

# Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: landscape-scale management implications for Amazonia

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## Summary

1. Widespread hunting throughout Amazonia threatens the persistence of large primates and other vertebrates. Most studies have used models of limited validity and restricted spatial and temporal scales to assess the sustainability.

2. We use human-demographic, game-harvest and game-census data to parameterize a spatially explicit hunting model. We explore how population growth and spread, hunting technology and effort, and source–sink dynamics impact the density of black spider monkeys *Ateles chamek* over time and space in the rainforests of south-eastern Peru.

3. In all scenarios, spider monkey populations, which are vulnerable to hunting, persist in high numbers in much of Manu National Park over the next 50 years. Nonetheless, shotguns cause much more depletion than traditional bow hunting by Matsigenka (Machiguenga) indigenous people.

4. Maintenance of the current indigenous lifestyle (dispersed settlements, bow hunting) is unlikely to deplete spider monkeys and, by extension, other fauna, despite rapid human population growth. This helps explain why large, pre-Colombian human populations did not drive large primates to extinction. When guns are used, however, spider monkeys quickly become depleted around even small settlements, with depletion eventually reversing the short-term harvest advantage provided by shotgun hunting. Thus, our models show that when guns are used, limits on settlement numbers can reduce total depletion.

5. *Synthesis and applications.* Our framework lets us visualize the future effects of hunting, population growth, hunting technology and settlement spread in tropical forests. In Manu Park, the continued prohibition of firearms is important for ensuring long-term hunting sustainability. A complementary policy is to negotiate limits on new settlements in return for development aid in existing settlements. The advantage of the latter approach is that settlement numbers are more easily monitored than is hunting effort or technology. Similar policies could help to reduce landscape-scale depletion of prey species in human-occupied reserves and protected areas throughout the Amazon.

**Key-words:** biodiversity conservation, bushmeat, community-based conservation, indigenous peoples, protected-area management, source–sink dynamics, spatial ecology, subsistence hunting, wild meat, wildlife management

## Introduction

Most of the Amazon Basin is accessible to hunting (Peres & Lake 2003), and almost all Amazonian-protected areas, from indigenous territories and extractive reserves to

national parks, are occupied by human populations (Brandon, Redford & Sanderson 1998; Terborgh & Peres 2002). Hunting threatens the persistence of large vertebrates and the loss of their ecological functions (Peres & Palacios 2007). Large primates – keystone seed dispersers upon which much plant diversity depends (Terborgh *et al.* 2008) – are especially threatened (Peres 1990).

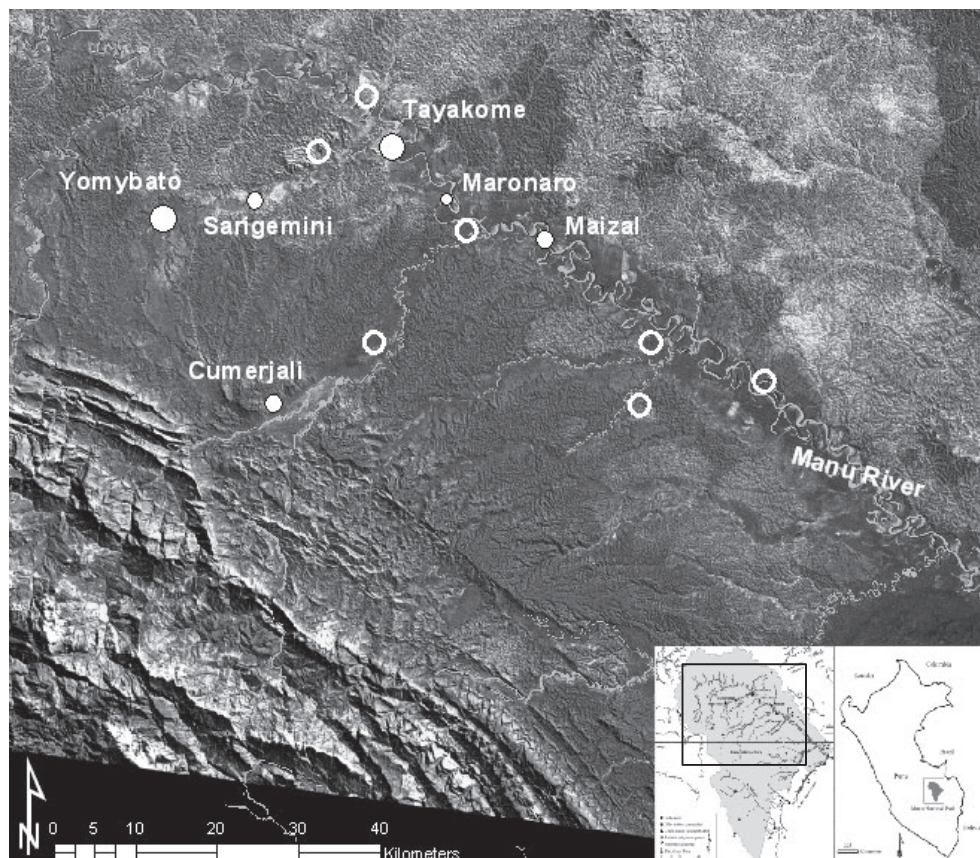
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Conversely, game species are themselves an ecological benefit for millions of forest-dwelling humans. In the Brazilian Amazon, the annual wild meat harvest exceeds 89 000 tons (Peres 2000). Moreover, under some conditions, forest dwellers can prevent forest conversion to industrial agriculture and logging, especially in indigenous territories (Schwartzman & Zimmerman 2005; Nepstad *et al.* 2006). The conservation challenge, therefore, is not to prevent hunting *per se* but to prevent hunting from depleting forests of their wildlife, ultimately costing forest dwellers their food supply, and, potentially, ecotourism revenue and/or the political will to maintain defaunated forests in the face of alternative land uses.

We first distinguish between depletion around a settlement and defaunation on a large spatial scale. With regard to ecosystem collapse, large-scale defaunation is the greatest concern, but hunting studies are typically small scale, limited to  $\approx 300$  km<sup>2</sup> hunting zones and 1–2 years (Alvard *et al.* 1997; Bodmer, Eisenberg & Redford 1997; Sirén, Hamback & Machoa 2004; Peres & Nascimento 2006; Ohl-Schacherer *et al.* 2007; Smith 2008). However, to explore the effect of human population growth, we cannot just increase offtake linearly and recalculate the sustainability index. Apart from the considerable errors (Milner-Gulland & Akçakaya 2001), the relationship of offtake to hunter number is not straightforward; adding more hunters to a village increases pseudointerference, reducing per-hunter offtake.

Thus, to explore the long-term effects of different management options on sustainability, we use a spatially explicit model to explore how human population growth, settlement spread and weapon technology impact prey density over time and space. Our study area is the 1.7-Mha Manu National Park in the lowland rainforests of south-eastern Peru (Fig. 1). Manu is a UNESCO World Heritage site and Biosphere Reserve inhabited by native Amazonians (Shepard *et al.* in press). The largest such group is the Matsigenka, who engage in a traditional economy of swidden horticulture, fishing, hunting and gathering of forest resources. Most of the Matsigenka live in the two legally constituted native communities of Tayakome and Yomybato, with a combined population of 460+ as of late 2007. Three to four hundred more reside in isolated settlements in the Manu headwaters, and there are unknown numbers of uncontacted hunter-gatherers.

Almost all hunting in Manu is carried out with bow and arrow (Shepard 2002; Ohl-Schacherer *et al.* 2007). However, wage work, some from an ecotourism project (Ohl-Schacherer *et al.* 2008), has increased cash income in the past decade, and has increased the affordability of shotguns, despite contravening park regulations. Moreover, improved health care and immigration from isolated Matsigenka groups and from outside the park have resulted in rapid population growth; the settled population has doubled in the last 15 years (Ohl-Schacherer *et al.* 2007; Shepard *et al.* in press). Suggesting that



**Fig. 1.** Map of Manu National Park. Open circles are projected new settlements in the SPREAD scenario, placed in areas likely to be colonized based on current use as fishing and hunting grounds, location near Manu River tributaries, and/or proximity to other settlements or the 'Casa Machiguenga' lodge. Inset: The array used in the model covers the area encompassed by the rectangle.

'the park faces a demographic explosion for which it is completely unprepared', one author has called for the resettlement of Westernized Matsigenka outside park boundaries to prevent erosion of Manu's biodiversity (Terborgh 1999). In this context, we carried out a study to assess the impacts of hunting (Ohl-Schacherer *et al.* 2007), and we here develop a model to evaluate future scenarios.

## Materials and Methods

### GENERAL APPROACH

We choose black spider monkeys *Ateles chamek* Humboldt as our focal game species because they are very vulnerable to hunting (Peres 2000; Ohl-Schacherer *et al.* 2007), are prized by Matsigenka hunters (Shepard 2002; da Silva, Shepard & Yu 2005) and are keystone dispersers of many tree species (Terborgh *et al.* 2008). Spider monkeys act as an indicator species, as forests containing viable populations will generally contain other large vertebrates (Peres 2000; see also Ohl-Schacherer *et al.* 2007; Smith 2008; Alvard *et al.* 1997).

Because spider monkeys are extremely sensitive to hunting, we assume that the maximum distance that hunters are willing to walk varies on a slower time-scale than the time necessary for spider monkey populations to become depleted. Hunting studies in Amazonia bracketing the range of technological and demographic change that we consider in our model reveal similar maximum hunting distances (~10 km radius), regardless of the state of spider monkey populations (compare gun hunters in Alvard *et al.* 1997 and Smith 2008 with bow hunters in Ohl-Schacherer *et al.* 2007). This observed invariance is the product of both the high effort cost of multi-day forays and the ability to switch prey in multi-species communities. In economic terms, we assume that demand for spider monkey is elastic; alternate prey species are accepted as large primate populations are depleted.

To build the hunting model, we used four information sources: (1) a game-offtake data set from four Matsigenka settlements (October 2004 to October 2005; 102 397 consumer days: Ohl-Schacherer *et al.* 2007), (2) a hunting foray data set in which hunters recorded observed and pursued animals in addition to those killed (November 2004 to December 2005; 619 forays across 56 hunters: Ohl-Schacherer *et al.* 2007), (3) a terrestrial-vertebrate density data set in which linear 'Distance sampling' transects (Buckland *et al.* 1993) were run in five unhunted sites in Manu and within the hunting zones of the Tayakome and Yomybato settlements using Matsigenka hunters as spotters (January 2006 to August 2006, C. Peres and D. Yu, unpublished data, Supporting Information Appendix S1), and (4) a demographic data set of the studied Matsigenka communities (authors' unpublished data, Supporting Information Appendix S2).

Hunters are central-place foragers, and empirical studies in both bow- and gun-hunting settlements (Sirén *et al.* 2004; Ohl-Schacherer *et al.* 2007; Smith 2008) indicate that the distance distribution of hunter forays can be modelled as a Gaussian centred on the settlement, reflecting the decline in hunting effort with distance. We assume an isotropic distribution of hunting effort to isolate the effect of distance walked on effort. Matsigenka hunters kill over 30 game species (Ohl-Schacherer *et al.* 2007) and so do not focus exclusively on spider monkeys, but, as spider monkey is highly desired, they are nearly always pursued when encountered (T. Levi and G. Shepard, personal observations; Shepard 2002). Fission-fusion groups of spider monkeys exhibit site fidelity over large 'community' home ranges; so, their dispersal into hunting zones

can be modelled as a diffusion process. The result is that hunting creates depletion zones, and our objective is to project the growth and arrangement of those zones as a function of the growth and spread of Matsigenka settlements, which we determine exogenously.

Using the model, we explore management interventions that could harmonize biodiversity conservation with legally guaranteed indigenous rights to traditional livelihoods (Shepard *et al.* in press). Any attempt to manage the adverse effects of hunting must acknowledge logistical limitations on monitoring and verification (Damania, Milner-Gulland & Crookes 2005).

### THE MODEL

We construct a two-dimensional  $140 \times 95 \text{ km}^2$  ( $13\,300 \text{ km}^2$ ) array of bins (Fig. 1), where each bin represents  $1 \text{ km}^2$ , holding a value for the density of spider monkeys,  $N$ . The array is smaller than the actual park to exclude edges and high-altitude zones. On the array, we set a spatially explicit, reaction-diffusion harvest model in discrete time for monkey density,  $N_{x,y,t}$ .  $N_{x,y,t+1}$  is a function of population growth  $R(N_{x,y,t})$ , migration  $M(N_{x,y,t})$  and offtake, which is itself a function of both spider monkey and human populations  $O(N_{x,y,t}, p_t)$ .

$$N_{x,y,t+1} = N_{x,y,t} + R(N_{x,y,t}) + M(N_{x,y,t}) - O(N_{x,y,t}, p_t) \quad \text{eqn 1}$$

### PREY POPULATION GROWTH

We assume logistic population growth in each bin. The theta logistic ( $\theta > 1$ ) may be more realistic but also makes small populations more resilient to harvest, and we choose to be conservative.

$$R(N_{x,y,t}) = rN_{x,y,t} \left( 1 - \frac{N_{x,y,t}}{K} \right) \quad \text{eqn 2}$$

where  $r = 0.07$  is the maximum intrinsic growth rate (Robinson & Redford 1991), and  $K = 25 \text{ km}^{-2}$  is the carrying capacity (Janson & Emmons 1991). We previously calculated a higher  $r$  using data from nearby Cocha Cashu Biological Station (Fig. 1, Ohl-Schacherer *et al.* 2007; Symington 1988), and densities reach higher levels in Manu (authors' unpublished data), but we use lower literature values here.

### OFFTAKE AS A FUNCTION OF PREY DENSITY

The number of monkeys killed, or Offtake  $O(N_{x,y,t}, p_t)$ , in each bin and year ( $x, y, t$ ) increases with hunting effort, the monkey encounter rate and the rate of kills per encounter,  $d_r$ . Thus,

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

The encounter rate term,  $E_{x,y,t}$ , is dependent on spider monkey density by  $E_{x,y,t} = e_r \times N_{x,y,t}$  with the encounter rate constant,  $e_r$ , determined empirically by distance sampling using Matsigenka spotters (Buckland *et al.* 1993) (see Supporting Information Appendix S4). The kill-rate constant,  $d_r$ , depends on the hunting technology employed.

SPATIAL DISTRIBUTION OF HUNTING EFFORT

A non-mathematical description of the following is in Supporting Information Appendix S3. The hunting effort term (km walked) in each bin and year,  $h_{x,y,t}$ , incorporates human population size in each settlement, hunts per hunter per year and the location of human settlements (because effort declines with distance from settlement). Hunting effort (km walked) is modelled as a two-dimensional Gaussian centred on each settlement.

This is not a trivial task, because our Cartesian ( $x$ - $y$ ) coordinate system does not lend itself to modelling hunter trajectories that emanate from a single starting point. We convert the area integral to the bivariate normal distribution into a polar coordinate system (radius  $r$ , angle  $\theta$ ) to find the probability that a hunt is walked past  $s$  distance units

$$\begin{aligned} & \iint \frac{1}{2\pi\sigma^2} \exp\left[-\frac{1}{2\sigma^2}(x^2 + y^2)\right] dx dy \\ &= \iint \frac{r}{2\pi\sigma^2} \exp\left[-\frac{r^2}{2\sigma^2}\right] dr d\theta \end{aligned} \tag{eqn 5}$$

The probability that a hunt is walked at least  $s$  distance units away from a settlement is now the area integral from  $s$  to infinity over the interval  $(0, 2\pi)$

$$\int_0^{2\pi} \int_s^\infty \frac{r}{2\pi\sigma^2} \exp\left[-\frac{r^2}{2\sigma^2}\right] dr d\theta = \exp\left(\frac{-1}{2\sigma^2}s^2\right) \tag{eqn 6}$$

We want to scale this term to find the fraction of hunts that not only went past  $s$  but were also on a trajectory passing through a particular bin ( $x, y$ ). We return to Cartesian coordinates and scale the effort by the circumference  $+1$ , which: (1) divides the fraction of hunts walked past  $s$  into the fraction that also walk past an arc that is a fraction of the total circumference, and (2) avoids division by zero at the settlement centre so that no more than the total number of hunts pass through the settlement centre. This scaling method is an approximation, but it gives near-true estimates without requiring numerical integration (Supporting Information Appendix S3, authors' unpublished data). Using the approximation, total annual effort at ( $x, y, t$ ) is

$$h_{x,y,t} = \text{hphy} \frac{\sum_{i=1}^{\text{settlements}} p_{i,t} \exp\left[\frac{-1}{2\sigma^2}[(x_{0,i} - x)^2 + (y_{0,i} - y)^2]\right]}{1 + 2\pi\sqrt{(x_{0,i} - x)^2 + (y_{0,i} - y)^2 + 1}} \tag{eqn 7}$$

where  $(x_{0,i}, y_{0,i})$  is the coordinate of the  $i$ th settlement, and  $p_{i,t}$  is the population of hunters (males aged 14–49 years) in settlement  $i$  at time  $t$ .  $\sigma$  is the standard deviation of hunting distances, which can be thought of as scaling the concentration of effort. 'hphy' is the number of outgoing hunting trajectories per hunter per year, and we must augment this number to include kills made on the return legs of hunting trips. Return legs should result in fewer kills than outgoing legs because: (1) game might already have been caught and there is less interest in pursuing, (2) the afternoon encounter rate is lower than the morning encounter rate due to reduced prey foraging activity and (3) given a failed outgoing hunt, the returning hunt is more likely

to fail, as the trajectories correlated in space and time. Thus, doubling hphy to account for hunting on return trips should overestimate total effort, and we run the model with both hphy and double hphy.

MONKEY MIGRATION

On the prey side, we model migration of the spider monkeys as a diffusion process, meaning that monkeys move from more crowded bins into less crowded neighbouring bins and that the rate of doing so is faster if the density difference between bins is greater. Thus, migration is given by

$$M(N) = D \times \nabla^2 N \tag{eqn 8}$$

where  $D$  is the diffusivity constant (distance<sup>2</sup>/time), which is estimated, and  $\nabla^2$  is the Laplace operator, which gives the density gradient and in two dimensions is

$$\nabla^2 N = \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \tag{eqn 9}$$

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 values of the four nearest neighbour bins (up, down, left and right) are used to approximate derivatives on a grid for a 1-year time step

$$D \times \nabla^2 N \approx D \times (N_{x+1,y,t} + N_{x-1,y,t} + N_{x,y+1,t} + N_{x,y-1,t} - 4N_{x,y,t}) \tag{eqn 10}$$

The array perimeter bins are set equal to  $K$  (Dirichlet boundary condition).

PARAMETER ESTIMATION

We explore hunting dynamics by generating scenarios along which the Matsigenka develop. Wildlife populations are affected by five factors: the range of distances walked by hunters ( $\sigma$ ), hunter population growth (i.e. the male population at hunting age, 14–49 years), human population spread (new settlements), hunting effort (hunts/hunter/year, hphy) and hunting technology (shotguns vs. arrows,  $d_r$ ) (Table 1). Parameter estimation is described in Supporting Information Appendix S5.

**Table 1.** Parameter values and meanings

Parameters	Values	Interpretation
$r$	0.07	Maximum growth rate
$K$	25 km <sup>-2</sup>	Population ceiling of spider monkeys
$d_r$	0.1, 0.9, 1.7	The number of spider monkeys killed if encountered
hphy	40–80	Range of mean number of hunts per hunter per year
$D$	0.02–0.1	Diffusivity range of spider monkeys
$E_{x,y,t}$		Encounter rate in bin( $x, y$ ) at time $t$
$(x_{0,i}, y_{0,i})$		Coordinate of $i$ th settlement
$p_{i,t}$		Population of $i$ th settlement at time $t$

## SETTLEMENT SCENARIOS

We generate two settlement scenarios. In the ‘Sedentary Settlements’ scenario (SEDENTARY), the Matsigenka population remains in the six currently extant settlements (Fig. 1). In the ‘Settlement Spread’ scenario (SPREAD), the human population grows and spreads over 13 settlements: the six current ones, plus seven hypothetical new settlements along the Manu River and tributaries (Fig. 1), sited according to our understanding of Matsigenka village fissioning dynamics and settlement choice criteria and irrespective of current park zoning. Note that the SPREAD scenario assumes total non-governance in Manu Park such that indigenous communities occupy portions of the Manu River now zoned exclusively for tourism and research.

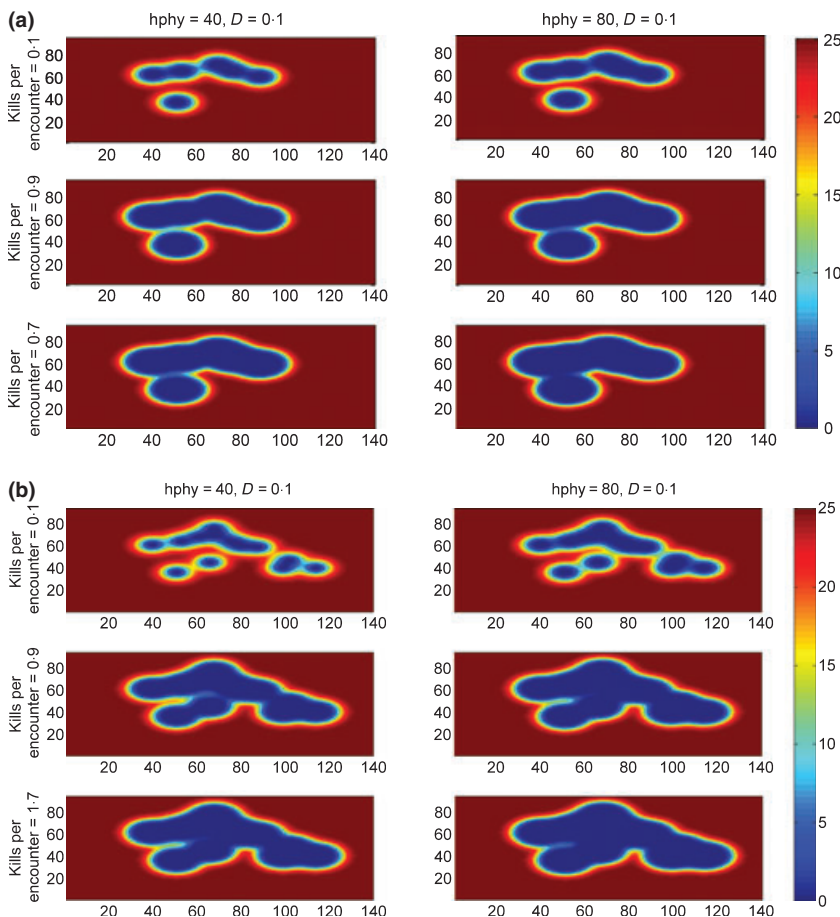
Both scenarios are initialized by following the historical trajectory of population growth and settlement spread from 1960 to 2008 (Shepherd *et al.* in press), hunting only with bow and arrow (Supporting Information Appendix S2). Our demographic data set allows us to track the number of hunters from 1960 to 2008 in all the study settlements, after which we grow the population according to an age-structured matrix model parameterized to the entire Matsigenka population, from which we extract hunter numbers (Supporting Information Appendix S2).

In the SEDENTARY scenario, the 2009 population (131 hunters) is immediately distributed evenly amongst the six current settlements, and all subsequent growth takes place in the same settlements. In the SPREAD scenario, the 2009 population is immediately distributed evenly amongst 13 widely dispersed settlements (six existing plus seven hypothetical settlements) throughout Manu Park. Both scenarios then grow at the current rate for 50 more years, to 770 hunters

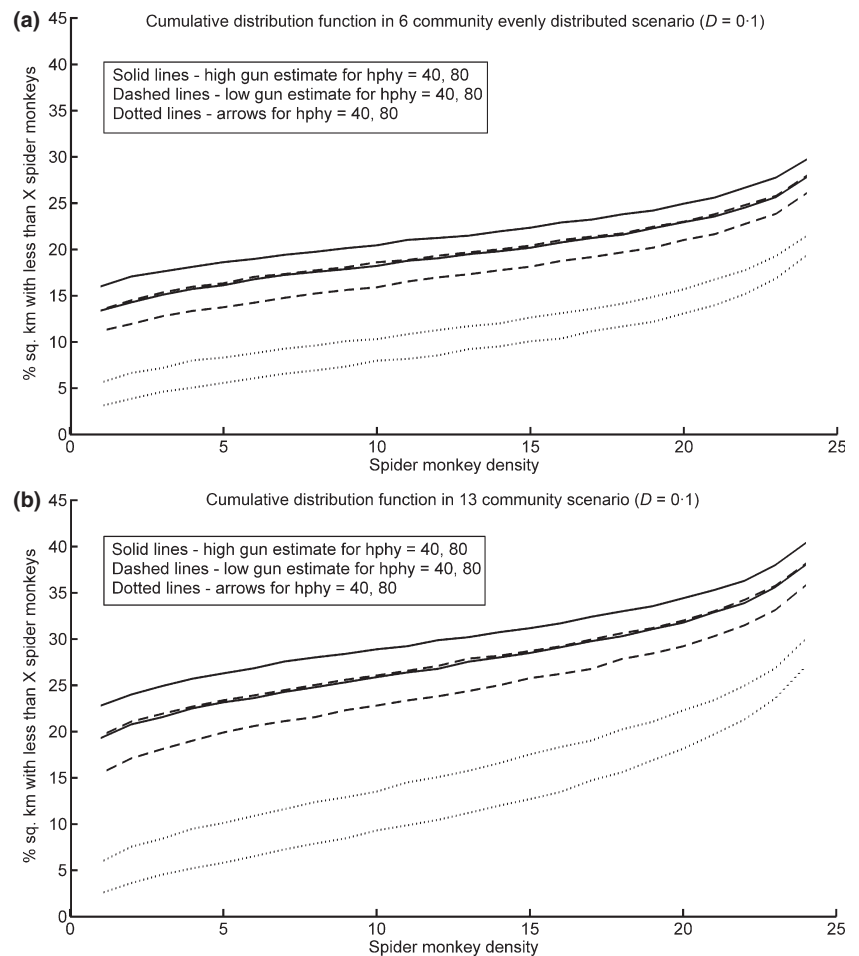
( $n_{\text{tot}} = 3560$ ). Note that we redistribute the population in this pair of scenarios to focus on the effect of settlement spread alone; the effect of variable population across settlements is evaluated in the hunting technology scenarios below. Both scenarios assume continued population growth at current rates with little or no birth control. However, there is a small but growing use of birth control among the Matsigenka.

## HUNTING TECHNOLOGY SCENARIOS

We explore the effect of hunting technology by crossing the two settlement scenarios with two hunting technology scenarios, one in which all hunters take up guns in 2009 ( $d_r = 0.9$ – $1.7$  for low and high gun estimates) and another in which all hunters continue to use bow and arrow ( $d_r = 0.1$ ). In this set of scenarios, unlike the above settlement scenarios, we do *not* redistribute the Matsigenka population across settlements but use the 2009 populations of each settlement as a basis for future population growth, allowing us to focus on the effect of settlement size. Shotguns initially increase the offtake of the hunters who use them but deplete monkey populations so severely that offtake eventually drops to levels similar to or below those of bow hunters. To demonstrate this and to estimate the time-scale over which this occurs, we calculate catch per unit effort (CPUE) over time for gun-only and arrow-only scenarios, where effort is total km walked. Runs are initialized as above and grown with the same age-structured matrix until 2059.  $h_{\text{phy}}$  is varied between 40 and 80, and diffusivity,  $D$ , ranges from 0.2 to 1.0 (Supporting Information Appendix S5).



**Fig. 2.** Density maps of spider monkey populations after 50 years over different scenarios and parameter combinations. Settlement locations are as depicted in Fig. 1. (a) The SEDENTARY scenario, in which the human population is evenly distributed among six settlements in 2009. (b) The SPREAD scenario, with 13 settlements. Settlement spread and shotguns (kills per encounter  $d_r = 0.9$  and  $1.7$ ) combine to create large defaunated areas, whereas bow hunting ( $d_r = 0.1$ ) causes much less depletion.



**Fig. 3.** Cumulative distribution functions (CDFs) of spider monkey densities calculated from the density maps in Fig. 2. (a) The SEDENTARY scenario. (b) The SPREAD scenario. The y-axis is truncated at 24 spider monkeys per km<sup>2</sup> in order to zoom in on depletion, as, in all scenarios, the CDFs reach 1.0 at  $N = 25$  spider monkeys. Kills per encounter are  $d_r = 0.1$  for arrows, and  $d_r = 0.9$  and  $1.7$  as the low and high shotgun kill-rate estimates respectively.

## Results

After 50 years of Matsigenka population growth and hunting, spider monkey populations are projected to remain at carrying capacity over the majority of Manu Park under all four scenarios. This is the direct result of central-place foraging by hunters and limited dispersal by monkeys, such that depletion is concentrated around settlements. The patterns of depletion can be visualized with colour maps (Fig. 2) and summarized using cumulative distribution functions (Fig. 3), which reveal clear differences amongst the scenarios, varying from mere local depletions to large, contiguously defaunated areas across overlapping hunting zones.

Shotgun hunters are expected to empty almost their entire hunting zones of spider monkeys, whereas bow hunters create the 'empty forest' syndrome only directly adjacent to their settlements (Fig. 2). The degree of depletion around gun-hunting settlements varies because those that have overlapping hunting zones create contiguous bands of depleted landscape. In general, however, after 50 years of shotgun use, spider monkeys exhibit local collapse (defined here as  $\geq 90\%$  depletion in a bin, or  $\leq 2.5$  monkeys per km<sup>2</sup>) in 12–25% of the landscape across both settlement scenarios, and for all values for diffusivity ( $D$ ), kills per encounter ( $d_r$ ) and hunting effort (average hunts per hunter per year, hphy). By contrast, if restricted to

bow and arrow, only 4–10% of the landscape will be similarly depleted (Fig. 3).

There is also an important interaction between hunting technology and settlement spread. With arrows ( $d_r = 0.1$ ), increasing settlement number from 6 to 13 has little effect on landscape-wide defaunation. Indeed, the SPREAD scenario with low hunting effort (hphy = 40) results in slightly less depletion compared with the SEDENTARY scenario (upper left panels in Figs 2a vs. b and 3); as there are fewer hunters in each community, each of the 13 hunting zones is less depleted. Furthermore, immigration from source populations is higher because the total perimeter of hunting zones has increased. In summary, spreading a rapidly growing population of bow hunters across the landscape does not threaten spider monkey viability in Manu Park over the next 50 years but does produce localized areas of depletion.

By contrast, spreading shotgun hunters across the park does increase the proportion of defaunated landscape (corresponding mid- and lower panels in Figs 2a vs. b and 3). Even small numbers of hunters wielding shotguns can deplete local populations; so, spreading hunters across more settlements simply increases the number of areas emptied by hunting. Furthermore, where communities are sufficiently close so that their hunting zones touch (approximately  $< 20$  km apart), contiguous regions of local extinction are

created (mid- and lower panels in Fig. 2a,b), which decreases the perimeter available for monkey immigration. As new settlements will tend to be located along rivers, hunting with guns could cause spider monkey population collapse in a substantial proportion of the lowland rainforest bordering the Manu river.

#### HUNTING EFFORT

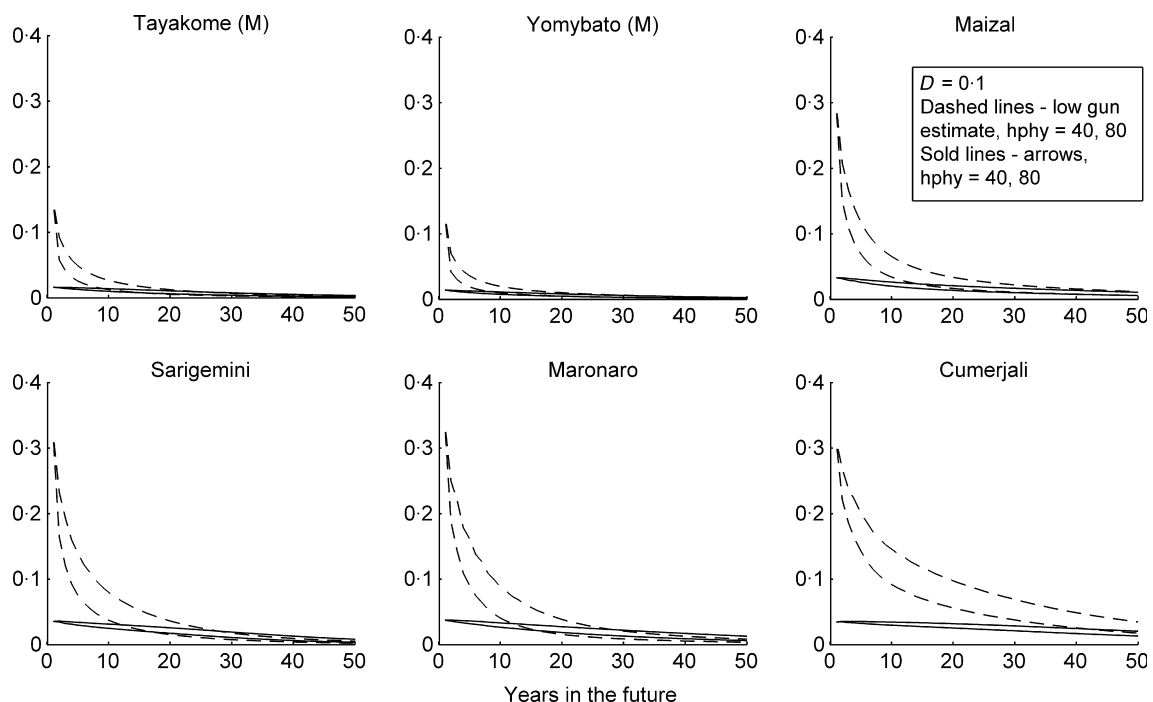
Increasing hunting effort ( $h_{phy}$ ) increases depletion in all scenarios (left vs. right panels in Figs 2 and 3). Total hunts per year is the product of  $h_{phy}$  and the number of hunters. Using a higher value of  $h_{phy}$  is more conservative, correcting for a number of potential underestimates in the model, e.g. not counting kills made on return trajectories of forays or underestimating the hunter growth rate (Supporting Information Appendix S2).

Importantly, shotgun hunting would also be expected to reduce the considerable observed variation in hunting skill observed among Matsigenka bow hunters (Supporting Information Appendix S5). Less skilled bow hunters hunt less effectively and less frequently, and many hunters kill no spider monkeys. We therefore expect that guns should make all Matsigenka men more effective *and* more frequent hunters (higher  $d_r$  and  $h_{phy}$ ). Thus, for a realistic sense of the long-term impact of shotguns, the more relevant comparisons are between low- $h_{phy}$  bow and arrow and high- $h_{phy}$  gun scenarios (Fig. 3).

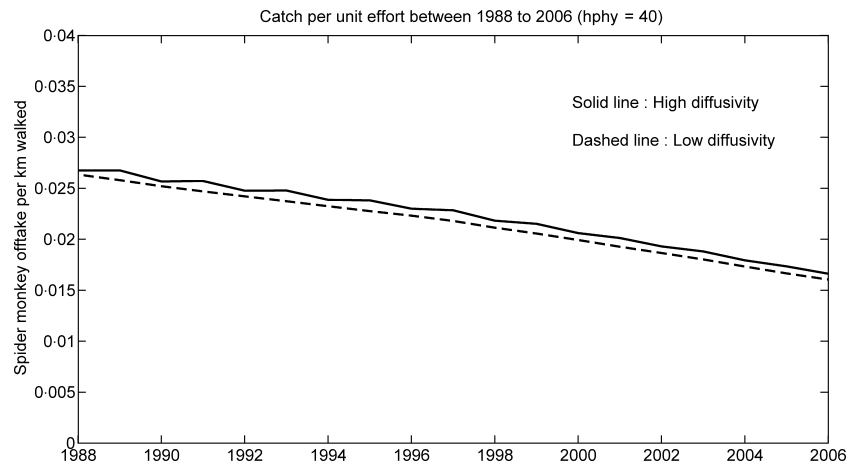
#### CATCH PER UNIT EFFORT AND SOURCE-SINK DYNAMICS

During 50 years of human population growth in each settlement, the CPUE in the gun-hunting scenario starts high and decreases steeply as spider monkey populations are 'mined'. CPUE then stabilizes to a level at or below that modelled in the bow-hunting scenario (Fig. 4). CPUE for bow hunters is also projected to decline but gradually. The larger the settlement, the more transient is the advantage of guns (Fig. 4); in the two main settlements of Tayakome and Yomybato, with populations of  $\sim 200$  people, the CPUE advantage of guns is predicted to disappear in  $< 10$  years, most in the first few years. This has an important implication. Although we assumed a wholesale switch to guns in the first year (2009), gradual adoption is more realistic. However, even gradual adoption will still cause rapid reduction in CPUE because a small number of gun hunters in a large settlement is similar to wholesale adoption in a small settlement.

We also present the estimated historical CPUE trajectory for Yomybato from 1988 to 2006 (Fig. 5), during which time the hunter population grew from 21 to 54. Despite the fact that spider monkey offtake is thought to have exceeded the local maximum sustainable yield since at least 1988 (Alvard *et al.* 1997; Ohl-Schacherer *et al.* 2007), the estimated CPUE declined only gradually. This is consistent with our observation that the proportion of large primates out of all primate offtake has not declined between 1988 and 2005, remaining above



**Fig. 4.** Catch per unit effort over the next 50 years in the six existing settlements, with different hunting technologies. Here, we use the low estimate for the gun kill rate of  $d_r = 0 \times 9$ . Convergence of CPUEs for guns and arrows is more rapid with the high gun kill rate of  $d_r = 1 \cdot 7$ . The two main settlements are marked with (M); the other settlements consist of a few isolated households. In each category, upper lines are for  $h_{phy} = 40$ , and lower lines for  $h_{phy} = 80$ . Diffusivity  $D$  is set to  $0 \cdot 1$ .



**Fig. 5.** Estimated historical trajectory of catch per unit effort (CPUE) from 1988 to 2006 in the Yomybato main settlement. Diffusion maintains populations via source–sink dynamics to some degree, but, even with low diffusion, the fall in CPUE is not extreme and may go unnoticed in prey profiles.

80% (Ohl-Schacherer *et al.* 2007), which in turn suggests that local large primate populations have not declined appreciably. Even if we reduce or eliminate monkey immigration (diffusivity  $D = 0.02, 0$ ), we still find a flattish CPUE trajectory (Fig. 5).

## Discussion

Our modelling framework allows us to incorporate and grow multiple human settlements, allow overlapping hunting zones and project game offtake and depletion over a landscape over time. This method converts assessments of sustainability from a yes-or-no question for fixed amounts of habitat and offtake (the sustainability index approach) to quantified levels of depletion that can be projected over time and space and visualized on landscapes.

Over the next half a century, none of our scenarios or parameter combinations – even the most extreme ‘no governance’ scenario with immediate shotgun adoption and settlement spread – threatens the persistence of spider monkeys in Manu Park. Because spider monkeys are one of the species most vulnerable to hunting, it follows that subsistence hunting is unlikely to threaten other large vertebrate species over most of Manu in the next half a century (Figs 2 and 3), except possibly some rare and patchily distributed species such as giant river otter *Pteronura brasiliensis* Gmelin and Orinoco goose *Neochen jubata* Spix. However, gun hunting does have the potential to defaunate large portions of the park, particularly lowland forest, which is floristically distinct.

Our projections are not meant to be exact as we do not incorporate large-scale landscape features that might affect game species densities, such as bamboo forests, palm swamps or the soil fertility difference between flood plain forests vs. upland *terra firme*. Instead, we use a conservative estimate of spider monkey density for Manu, and the model therefore provides a quantitatively conservative approximation of depletion over space. In addition, due to the complexity of foraging in a multi-species framework and to the complex spatial dynamics

of non-territorial species, certain species are not amenable to modelling this way. For example, herds of white-lipped peccaries, *Tayassu pecari* Friedrich, a major protein source in Amazonia, move rapidly over the landscape and blur the distinction between source and sink, which makes it difficult to project their populations within our framework. A similar caveat applies to large carnivores.

Our models do not anticipate the effects of climate change on forest fires and, thus, on the persistence of vertebrate populations (Barlow & Peres 2008) nor can they address a major policy change that might de-gazette a national park for resource exploitation. Nor have we considered socioeconomic change among the Matsigenka beyond hunting technology: for example, the substitution of game with protein acquired from fishing, food purchase, aquaculture, small animal husbandry or increased hunting in agricultural fallows. Substitutes, by definition, reduce hunting effort, and therefore reduce the impact of hunting on game populations (Bulte & Horan 2002; Damania *et al.* 2005; Ling & Milner-Gulland 2006). Additionally, we do not consider the effect of mechanized transport along rivers or roads (Souza-Mazurek *et al.* 2000; Peres & Lake 2003), a source of anisotropic hunting effort that is nearly absent from Manu. Our purpose here is to ask to what extent endogenous growth and technology change by the Matsigenka poses a large-scale threat to the biodiversity of Manu Park. For other settings, anisotropically distributed hunting effort can be added to our modelling framework. We also refer readers to Ohl, Wezel & Yu (2007) for a complementary analysis of Matsigenka swidden agriculture, which we project will have a small impact on forest cover. Even if gardens are limited to 500 m of the two main settlements and given multi-decadal fallow periods, swidden can still support 2100–2800 Matsigenka indefinitely.

## WEAPONS TECHNOLOGY VS. HUMAN POPULATION SIZE

The greatest increase in game depletion results from increasing the kill rate ( $d_i$ ) from values typical of bow hunting to those



associated with guns (Figs 2 and 3). This effect far outstrips that produced by doubling hunting effort (hphy), which is equivalent to doubling the number of hunters. The decline in game species is typically blamed on human population increase *per se* (Alvard *et al.* 1997; Redford 2000; Terborgh 2000). However, the more important proximate reason for decline has been the adoption of shotguns, thereby increasing hunting efficiency by an order of magnitude or more (Table 1, Supporting Information Appendix S5).

Our results also suggest that when shotguns are newly introduced, hunters will enjoy a short period of high offtake (Fig. 4). For example, Peres (1990) reported that a single family of hunters in a new hunting zone killed more than 200 woolly monkeys, 100 spider monkeys and 80 howler monkeys from 1985 to 1986. Eventually, overhunted spider monkey populations become so depleted in our gun scenarios (Peres & Palacios 2007) that offtake is limited to stray migrants (Sirén *et al.* 2004) or kills on the edges of hunting zones (Smith 2008).

Our results therefore contradict Alvard's (1995) conclusion that hunting technology is less relevant than consumer population in producing depletion. Alvard found similar return rates for bow-hunting Matsigenka in Manu Park and shotgun-hunting Piro on the border of Manu Park. He concluded that if shotguns were permitted in Manu, they would not cause further depletion. On the contrary, our model suggests that introducing guns to Manu will cause CPUE to decline to levels associated with bow hunting in just 15 years (Fig. 4), which happens to be the time elapsed from the inception of the Piro community to Alvard's fieldwork (1974–1989). Indeed, a census conducted after Alvard's study found far greater depletion of spider monkeys in the Piro settlement than at bow-hunted sites in Manu (Mitchell & Raéz-Luna 1991).

We must also re-evaluate our own previous conclusion (da Silva *et al.* 2005; Ohl-Schacherer *et al.* 2007) that source–sink dynamics maintain large primate populations in the hunting zones of Matsigenka settlements. We find that realistic values of diffusivity have only a small replenishing effect (Fig. 5). Thus, the most parsimonious explanation for sustained high offtake of large primates appears to be that bow hunting has not yet caused serious depletion (Fig. 5). Turned around, the correspondence between our observations of continued high levels of large primate offtake (Ohl-Schacherer *et al.* 2007) and the estimated slow decline in CPUE over the same time period (Fig. 5) provide some empirical validation of our model.

#### EFFICIENT MANAGEMENT OF HUNTING IN MANU PARK

One of our most important results is that if the Matsigenka continue to use bow and arrow, then even 50 years of rapid human population growth and unfettered settlement spread will not cause large-scale depletion of spider monkeys within Manu Park (Figs 2b and 3b). Over the range of hunting effort (hphy) values used in our projections, > 80% of the landscape is projected to contain more than 20 spider monkeys per km<sup>2</sup>. Bow and arrow hunting is just not efficient enough to cause large-scale defaunation, even at much higher human numbers

than are currently observed. Thus, we can understand how it is that indigenous hunting did not drive large primates extinct in the thousands of years before the introduction of firearms, despite high, pre-Colombian densities of native Americans (Denevan 1976; Heckenberger *et al.* 2008). In fact, Manu River, which is now touted as a pristine wilderness, was once known by its former inhabitants, the Toyeri (driven essentially to extinction in the early 20th century), as *Hak'wei* or 'River of Houses', reflecting a very different reality only a century ago (Shepard *et al.* in press). On these grounds, a *laissez-faire* park policy toward indigenous hunting and settlement spread might seem reasonable if bows remain the dominant weapon.

The park should therefore maintain its ban on firearms, ideally in consultation with the Matsigenka themselves, so that they understand the consequences of shotguns. Most Matsigenka already associate the defaunation observed outside park boundaries with shotgun use (Shepard 2002). However, given the increasing Westernization, market integration and political organization of the Matsigenka, the dramatic (but transient) hunting advantage of shotguns and the widespread adoption of firearms by indigenous Amazonian hunters (Hames 1979), it is prudent to consider worst-case scenarios. With guns, we expect a substantial portion of flood plain forest to become depleted of large primates (Figs 2b and 3b), which should strangle the recruitment success of large monkey-dispersed tree species restricted to flood plain habitats (Terborgh *et al.* 2008).

The management challenge therefore is to find a way to mitigate the depleting potential of shotguns in the future. We found that when guns are used, spider monkey depletion is approximately a third less in the SEDENTARY scenario (6 settlements) relative to the SPREAD scenario (13 settlements) (compare corresponding gun cumulative distribution function lines between Figs 2a,b and 3). This is because gun hunters pseudointerfere with each other; so, fewer settlements with more hunters result in less total offtake than more settlements each with fewer hunters. As settlement numbers and locations are more easily monitored by outsiders than is shotgun use, we recommend that the park administration adopt policies to discourage the establishment of new settlements, while promoting infrastructure and service investments in the existing settlements.

Matsigenka settlement dynamics in Manu have been determined by countervailing 'centripetal' and 'centrifugal' forces (Shepard & Chicchón 2001; Shepard *et al.* in press). Centripetal forces toward aggregation have prevailed when, for example, missionary or government organizations have invested in infrastructure or provided services such as education, health care and wage-earning opportunities. Centrifugal forces leading to social conflict and community dispersal have prevailed when these services have been removed – such as when the park administration expelled missionaries in 1973 – or their quality has declined – such as when recently a population block of Yomybato fissioned from the main community to establish a new settlement over dissatisfaction with the education and healthcare professionals present.

Because settlement limitation eventually reduces per capita offtake (Fig. 4), some protein substitutes will ultimately be

needed. In already defaunated Matsigenka communities on the neighbouring Urubamba river, where shotguns are the main weapon, the Peruvian government has introduced small-scale aquaculture. Investing in this infrastructure in Manu before defaunation could have the effect of both stabilizing settlements and lowering hunting effort.

In conclusion, our framework for analysing the landscape sustainability of hunting gives us a tool for visualizing the future effects of hunting, population growth and settlement spread in tropical forests. We anticipate that one of the most useful aspects of this approach will be the ability to use cheaply obtainable data. Quantifying offtake in a new site can require a year or more of fieldwork, while the numbers and sizes of human settlements are often available in public data bases and satellite imagery. These data can be combined with literature parameter values for hunter behaviour (e.g. Supporting Information Appendix S5) and game species population growth rates, to project the sizes of depletion zones and, thus, to provide semi-quantitative guidelines with which to manage human-inhabited protected areas. Future studies wishing to apply our framework should devote effort to improving our parameter estimates, especially hunts per hunter year (hphy) and kill rates ( $d_r$ ). Note that such data should be collected on all individuals who could hunt (e.g. all adult males), not just on the major hunters. Improved estimates of these parameters will influence the model output, but the qualitative dynamics and our policy conclusions are unlikely to change.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Terrestrial vertebrate density censuses

**Appendix S2.** Matsigenka demography

**Appendix S3.** The true effort function and a non-mathematical description

**Appendix S4.** Relating Density and Encounter Rate

**Appendix S5.** Parameter estimation

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