from the settlement.

Analytical, multiple-settlement model

For both gun- and bow-hunters, we analyze the long-term impact of different settlement arrangements in space (Fig. 5). Gun-hunters create larger defaunated regions than do the same number of bow-hunters, leaving fewer refugia around settlements to act as a source of game. The two configurations for gun- and bow-hunters can be compared by the "fraction extirpated" (Fig. 5); a smaller fraction of the landscape is
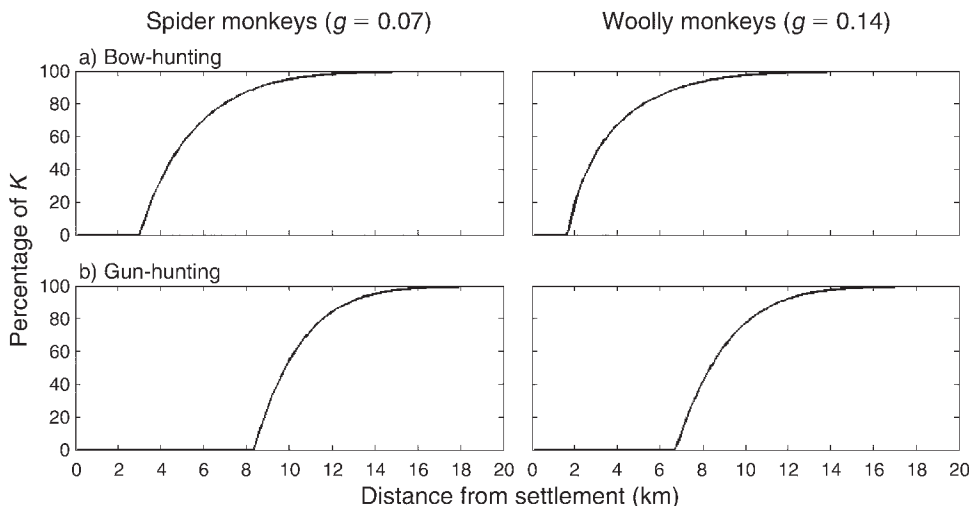
FIG. 4. The spatial distribution, in relation to distance from human settlement, of steady-state (K is carrying capacity) game species densities for spider monkeys and woolly monkeys (*Lagothrix* spp.), with different maximum intrinsic population growth rates, g. (a) Bow-hunting, kill rate $d = 0.1$. (b) Gun-hunting, $d = 0.9$. All four panels assume 20 hunters (the approximate number in Yomybato from 1976 to 1991), each hunting 40 times per year. The x-intercept indicates the radius of the extinction envelope ($N_{x,y} = 0$). Bow-hunting creates smaller areas of local extinction than does gun-hunting.

extirpated by bow-hunters. After controlling for weapons used, there is a secondary effect of the spatial arrangement of the settlements (Fig. 5). The more concentrated in space are the settlements, the more limited the depletion across the landscape, as hunters from different settlements pseudo-interfere with each other (Levi et al. 2009).

However, concentrating settlements on the landscape comes with the cost of lower catch per unit effort (Fig. 5). The guns scenario with clumped settlements had the lowest global CPUE of 0.0040 spider monkey kills/1000 km walked. The guns scenario with dispersed settlements had a 4.6-fold higher CPUE of 0.0185 kills/1000 km walked, but in both gun scenarios, spider monkeys were so depleted that they no longer contributed materially to human protein needs. Both clumped and dispersed bow-hunting scenarios had much higher CPUE values of 2.351 and 4.662 kills/1000 km walked, respectively. Some settlements in these two scenarios maintained access to spider monkeys, while others were so surrounded by other settlements that no spider monkeys remained within walking distance. The low CPUE for gun hunters does not imply that protein acquisition is difficult overall; spider monkeys are one of many alternate, and less vulnerable, game species. That said, the higher CPUE of bow-hunters does imply that other game species are more likely to be present near many settlements.

Validation results

We compare the numerical and empirical cumulative distribution functions of spider and woolly monkeys. By inspection, it is clear that the model fits the two transect data sets closely (Fig. 6). More formally, the Kolmogorov-Smirnov test could not detect any difference between the numerical model and the 1991 data ($P = 0.98$ for spider monkeys, $P = 1.00$ for woolly monkeys; Fig. 6a). Similarly, using the 2006 data, we recover a P value of 1.00 for both monkey species. In Fig. 6a, we also show the cumulative distribution function predicted by the analytical, steady-state model for Yomybato in 1991. This model, as expected, predicts a larger extinction envelope than does the numerical model, because Yomybato was still growing since first being settled in the 1970s and had not yet reached steady state (Levi et al. 2009, Shepard et al. 2010). We do not include an analytical solution for the current, rapidly growing population in Manu (Fig. 6b) because the analytical solution is a reasonable approximation only if the population size is stable or very large, such that additional population growth has little effect. However, see Levi et al. (2009) for projection scenarios of hunting impact in Manu Park.

As expected, the numerical and analytical solutions are more similar for woolly monkeys than for spider monkeys. Woolly monkeys, having a faster reproductive rate, can better compensate offtake with reproduction and will stabilize more quickly. Spider monkeys will

continue to be depleted farther from settlements, even by low levels of hunting effort.

The data from the large gun-hunting settlement, Sarayacu, show that catch per unit effort of woolly monkeys spikes upward after 14 km (Fig. 6b). This is consistent with the steady-state analytical solution, which shows heavy depletion up to 14 km from the settlement and rapid recovery beyond that point. In this analysis, we empirically estimated parameter values for gun-hunters and a hunter population estimate of 200, given that Sarayacu has 960 total inhabitants. The idea is not to have an exact match, but to show that the observed data are consistent with what the model predicts for a reasonable hunter population estimate. These examples show that the model is flexible and robust enough to characterize depletion caused by both bow- and gun-hunters in large and small settlements.

Note that neither model has been "fit" to the data; rather, we used parameter estimates determined a priori through fieldwork to run a purely mechanistic model and compare the predictions to data. Given this approach, the high degree of fit suggests that our model adequately captures the relevant dynamics.

Discussion

Indigenous peoples' territories present both tremendous opportunities and challenges for tropical biodiversity conservation worldwide, perhaps nowhere more so than in the Amazon basin (see Shepard 2002, Shepard et al. 2010), where fully 21% of the landscape is under the stewardship of indigenous peoples, constituting 54% of the total forest cover under some form of state protection (Peres 1994). Moreover, >70% of strictly protected national parks and analogous reserves include resident human populations (Brandon et al. 1998). In Brazilian, Peruvian, and Bolivian Amazonia, indigenous reserves together total >130 million ha of largely intact forestlands that can safeguard both full complements of biodiversity and important ecosystem services, such as carbon storage and hydrological cycles. Remote-sensing analyses have shown that indigenous reserves can be equally or more effective (when the surrounding landscape mosaic is considered) than strictly protected parks at preventing deforestation and forest fires (Nepstad et al. 2006). However, human-occupied reserves are beset by several internal threats to biodiversity, including high levels of population growth (McSweeney and Arps 2005), rapid cultural change, and overhunting associated with the recent adoption of firearms. The modeling framework that we have developed allows us to generate a map of game density, and therefore to assess the sustainability of hunting over space and time, which is an improvement over current sustainability indices (Appendix F). Moreover, we can do this with easily obtainable data, using maps of human settlements plus reliable literature values for key parameters (Table 1). The ability to assess and project game density over space and time under different
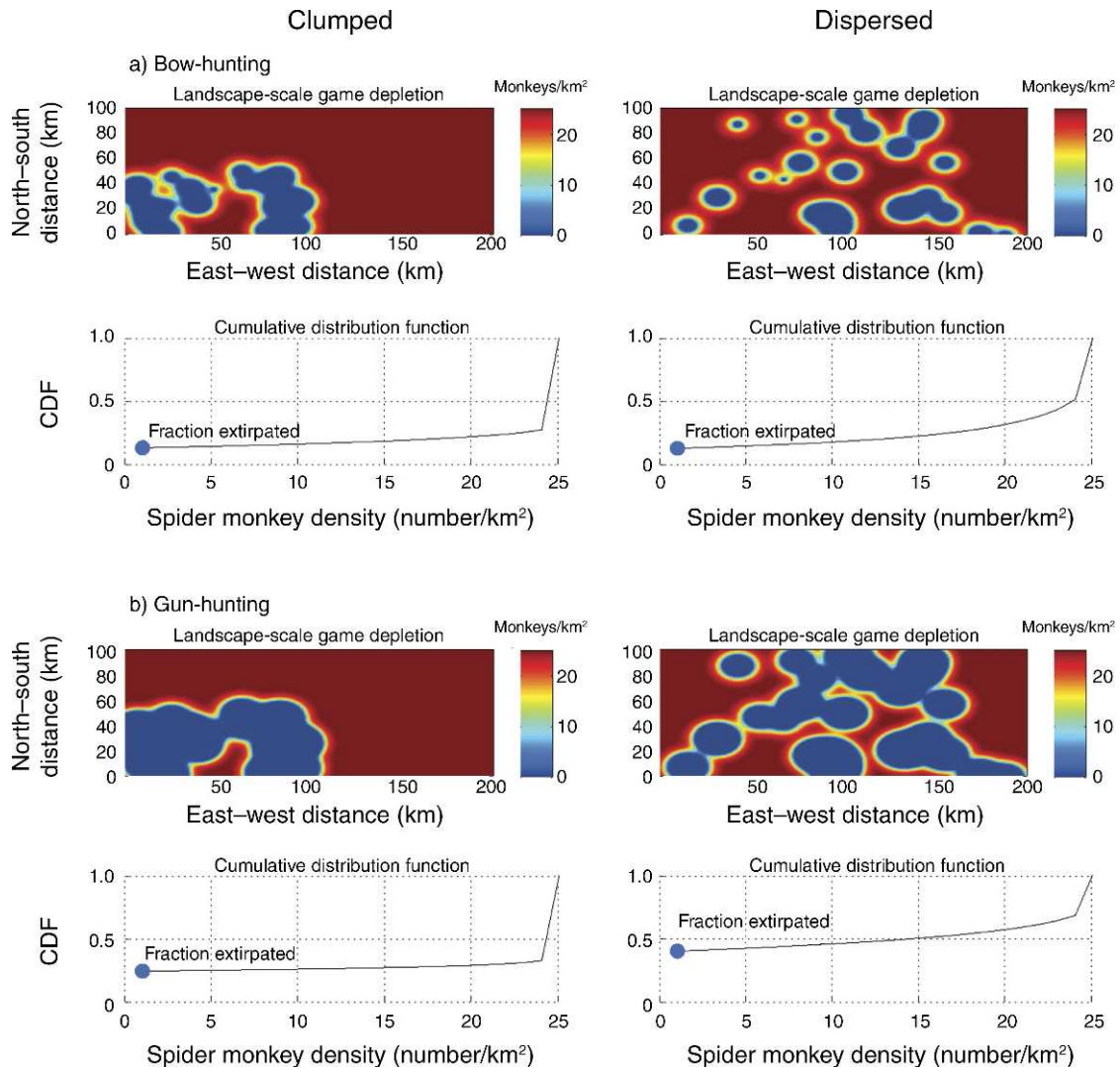
FIG. 5. The long-term, steady-state spatial distribution of spider monkey densities under hunting by (a) bow-hunters ($d = 0.1$) and (b) gun-hunters ($d = 0.9$) for a clumped and a dispersed spatial arrangement of 25 settlements. The landscape-scale depletion can be visualized with a color map, where dark blue indicates local extirpation and dark red indicates no exploitation (monkeys at or near carrying capacity), and summarized with a cumulative distribution function, CDF (the proportion of the landscape below a given density). The blue dot signifies the fraction of the landscape that is locally extirpated (<1 monkey/km^2), which is an analogue of the "extinction envelope" used in the single-species model. There is nearly twice as much extirpation in the dispersed-settlement than the clumped-settlement gun-hunting scenario, but settlement pattern makes little difference in the bow-hunting scenario. Actual settlement populations and coordinates can be found in Appendix D.

management scenarios, through demographic change, and over large spatial scales is a key result for application to the management of reserves and landscapes. For example, in Levi et al. (2009), we were able to assess the sustainability of hunting in the 1.8-Mha Manu National Park of southern Peru over the next 50 years, considering two divergent scenarios of human settlement growth and spread.

Here, our purpose has been to validate the approach taken by Levi et al. (2009) and to make its methods available to nontechnical users via two analytically tractable models and via our Python script, which uses

ArcGIS to automate the mapping of game depletion in space over a defined time frame under variable spatial configurations of settlements with overlapping hunting zones (Fig. 7; see Levi et al. 2009). We also (1) demonstrate that the hunting effort approximation used in Levi et al. (2009) closely approximates the results expected under a mechanistically derived model (Fig. 1); (2) show how weapon technology is more important than human population size per se in determining the spatial pattern of game depletion and catch per unit effort (Figs. 2–6); (3) provide a simple method to calculate the steady-state distribution of
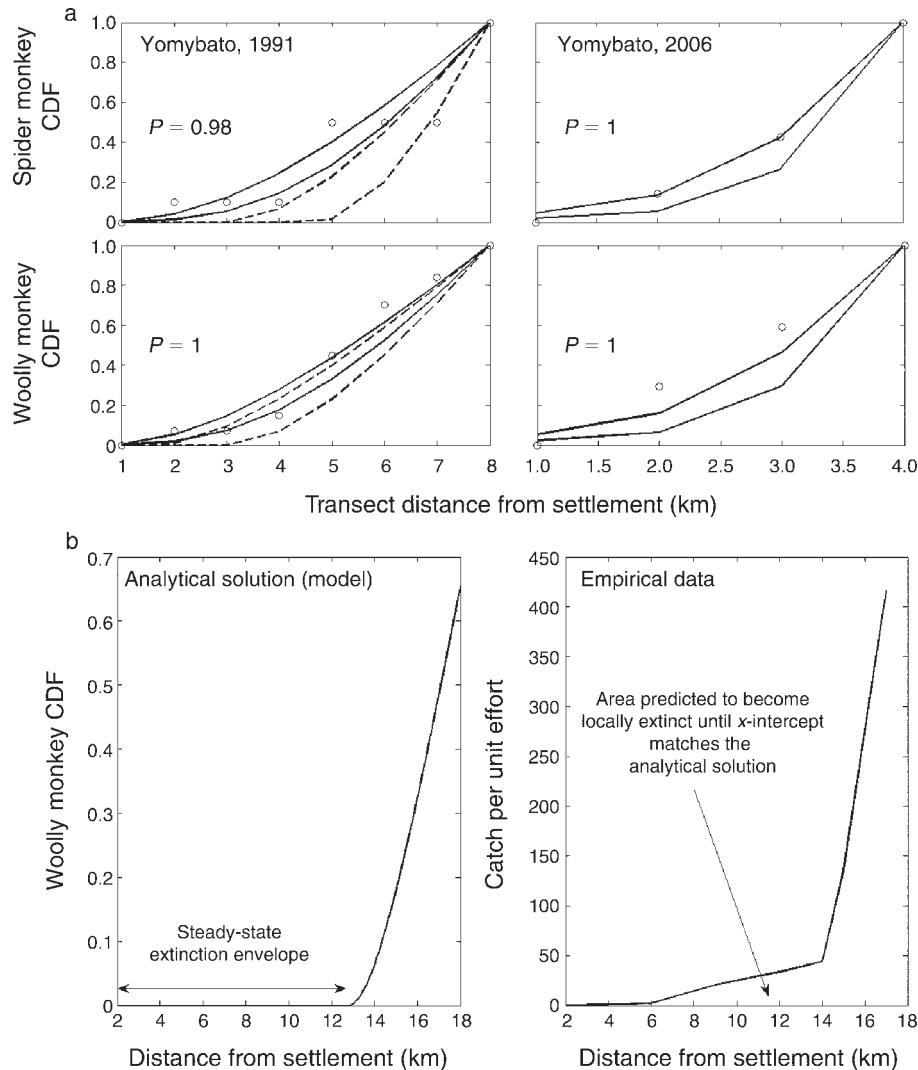
FIG. 6. Comparing model output and empirical data to validate the biodemographic models. (a) Cumulative distribution functions (CDFs) of spider and woolly monkey (population growth rate, *g*) encounters, with radial distance from the Yomybato settlement in 1991 and 2006, using the numerical model with one settlement. Empirical data points (open circles) for the cumulative distribution functions are the fraction of observations from line transects occurring before the distance specified on the *x*-axis, where each fraction is the number of encounters on a transect before the distance on the *x*-axis divided by the total number of encounters. Thus, there are few spider monkey encounters near settlements (flat slopes) and many encounters far from settlements (steeper slopes). Solid lines correspond to numerical model outputs, and dashed lines to the analytical steady state (Eq. 9), with hphy = 40 and 80 hunts per hunter per year for the upper and lower lines of each pair, respectively. A *P* value near 1 indicates that the model and data are statistically indistinguishable. (b) Steady-state (long-term) cumulative distribution function of woolly monkeys given by the analytical, single-settlement model of a gun-hunting community with 200 hunters and hphy = 80 (left), compared to the data from Sarayacu (Sirén et al. 2004) (right). The model produces a reasonable fit of an extinction envelope to the observed spatial pattern of depletion in Sarayacu, as measured by catch per unit effort (CPUE). Note that we start the *x*-axis at 2 km, because there is local extirpation from 0 to 2 km.

large-bodied primates, catch per unit effort, and the "extinction envelope" around single settlements (Eqs. 9, 11, 13, 14; Figs. 2–4); and (4) use published spatial data sets to provide empirical validation for the model (Fig. 6).

Neither of the analytical models can project the impact of hunting to a particular time with a growing human population because they are designed to give a steady-state solution. However, steady-state predictions are useful when considering the long-term effects of an arrangement of settlements or the long-term conservation value of no-take areas. As such, the "fraction extirpated" index can be used to identify the amount of area where an indicator game species, such as the spider monkey, will persist, and by extension, so will all other species that are less vulnerable to hunting. A major advantage of the analytical approach is the simplicity of implementation on very large spatial scales. The

Spider monkey density

$K = 25/km^2$

Extirpation
($<1/km^2$)
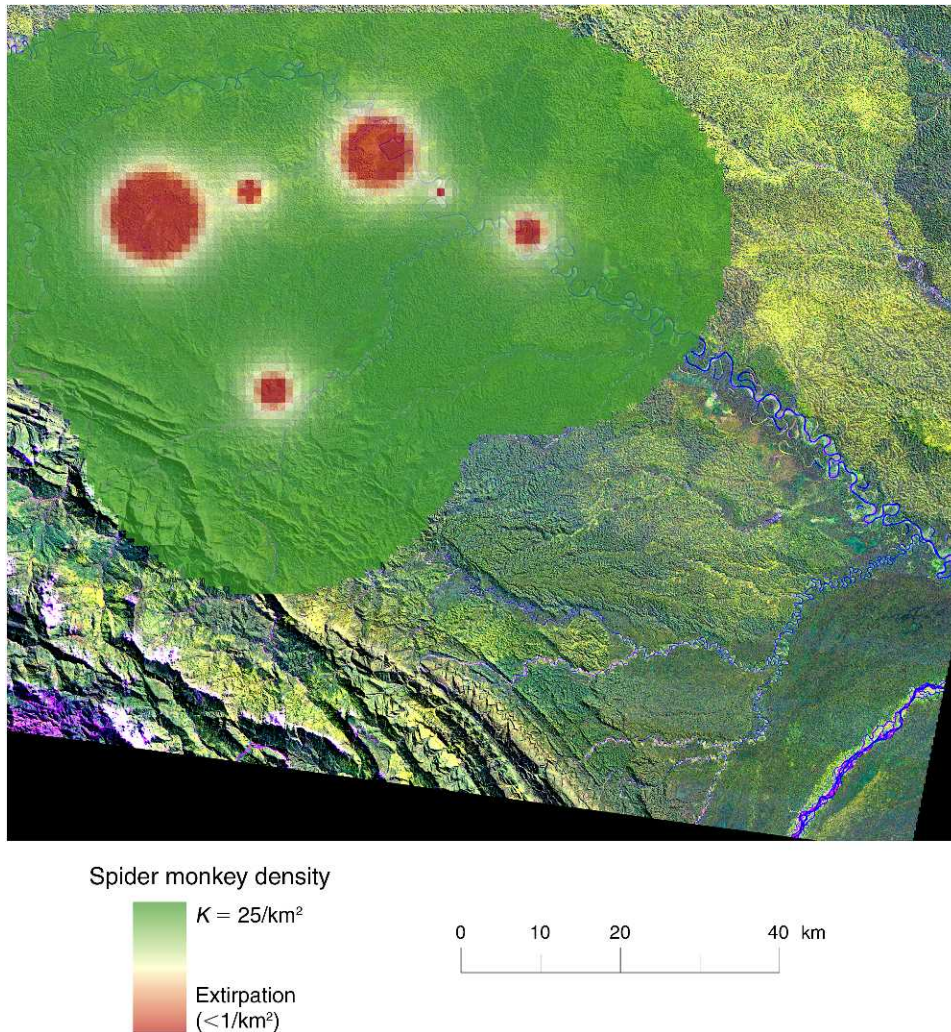
0   10   20   40   km

FIG. 7.   Example output of the GIS script to project the present depletion of spider monkeys for settlements in Manu National Park, Peru. Larger and older settlements have more local depletion than smaller and newer settlements.

computer memory requirements are minimal, and the model runs extremely quickly. In contrast, the numerical model must iterate over every grid cell, for every settlement and year, making it computationally expensive to implement on large spatial and temporal scales. If settlement data are available by remote-sensing or by government census, the long-term sustainability of hunting over very large spatial scales can now be modeled in order to assess likely trends and impacts over various scenarios without necessarily having to first invest in expensive and time-consuming fieldwork. The modeling results could later be tested and refined through more detailed fieldwork in specific study regions.

The analytical model cannot account for the movement of game from more distant source areas to the hunted sinks near settlements. Depending on the diffusivity, detectability, and reproductive rate of a game species, the analytical model may over- or underestimate the level of depletion. For slowly reproducing and easily encountered species, such as large primates, immigrants are quickly killed as they approach settlements. In this case, game animal diffusion toward settlements could deplete source areas at greater distances than those predicted by the model. This is not significant for isolated central-place foragers because there is so much more source than sink, but as multiple settlements are considered, the spatial arrangements of sources and sinks may become important. The numerical model is useful even when considering long-term depletion where there are few small source areas amid a heavily hunted landscape. In this case, the model becomes a useful tool for systematic conservation planning by guiding decisions concerning the size and spatial arrangement of "no take" source areas.

The assumption that we make throughout this work is that hunters are limited by distance, causing hunting effort to be concentrated in space. As a result, game

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populations outside hunting zones are given refuges from human predation. Because both effort and the impact of hunting are concentrated near settlements, CPUE must decline at a rate that is largely dependent on the hunting technology used (Fig. 3). With bow and arrow, large primates remain in the hunting zone, and more can be killed for a given amount of effort because the rate of offtake is slow enough to allow for reproduction and migration to compensate.

In rural areas, the wide dispersal of human settlements even with low population numbers, when coupled with firearm use, can cause extirpation of large primates on a landscape scale (see also Levi et al. 2009). We find that traditional indigenous bow-hunting ultimately may be better for both humans and wildlife by putting a technological limit on hunting efficiency, thereby capping the extent of the extinction envelope and thus enforcing landscape-level sustainability. However, actually enforcing a ban on firearms or otherwise regulating hunting is impractical in many regions of Amazonia, even in strictly protected parks, unless the sale of ammunition can be effectively restricted. We thus recommend settlement stabilization as an alternative means of achieving both biodiversity conservation and sustainable resource use in Amazonia. In the era of firearms, reducing the dispersion of human settlements and thereby creating de facto no-take zones can greatly increase large-primate population sizes (Fig. 5), even in the absence of controls on gun use. Moreover, settlement stabilization can be monitored and therefore, in principle, is enforceable as a management approach (Levi et al. 2009, Yu 2010). The logic behind settlement stabilization is that adding consumers to an already existing human settlement causes less per capita depletion of wildlife (see Fig. 2) than the same number of consumers establishing a new settlement, or, in economic terms, the marginal cost to wildlife decreases with in situ human population growth. Settlement stabilization may be achieved in congruence with payments for ecological services schemes (e.g., REDD+, the United Nations Program on Reducing Emissions from Deforestation and Forest Degradation), and social service provision programs such as improved schools, medical care, fish aquaculture, and potable water, all of which can act as centripetal social forces preventing settlement sprawl and fission (Levi et al. 2009, Shepard et al. 2010). Aquaculture, which has been implemented in areas of the Peruvian Amazon where wildlife has been depleted, has the additional advantage of providing protein substitutes that could potentially lower the number of hunts (hphy) while bolstering human nutritional status.

Human hunting behavior in the Amazon cannot, of course, be described entirely by the assumption of central-place foraging (Peres and Lake 2003). For example, the use of motorized transport along roads and rivers causes the distribution of hunting effort to be anisotropic (Souza-Mazurek et al. 2000), and internal migration among camps and village sites can distribute effort over the landscape in a reticular fashion (Albert and LeTourneau 2007). These complications and the topography of forest landscapes, however, can be added to our modeling framework if required. For example, camps can be incorporated as new hunting foci, with an appropriate level of effort.

Our methods can currently project the impact of hunting in space and time for game species that are both profitable and vulnerable because, in the absence of a viable spatial human foraging model, we must hold hunter behavior fixed (hphy and σ are constant and monkeys are always pursued; see Methods). However, this assumption cannot always hold when considering multiple game species, particularly in the context of increasing market involvement and sedentarism. On the one hand, as game is depleted near settlements, hunting might become less attractive relative to alternate activities, causing hunting effort (hphy) to decrease. On the other hand, if alternate sources of protein are not available, hunters might need to hunt more frequently (hphy increases) to meet subsistence requirements. Additionally, depending on the spatial structure and profitability of the available game species, both human diet breadth and the spatial distribution of hunting effort, σ, will change. To account for these dynamics, a major direction for future work is the development of spatial human-foraging models that can account for the unique factors (central-place foraging on sequentially encountered prey, spatially circumscribed depletion of game, finite supply of ammunition, opportunity costs associated with alternate economic activities) that influence human hunting behavior. However, because the steady-state solutions provide long-term projections of game depletion, steady-state multispecies models are possible as long as reasonable approximations (or ranges) of long-term hunting effort (hphy and σ) can be intuited. Such approximations can be obtained by measuring hphy and σ at locations where game is already highly depleted, and at sites that have variable market involvement, to provide an empirical rather than model-based rationale for choosing parameter values.

Finding data to validate this modeling framework is challenging because much previous research on the impact of hunting has focused on offtake profiles rather than on human demography, hunter behavior, and the spatial distribution of effort and game populations. Nevertheless, our model output is remarkably similar to what is observed empirically for bow-hunters from Manu Park and gun-hunters from Sarayacu. We urge fieldworkers to publish data on human demographic structure, rates, and spatial distributions across the Amazon to improve available parameter estimates, especially hunts per hunter per year (hphy) and kill rates (d). Note that such data should be collected on all individuals who could hunt (e.g., all adult males), not just on the major hunters.

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APPENDIX A

Calculating the game encounter rate e from line-transect data (*Ecological Archives* A021-081-A1).

APPENDIX B

Equations for $r_{max}(\theta)$, $r_{min}(\theta)$, θ_{max}, and θ_{min} (*Ecological Archives* A021-081-A2).

APPENDIX C

Spreadsheet solver for the analytical solution (*Ecological Archives* A021-081-A3).

APPENDIX D

Matlab solver for the multiple-settlement analytical solution (*Ecological Archives* A021-081-A4).

APPENDIX E

Using the Python scripts in ArcGIS (*Ecological Archives* A021-081-A5).

APPENDIX F

How sustainability indices work and why we need better methods (*Ecological Archives* A021-081-A6).

SUPPLEMENT

Model implementation with Excel spreadsheet, Matlab, and Python script for ArcGIS (*Ecological Archives* A021-081-S1).