

Hunting in Ancient and Modern Amazonia: Rethinking Sustainability

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ABSTRACT We use a recently developed computerized modeling technique to explore the long-term impacts of indigenous Amazonian hunting in the past, present, and future. The model redefines sustainability in spatial and temporal terms, a major advance over the static “sustainability indices” currently used to study hunting in tropical forests. We validate the model’s projections against actual field data from two sites in contemporary Amazonia and use the model to assess various management scenarios for the future of Manu National Park in Peru. We then apply the model to two archaeological contexts, show how its results may resolve long-standing enigmas regarding native food taboos and primate biogeography, and reflect on the ancient history and future of indigenous people in the Amazon. [*Amazon prehistory, community-based conservation, indigenous peoples, Manu Biosphere Reserve, protected areas management, source–sink dynamics, subsistence hunting, Xingú River*]

RESUMEN Una técnica de simulación con computadora, recientemente desarrollada por los autores, fue aplicada para interpretar los impactos de la caza indígena amazónica en el pasado, el presente y el futuro. La simulación permite redefinir la sostenibilidad en términos espaciales y temporales y representa un avance sobre los “índices de sostenibilidad” estáticos usados actualmente en estudios de caza en bosques tropicales. Las proyecciones de la simulación fueron verificadas usando datos de campo de dos regiones de estudio en la Amazonia contemporánea y fueron aplicadas para evaluar diferentes escenarios de manejo para el futuro del Parque Nacional del Manu en Perú. La simulación también fue aplicada a dos contextos arqueológicos, donde fue útil en interpretar algunos enigmas como la existencia de tabús alimentares y la distribución desigual de primates en algunas regiones. Finalmente, los resultados son usados para reflejar sobre la historia y el futuro de los pueblos indígenas en Amazonia.

RESUMO Uma técnica de modelagem com computador, recentemente desenvolvida pelos autores, foi aplicada para interpretar os impactos da caça indígena amazônica no passado, no presente e no futuro. A simulação permite redefinir a sustentabilidade em termos espaciais e temporais e representa um avanço sobre os “índices de sustentabilidade” estáticos usados atualmente em estudos de caça em bosques tropicais. As projeções da modelagem foram verificadas usando dados de campo de duas regiões de estudo na Amazônia contemporânea e foram aplicadas para avaliar diferentes cenários de manejo para o futuro do Parque Nacional do Manu em Perú. A modelagem também foi aplicada a dois contextos arqueológicos, onde foi útil para interpretar alguns enigmas como a existência de tabús alimentares e a distribuição desigual de primatas em algumas regiões. Finalmente, os resultados são usados para uma reflexão mais geral sobre a história e o futuro dos povos indígenas na Amazônia.

INTRODUCTION

Contradicting long-standing stereotypes of Amazonian peoples as seminomadic hunter-farmers within

a challenging, nutrient-poor ecosystem (Gross 1975; Meggers 1971), a growing body of evidence demonstrates that parts of pre-Colombian Amazonia supported large

populations living in complex, hierarchical societies unlike those observed ethnographically (Denevan 1976; Heckenberger et al. 2008; Hemming 2008). Recent archaeological discoveries reveal large, sedentary settlements that practiced intensive agriculture and agroforestry, invested in major earthworks, and otherwise modified and managed their environments (Erickson 2006; Heckenberger 2005; Myers 2004; Neves and Petersen 2006; Rostain 2008). Yet soon after European conquest, these lowland civilizations were all but erased, surviving only in the accounts of a few explorers and through an enduring legacy in some Amazonian landscapes (Arroyo-Kalin 2012; Balée 1989; Shepard and Ramirez 2011). Conquest and introduced diseases, more than environmental limitations, shaped the social formations and subsistence strategies of subsequent indigenous populations (Beckerman 1979).

As indigenous people have mobilized politically, fought for legal recognition, and gained access to governmental health and education services, their populations have rebounded from a demographic nadir (McSweeney and Arps 2005). Most indigenous Amazonian groups have also joined the global marketplace and acquired guns, steel tools, fishing gear, chainsaws, and motorized transport. Many conservationists fear that growing, Westernizing indigenous populations will decimate biodiversity (Peres 2011; Robinson 1993; Terborgh 1999). Others have contested that indigenous reserves are as efficient as parks at preventing deforestation and fires (Nepstad et al. 2006) and that the “biodiversity cost” exacted by indigenous groups is compensated if they are empowered to deter incursions by more destructive loggers, miners, and ranchers (Ohl-Schacherer et al. 2007; Shepard 2009; Yu et al. 2010; Zimmerman et al. 2001).

A considerable body of work has addressed the impacts and sustainability of hunting in Amazonia (Alvard et al. 1997; Forline 2001; Robinson and Bodmer 1999; Sirén et al. 2004; Smith 2008). “Sustainability indices” have been used to calculate the maximum sustainable harvest for different animal species (Milner-Gulland and Akçakaya 2001; Robinson and Redford 1991; Slade et al. 1998; Stephens et al. 2002). Such indices treat sustainability as a static “yes”/“no” question, and the result depends largely on the arbitrary choice of the size of the catchment area (Levi et al. 2009). The indices also depend on detailed quantitative inputs about hunting activity in the study communities, requiring extensive fieldwork. Ongoing empirical research is essential, but it is impractical to conduct hunting surveys in every community to develop case-by-case management strategies.

To address these shortcomings, we developed a novel, computerized modeling technique that simulates the intensity and extent of game depletion through space and time, using five main inputs: demographic and ecological parameters for prey species, human-population distribution and growth, hunting efficiency (as determined by technology), cultural preferences among different game animals (used to identify appropriate indicator species), and the average

annual effort devoted to hunting. This dynamic model can be used to project the future impacts of hunting under different scenarios of population growth and technological change (Levi et al. 2009). A “steady-state” version of the model (Levi et al. 2011b) has been tested and validated for the main study site as well for a second site in Ecuador using published results. The close fit between the model’s projections and empirical field data in two distant regions suggests that the model captures the essential dynamics of subsistence hunting in Amazonia (Levi et al. 2011b). The model’s inputs are fairly easy to obtain from publications, maps or satellite images, and interviews, as opposed to the labor-intensive quantitative data required to calculate sustainability indices. Thus, it provides a particularly effective and efficient tool for conservation planning.

The purpose of modeling is to simplify complex interactions and identify the main parameters that shape observed outcomes. Given a working model, one can design scenarios in which possible futures are projected. Projections are not predictions: a projection helps us to understand what is going on now by extending the present into the future (or the past). A prediction, by contrast, needs to take all information into consideration, and as physicist Niels Bohr famously said, “Prediction is very difficult, especially about the future” (Pors 2007). A more realistic approach is to project multiple scenarios that encompass the range of reasonable, possible futures and then ask whether a given policy intervention achieves the desired effect across all or most of those futures. New scenarios can always be added that contemplate animal or human epidemics, fundamental changes in land use, major climate events, and so on.

In this article, we first synthesize our previous work on the modeling technique and its utility for conservation planning in contemporary Amazonia. In the second half, we develop a new application, modeling the hypothetical effects of hunting by large, sedentary indigenous populations in ancient Amazonia. Finally, we reflect on the evolution of subsistence strategies in Amazonia and suggest a new paradigm for addressing sustainable hunting in tropical forests.

MODELING HUNTING IN CONTEMPORARY AMAZONIA

The quantitative data and conceptual insights that shaped our model were gleaned during a three-year field study of Matsigenka hunting in Manu National Park, Peru (Ohl-Schacherer et al. 2007). Matsigenka hunting is governed by a rich suite of beliefs and practices that reflect practical and cosmological concerns (Campos and Shepard 2012; da Silva et al. 2005; Shepard 2002, 2004): large game is hunted in the rainy season when animals are “fatter”; howler monkeys are taken infrequently, as they are viewed as lazy, parasite-infested, and spiritually dangerous because of their shamanic “singing”; deer are mostly avoided because they are considered succubus-like demonic seducers; armadillos, capybara, and caiman are shunned altogether; men avoid hunting and arrow making during the



FIGURE 1. *Matsigenka hunters prefer not to carry animals they have killed (like the woolly monkey pictured here) lest they lose their hunting skills. They leave this task to a brother-in-law or other male relative. Photo © G. H. Shepard Jr. (1995).*

“couvade” period before and after childbirth; hunters prefer not to carry animals they have killed to avoid offending animals spirits and losing their hunting skills (Figure 1); women use an arsenal of medicinal plants to protect babies from attack by vengeful animal spirits. Just as Amazonian hunting practices reflect complex notions about predator/prey interactions (Fausto 2007), so do indigenous diets reflect a wide range of preferences and prohibitions (Cormier 2006; Milton 1991). As a fluent speaker of Matsigenka with a thorough knowledge of the local communities and cultural norms, Glenn Shepard contributed to developing and implementing the game-monitoring protocol used in this study.

Manu National Park is located in southeastern Peru in the department of Madre de Dios and covers 1.7 million hectares. Created in 1973, the park constitutes the core area of a UNESCO Biosphere Reserve and was declared a World Heritage Site in 1987. The core area of the park, however, is the territory of a diverse indigenous population (Shepard et al. 2010). According to Peruvian law, indigenous peoples can legally occupy national parks and continue

traditional subsistence activities but are not allowed to sell park resources without special permits. Indigenous hunters in Manu are not allowed to use firearms or sell game-animal meat, restrictions that are enforced by park guards at several posts along the river. Although people occasionally trade smoked game with outsiders, the vast majority of game is hunted for local consumption.

We worked in the two Matsigenka native communities, Tayakome (pop. 149 as of December 2007) and Yomybato (pop. 183), and in the satellite communities of Maizal (pop. 46), Sarigemini (pop. 35), and Maronaro (pop. 8), all within the core area of Manu Park (Figure 2). Because of the park prohibition of guns, the Matsigenka in Manu mostly hunt with bow and arrow (Figure 3). The Matsigenka are cultural heirs to the “Arawak diaspora” of the first millennium C.E. (Heckenberger 2005). The Matsigenka hunt forest game mostly during the rainy season, focusing on fishing during the dry season, and these ethnographic observations are reflected in the model by adjusting hunter effort. This seasonal respite from hunting reduces the overall offtake for some species but does not change the fundamental assumptions of the model for large, low-fecundity species like spider monkey. “Garden hunting” of species like agoutis, collared peccaries, and avian seed predators that raid Matsigenka crops occurs year round is as much a matter of pest control as of obtaining protein. Our research team included indigenous monitors from 26 families who were trained to record comprehensive hunting data (Figure 4). In the first year alone, they registered 2,089 game animals killed by 99 hunters, totaling 144,153 consumer days of monitoring (Ohl-Schacherer et al. 2007). In all, the study registered over 300,000 consumer days and more than 4,300 animals killed, a thirty-fold increase in research effort over prior studies in the same region (cf. Alvard and Kaplan 1991). A complementary study quantified actual animal densities along 20 transects totaling 90 kilometers distributed among seven forest sites in hunted and nonhunted areas of the park (Endo et al. 2009).

Our research emerged in the context of John Terborgh’s (1999) influential book, *Requiem for Nature*, which warns of the existential threat to Manu Park posed by the Matsigenka. The only way to guarantee conservation in Manu and elsewhere, he claims, is by enticing native communities to relocate outside park boundaries. We have contested this view, pointing out its moral, political, and legal hazards (Shepard et al. 2010). Furthermore, studies of Matsigenka hunting and farming show that their impact on the park’s biodiversity is currently minimal (Ohl et al. 2007; Ohl-Schacherer et al. 2007) and will be more than compensated in the long run if the Matsigenka are empowered to defend the park from incursions by nearby loggers, gold miners, and ranchers.

The model was parameterized and tested using quantitative data and run to simulate the long-term results of different scenarios through space and time (for technical details, see Levi et al. 2009, 2011b). In sum, the simulation calculates the probability that an individual or group of a

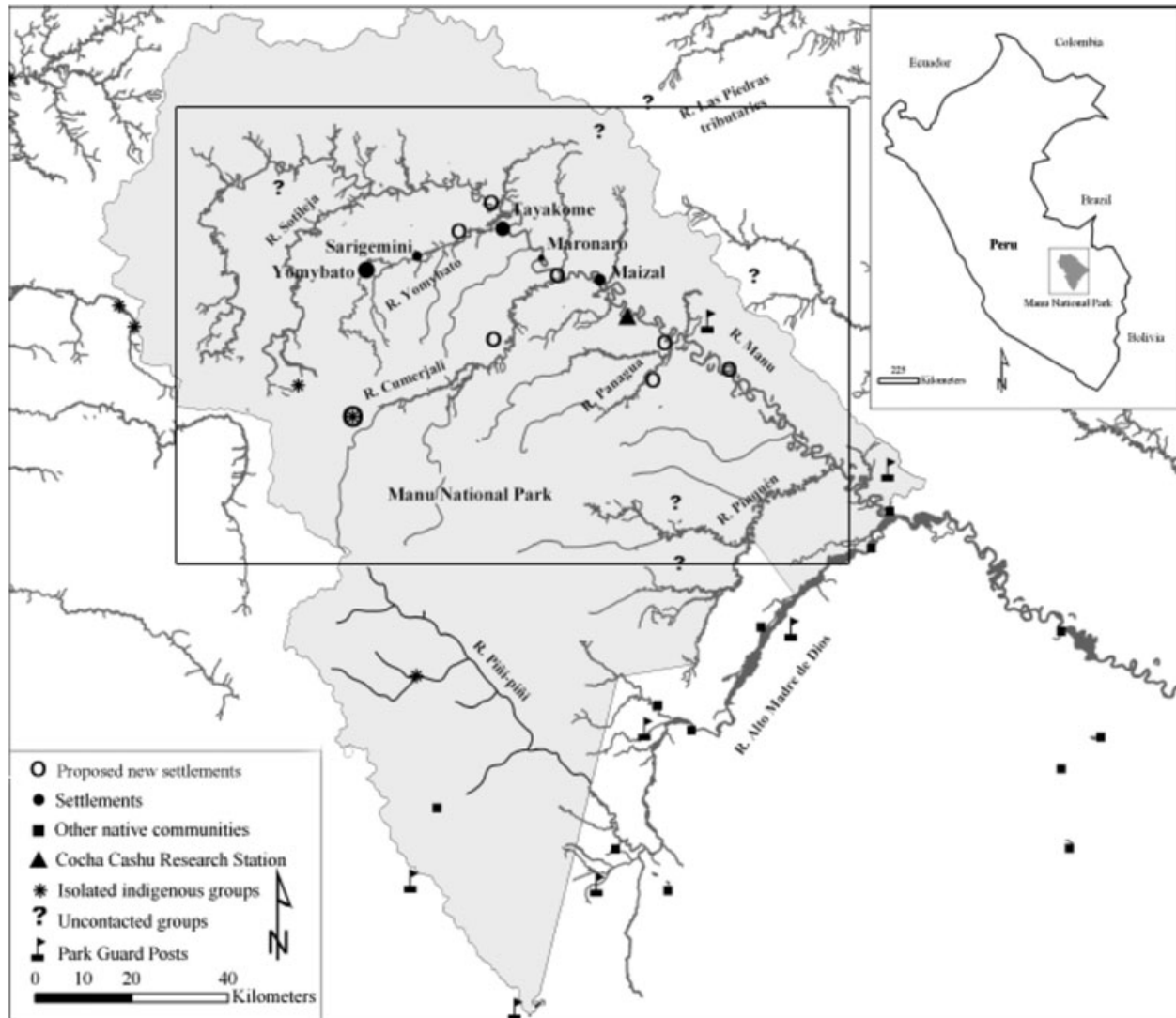


FIGURE 2. Manu National Park, showing communities and the rectangular modeling area (Figure 5). Solid circles represent current settlements; open circles represent hypothetical settlements for the SPREAD scenario in Figure 5. Other native communities and groups, Peruvian towns, and park guard stations are also indicated.

given animal species will cross paths with a hunter in any 1-kilometer-squared cell (bin) around the village during a single year and the probability that the hunter will kill or fatally wound that animal. The number of annual kills for any species will be a function of the desirability, vulnerability, and local abundance of the species, the human population, hunting effort and technology, and the distribution of population centers. The density of each species the following year will depend on its reproductive and migration rates. The output is a “heat map” showing estimated densities of the chosen species throughout the region (see Figure 5). The model is based on the assumption, widely supported in the literature, that indigenous hunters are central-place foragers who concentrate their effort near settlements (Levi et al. 2011a; Lu and Winterhalder 1997; Ohl-Schacherer et al. 2007; Sirén et al. 2004; Smith 2008). Moreover, government and NGO investments in schools, health posts, and water projects in recent decades have led native communi-

ties in and around Manu to become increasingly sedentary and concentrated around the central village area. Yet some authors have described exceptions to central-place foraging (Albert and LeTourneau 2007; Peres and Lake 2003; Read et al. 2010; Souza-Mazurek et al. 2000), which could be incorporated into the model by distributing hunting effort as desired. For the purposes of the current study, we use the simpler, central-place assumption.

We chose large primates (particularly spider monkeys, *Ateles* spp., and woolly monkeys, *Lagothrix* spp.) as our focal species because they are prized as game animals by the Matsigenka and other Amazonian groups (although not all; see Cormier 2006), their territoriality allows for reliable estimates of migration rate from “sources” into depleted “sink” zones, and their low reproductive rates and high visibility make them vulnerable to overhunting. Because of their size, arboreal agility, intelligence, and social organization, large primates are largely immune to attack by nonhuman



FIGURE 3. *Manu Park prohibits firearms, so the Matsigenka there mostly hunt with bow and arrow. Photo © G. H. Shepard Jr. (1995).*



FIGURE 4. *We trained Matsigenka monitors to collect systematic data on their hunting activities. Photo © Julia Ohl (2004), used with permission.*

predators other than harpy eagles, which occasionally take juveniles. Large primates, keystone seed dispersers on which much plant diversity depends, are rapidly depleted by hunting in Amazonian forests (Nuñez-Iturri and Howe 2007; Peres 1990, 2000) and are thus reliable indicators of hunting pressure. If hunting management plans can be developed to

preserve large primate species within the landscape, then a full suite of less-vulnerable game species will also be present, as will the ecological services these various species provide.

Using the model, we examined the future impacts of different management scenarios in Manu Park. Current demographic trends were used to grow the Matsigenka population and environmental footprint to its projected size 50 years in the future, making the conservative assumption of no decrease in the current high natural-fertility rates.¹ Hunting distances are modeled with a normal distribution, following our data on actual forays (Ohl-Schacherer et al. 2007). Long-distance, multiday expeditions are less frequent than single-day forays and only weakly deplete prey because the roughly circular hunting zone increases as the square of the radius from the village. We compared a number of alternative scenarios of population spread and technological change. First, we examine a status quo scenario (“sedentary”), in which the population continues growing at current rates but remains fixed in the current communities, versus the “spread” scenario, in which the same growing population is dispersed among a total of 13 suitable locations throughout the park, regardless of the park’s current zoning restrictions.² Second, we examine the role of hunting technology, modeling for current bow-and-arrow usage (with a low-efficiency rate of 0.1, or one kill for every ten times a monkey troupe is encountered, as observed in the field) versus a range of shotgun-hunting possibilities, from typical subsistence gun-hunting rates (much more efficient than bow and arrow, with 0.9 kills per encounter) to more aggressive surplus hunting that would permit commercial sale (1.7 kills per encounter because shotgun hunters often kill multiple individuals in the troupe). Finally, we model for two different scenarios of hunting effort, 40 hunts per hunter per year versus 80 hunts per hunter per year (hphy). The base value of 40 hunts per year corresponds to the current average hunter effort, taking into account seasonal preferences for hunting and fishing; doubling this to 80 hunts per year greatly overestimates the success rate of hunting on the return leg of forays and thus provides more conservative results. The model was run within an array of 140×95 kilometers for a total of 13,300 kilometers squared or 1.3 million hectares, smaller than the actual park size of 1.7 million hectares to exclude high-altitude zones and depleted regions toward the park’s edges. For purposes of the model, we assume a homogenous habitat and carrying capacity within the array. Although forest composition does vary (Shepard et al. 2001), large primate densities are mostly insensitive to this variation and are determined instead by proximity to human settlements (Endo et al. 2009). The “heat maps” can equally well be interpreted as representing relative density (percent of carrying capacity) rather than absolute density and, thus, still represent a valid metric of game depletion, regardless of local environmental variation.

Examining Figure 5, it is clear that technology (bow and arrow vs. guns) is the main parameter that affects depletion of primate populations. Even doubling hunting effort from 40 to 80 causes only a minimal increase in the depletion of

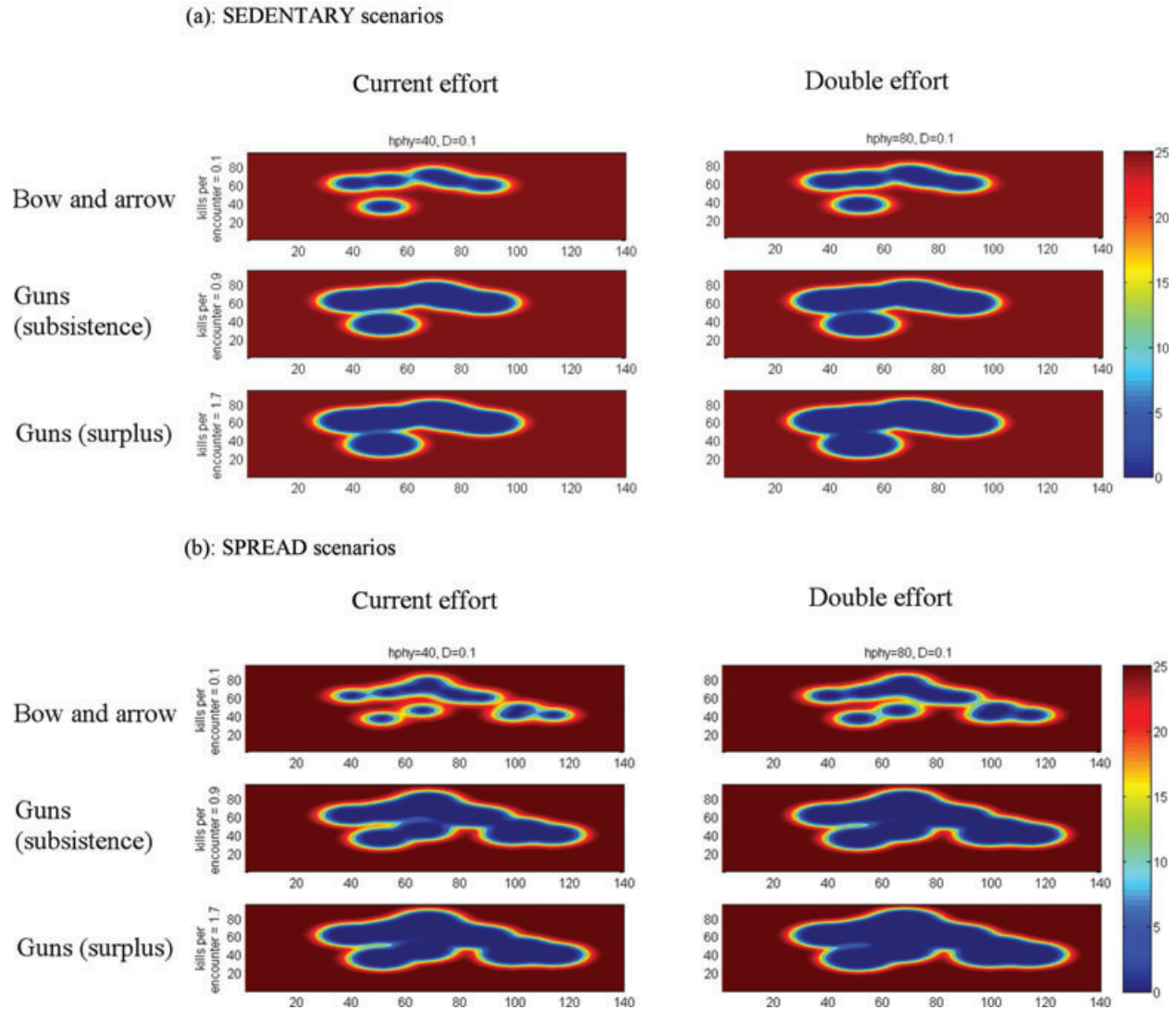


FIGURE 5. Projected density of spider monkeys in Manu Park 50 years in the future across different scenarios. *X* and *Y* axes both represent km distance (east–west and north–south, respectively) throughout the array, although the rectangular arrays (shown in Figure 2) have been somewhat flattened vertically so all scenarios can be viewed: (a) the “sedentary” scenarios maintains current population centers and population growth rates; (b) the “spread” scenarios divides the current population among the existing six settlements plus seven hypothetical settlements and grows them at the current rate. Bow-hunting scenarios use approximate current hunting efficiency rates (0.1 kills per encounter). The gun-hunting scenarios include a typical subsistence-hunting rate (0.9) and a higher surplus-hunting rate (1.7). Hunting effort is run at 40 and 80 hunts per hunter per year (hphy). “Heat-map” color gradations (right) represent density values: dark blue indicates areas with extreme local depletion (< 2 monkeys per km^2), dark red indicates areas at carrying capacity (> 24 per km^2).

animal populations in any given scenario. This is because more hunters traversing the same terrain from the same starting point (the “central place”) interfere with one another’s success: one hunter kills a monkey that another hunter might have encountered; because monkey dispersal is slow, the second hunter’s offtake is reduced by the first. In the various bow-and-arrow scenarios, our model projects that only 4–10 percent of the landscape is subjected to heavy depletion of large primates (dark blue zone in Figure 5), compared with 12–25 percent of the landscape depleted in the gun-hunting scenarios. In fact, in the “spread” scenarios with lower hunter

effort, bow hunters dispersed across the landscape actually produce slightly less long-term depletion than the “sedentary” scenario because the overall perimeter of the hunting area is greater and hence more amenable to migration of animals from nonhunted source areas and because bow-and-arrow kill rates are so low that even low reproductive rates in large primates can compensate. Once hunting effort or population increases beyond a certain threshold, however, the depleted areas of nearby settlements begin to overlap, creating contiguous overhunted regions. Hunting with firearms more than doubles the amount of animal depletion

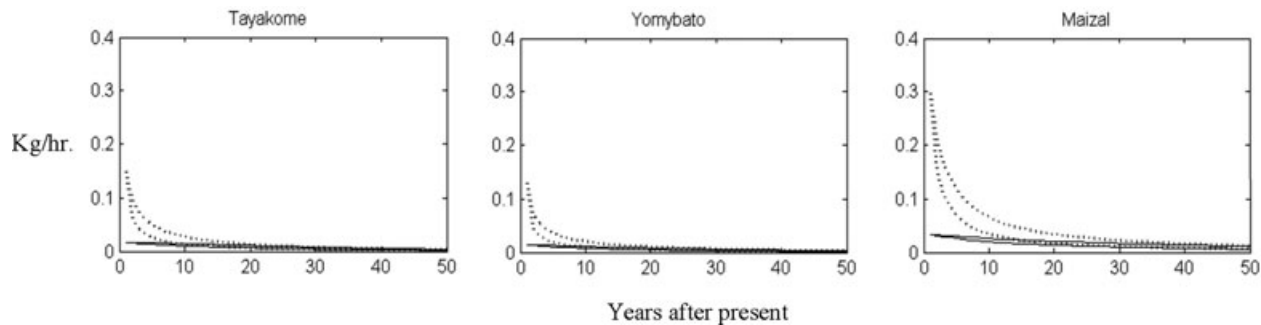


FIGURE 6. Projected catch-per-unit-effort (kg/hr) over the next 50 years in two native communities (Tayakome, Yomybato) and one small settlement (Maizal) in Manu Park, calculated for bow hunting (solid line) and subsistence gun hunting (dashed line). In each category, upper lines are for $h_{phy} = 40$, and lower lines for $h_{phy} = 80$.

in the landscape because of a much-greater killing efficiency (Alvard and Kaplan 1991). So efficient are firearms that hunters rapidly deplete nearby areas and must walk much farther to encounter game, eventually reducing their overall hunting returns per unit time. Figure 6 uses the model to project catch-per-unit-effort over the next 50 years for bow hunting versus gun hunting in the study communities. Within five to ten years for the two larger communities, and ten to 15 years for the smaller settlements, the short-term benefits of shotguns are counterbalanced by more severe local-game depletion, such that bow hunters and gun hunters ultimately spend the same amount of time hunting for a given return. In an independent confirmation of this conclusion, M. S. Alvard (1995:62) observed that catch-per-unit effort was nearly the same between Matsigenka bow hunters and Piro gun hunters in their respective communities. The Piro community is located just outside Manu Park's borders and thus is not subject to gun restrictions. Alvard, however, comes to the erroneous conclusion that guns could be introduced to Manu Park with no serious conservation consequences as long as indigenous population growth is checked:

The difference in total harvest is independent of technology and is simply a function of consumer population size in each village. It follows that if the [Matsigenka] were allowed to use shotguns inside the park they would not deplete their prey populations, but only if their numbers are not allowed to increase. [Alvard 1995:62]

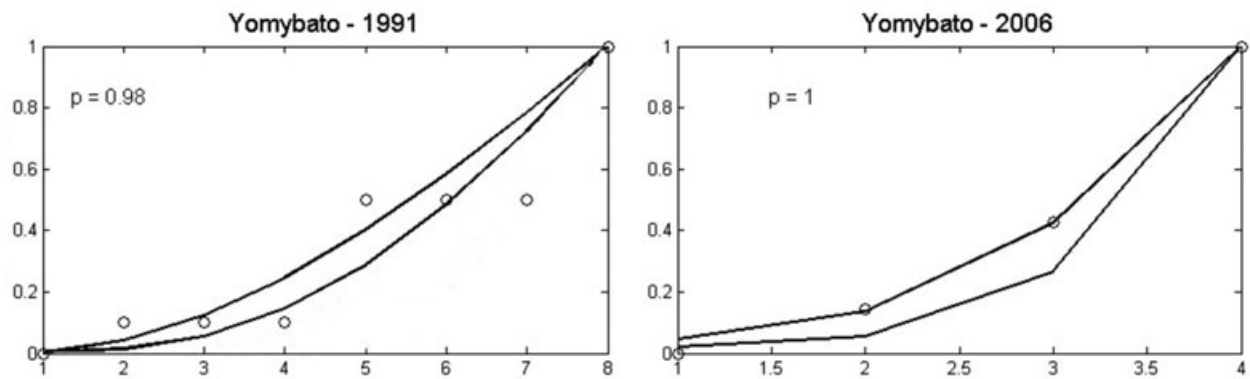
This conclusion derives from the linear logic that is inherent in traditional sustainability indices: a certain population size will consume a certain amount of a given prey species annually and, depending on the biology of the species, will require a hunting zone of a certain size ("minimum catchment area") to sustain this level of harvest, independent of technology: doubling the human-population size will simply double the minimum catchment area required. Our modeling framework reveals the underlying (and decidedly nonlinear) dynamics of hunting through space and time and suggests precisely the opposite conclusion: hunting technology has a far more significant impact on game depletion than population growth. Secondarily, the distribution

of human settlements in the landscape is more important than population growth per se. By analogy with Figure 6, we can understand how just 15 years of gun hunting at Alvard's study site—from 1974, when this Piro community was founded (see Shepard et al. 2010), to 1989, when Alvard began fieldwork—depleted animal populations so severely that hunters' return rates with guns had dropped to the same levels as bow-hunting Matsigenka inside the park.³ Thus, naïve comparisons of current catch-per-unit-effort values can lead to erroneous conclusions. Evaluating long-term impacts requires understanding the dynamics of hunting through space and over time.

Taking advantage of our demographic database, we used the dynamic model to "grow" the community of Yomybato and its hunting impacts from the time it was founded in the late 1970s until the years 1991 and 2006, when separate line-transect surveys of game animals were conducted (Endo et al. 2009; Mitchell and Luna 1991). The projected distances of spider monkey depletion, derived entirely from mathematical simulation using the chosen parameters, matched the actual survey data for both years to the point of statistical identity (Kolmogorov-Smirnov test, p values approaching 1.0; see Figure 7a), an impressive validation of the model's power (Levi et al. 2011b).

We then attempted to validate the model for an independent dataset from a region we have never visited: Sarayacu, a settlement of nonindigenous, gun-hunting colonists in the Ecuadorian Amazon with a total population of 960 (Sirén et al. 2004). Because we have no demographic data for the site, the dynamic model could not be used. Instead, we derived a "steady-state" solution to the model, running the model for a given population size until the depletion zone of large primate species stabilizes (Levi et al. 2011b). The model projects depletion to stabilize at a radius of approximately 14 kilometers from Sarayacu, with a rapid increase in spider monkey density beyond that point. A. Sirén and colleagues' (2004) quantitative study of hunters' catch-per-effort at different distances reveals a near-identical result (Figure 7b). We emphasize that the data has not been "fit" to the model in any way: actual field data match remarkably well with the results of purely mathematical calculations based on

a) Yomybato, Manu Park, Peru



b) Sarayacu, Ecuador

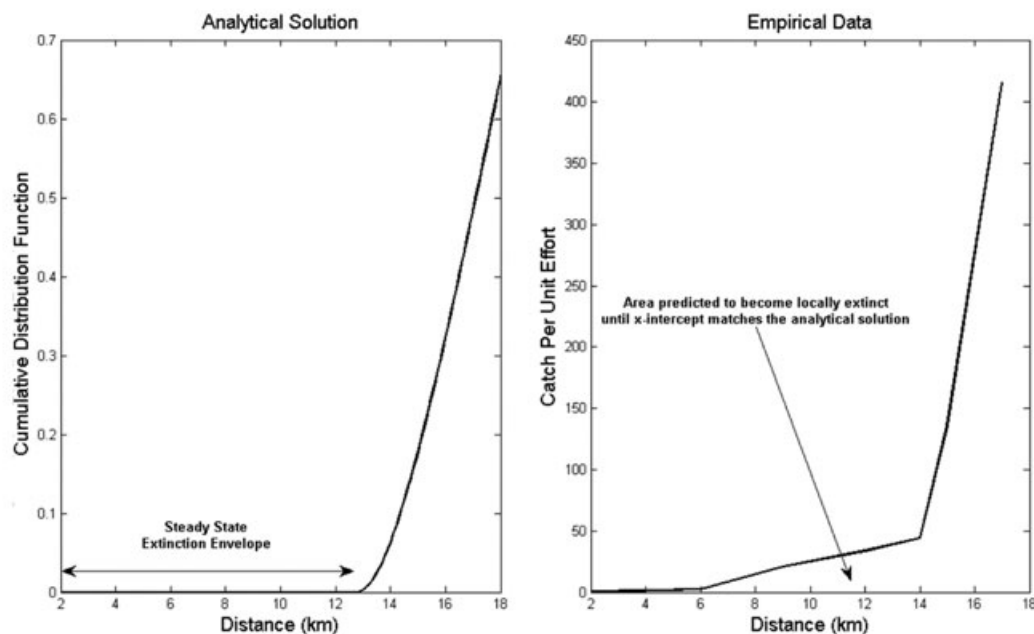


FIGURE 7. Empirical validation of the model: (a) Projected spider monkey encounter rates as a function of radial distance (km) from Yomybato community using dynamic model outputs (solid lines, 40 and 80 hphy for upper and lower lines) compared with actual transect data (circles) gathered in 1991 (Mitchell and Luna 1991) and 2006 (Endo et al. 2009); projected and actual encounter rates are statistically indistinguishable ($p \sim 1$). (b) Steady-state (long-term) distance distribution of spider monkeys given by the analytical model for a gun-hunting community (200 hunters, $h_{phy} = 80$), compared with empirical field data on catch-per-effort from the Ecuadorian Amazon (Sirén et al. 2004). The model projects depletion (“local extinction envelope”) of approximately 14 km radius from the community, just as was observed empirically in the field.

parameters that were determined beforehand. The close match between projected and actual animal densities in two distant locations in the Amazon, one of which we never visited, suggests that the model captures the essential dynamics of subsistence hunting.

MODELING HUNTING IN ANCIENT AMAZONIA

The “steady-state” solution to the model could be equally applied to any region where we have data on the spatial distribution and approximate population size of settlements and the hunting technology used. Here, we develop a novel

application of the model to data drawn from recent archaeological discoveries in the Brazilian Amazon: the Upper Xingú (Heckenberger et al. 2008) and the central Amazonian floodplain (Lima et al. 2006; Neves 2008; Neves et al. 2006), both of which supported large, sedentary occupations for hundreds of years prior to colonial conquest. Fishing appears to have been a major source of protein for these populations. However, as noted above, varying rates of hunting intensity are less influential on the outputs of the model than population distribution (see Figure 5). As long as some nontrivial level of hunting occurs, the perimeter of

depletion for any species is projected to stabilize within a decade or so for a given size, spatial arrangement, and hunting technology of human population. Even with intrinsic population growth, the size of the hunting depletion zone does not increase proportionately, as long as alternative protein sources are available close by (fish, opportunistic “garden hunting”): more hunters walking through the same central zone interfere with one another’s returns on preferred game species.

Most ethnographically observed riverine populations continue to hunt both seasonally and opportunistically even when fishing is the primary focus. Even the Tukanoan peoples of the upper Rio Negro, who focus exclusively on fishing and do not hunt, regularly trade for game meat with neighboring Maku people (Chernela 1985; Milton 1984). Even if game was not a major food source, occasional hunting by such large sedentary populations would have caused lasting impacts on vulnerable primate populations over the hundreds of years during which these settlements were occupied. Contemporary indigenous people in the Upper Xingú, direct heirs to the ancient Xingú civilization, maintain some of the most extensive food taboos on terrestrial mammals known for Amazonia, including spider monkeys and tapirs (Carneiro 1978; Carvalho 1951), among the most harvest-sensitive large mammals in Amazonia and, hence, the first to suffer local depletion from hunting. For the purposes of comparative modeling, we will ignore these contemporary food taboos. In the discussion, however, and following R. Carneiro’s (1978) lead, we use the modeling results to help explain how these taboos might have emerged.

For the Xingú sites, we use Michael Heckenberger’s (2005; Heckenberger et al. 2008) published data on settlement patterns and approximate population sizes for 31 mapped settlements occupied during the late first millennium. The settlements were built according to an intricate architectural plan oriented along cardinal points, connected with each other in concentric patterns by roads and causeways.

For the Central Amazon sites, we employ data from Eduardo Neves for 14 settlements near the modern city of Manaus, representing the Manacapurú and Paredão phases, which lasted from the fifth to 13th centuries C.E. (Neves et al. 2003). We do not include known cross-river settlements located on the east bank of the Negro and the south bank of the Solimões (see Figure 8b) because they are less well studied and because major rivers would have formed an impassable geographic barrier for game-animal dispersal. The Manacapurú and Paredão phases were but some of the archaeological components of the cultural sequence of the Central Amazon, preceded by distinctive sedentary occupations starting in the third century C.E. (Lima et al. 2006) and later occupied by another tradition, Guarita, from the 12th to the 16th century. Paredão and Manacapurú phase sites size vary, but the largest site, Açutuba, is at least 70 hectares and would have supported a population of well over a thousand (Appendix 1).

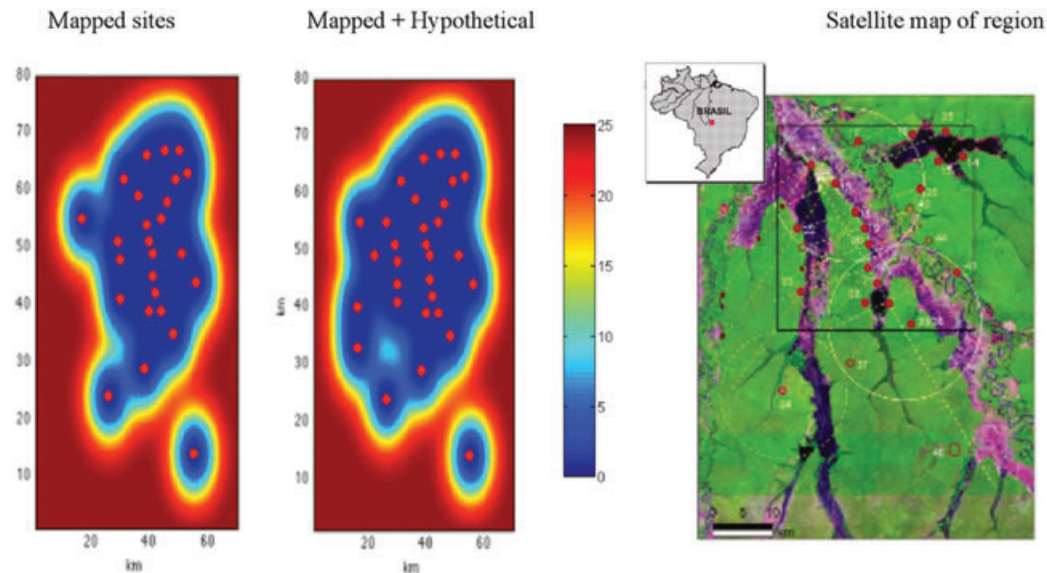
As in the contemporary cases, the model is run within rectangular, two-dimensional arrays encompassing areas where extensive archaeological surveys have been conducted. The array is divided into 1-km² bins, each holding a value for the density of spider monkeys; human settlements are placed in the appropriate locations. Population estimates for the Xingú sites (Heckenberger et al. 2008) were used to derive estimates for the Central Amazon region using the same proportion of 100–150 hectare occupation space for a population of about 2,500 (16.67–25 people per hectare). Given the high productivity of the várzea ecosystem, we use the higher density estimate of 25 people per hectare for the Central Amazon sites. To estimate the number of hunters present, we used our data from the Matsigenka, for whom active hunters represent about 20 percent of the total population. Because we are interested in the question of long-term sustainability, we hold human population constant and run the model until the distribution of spider monkeys in space reaches a steady state.⁴ To compensate for possible gaps in the survey effort in Xingú, we generate a second scenario by including hypothetical settlement locations suggested by Heckenberger et al. (2008).

In the Xingú example, the model results show local extirpation of spider monkeys around the central region of the polity, with moderate depletion in peripheral forests where spider monkey populations could persist in refuges between clusters of settlements. Given the size and spatial arrangement of settlements in the Central Amazon, the model projects an area of complete local extinction of spider monkeys in the interfluvial peninsula between the Negro and Solimões Rivers. This result is consistent with preliminary faunal analysis done with samples from the Hatahara site, showing a high frequency of fish and reptile bones, mostly catfish and turtles, and very few terrestrial mammal bones (Farias 2007). The location of the site, adjacent to the Amazonian floodplain, certainly contributes to the dietary composition, but the relative paucity of mammal bones suggests a degree of terrestrial faunal depletion. No archaeological data is yet available on faunal components of the ancient diet in the Xingú, but given the extent of waterway modification, as well as ethnographic comparison with modern Xingú peoples, fish were a likely a major component of the diet.

DISCUSSION

Once considered environmentally inhospitable to human cultural development, we know now that Amazonia was in fact an important cradle of civilization, showing some of the earliest innovations in crop domestication and ceramic production in the Americas (Lathrap 1970; Neves et al. 2006; Piperno and Pearsall 1998). Unlike other centers of crop domestication throughout the world, however, Amazonia presents a long lapse between the emergence of plant domestication 8,000 years ago and the development of sedentary lifestyles about 2,000 years ago (Neves and Peterson 2006). Although there are still many gaps in the

a) Xingú archeological sites



b) Central Amazon archeological sites

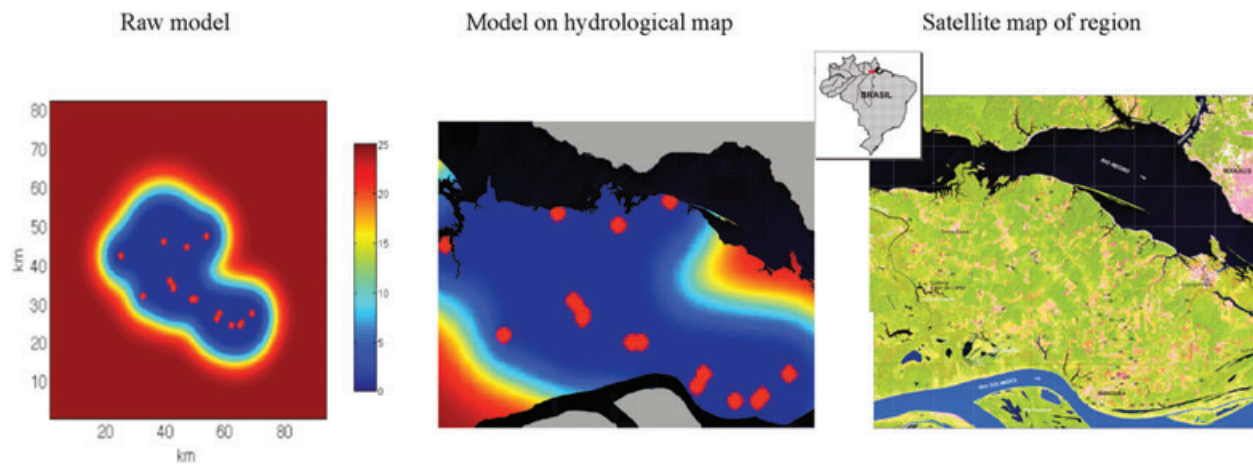


FIGURE 8. Projected densities of spider monkeys around ancient population centers in the (a) Xingú region and (b) Central Brazilian Amazon. Bright red dots indicate the location of archaeological sites. *X* and *Y* axes represent km east–west and north–south, color scale indicates spider monkey density (individuals per km^2) as in Figure 5. (a) Modeling results for the Xingú sites. The figure on the left is based on mapped archaeological sites, the figure to the right includes hypothetical settlements suggested by Heckenberger et al. (2008). Spider monkeys are expected to persist only in forested areas at the periphery. On the far right is a satellite image of the sites adapted from Heckenberger et al. (2008). (b) Modeling results for the Central Amazon. The figure on the left shows the raw modeling results, the figure to the right projects the results onto a hydrographic map showing rivers (black) and cross-river areas (gray), which are excluded. Spider monkeys are expected to have been driven to extinction in the interfluvial peninsula between the Rio Negro and Solimões. On the far right is a satellite image of the sites.

archaeological record, it appears that until the first millennium C.E., most regions of Amazonia were occupied by mobile, small-scale horticulturalists who planted crops but probably depended less on manioc agriculture than contemporary groups, relying on a wide menu of plants including palms and other nondomesticates (Heckenberger and Neves

2009; Morcote Rios et al. 2006; Neves 2007). Variable cultural and cosmological predispositions toward forest life were a factor shaping ancient peoples' livelihoods. Yet our modeling results suggest that seminomadic hunter-farmers, analogous to the modern Matsigenka, could have sustained a growing, spreading population with bow hunting. Such

expanding hunting groups would benefit from periodic migrations through the landscape to seek out game animals once preferred species became depleted nearby (see Figure 5, “spread” bow-hunting scenario). As populations grew, spread, and became territorially circumscribed, they would have exacted more severe local depletion on game, especially once adjacent hunting zones began to overlap. Because of the nonlinear nature of hunter–prey dynamics evidenced in our models, we can imagine steplike transformations that would occur between various subsistence technologies: once the human population and, more importantly, its spatial distribution in the landscape causes a certain degree of game depletion, the comparative efficiencies and per-capita returns of seminomadic hunting versus sedentary agriculture and a more intensive focus on fishing might cross a threshold and suddenly shift.

Robert Carneiro (1978:19–20), while criticizing Eric Ross (1978) for pushing “ecological explanations too far” in an analysis of Amazonian dietary taboos, provides his own “conjectural reconstruction” of how game-animal taboos might have emerged in modern Xingú cultures:

When the ancestors of the present inhabitants of the Upper Xingú first entered the area, they very likely relied on hunting. . . . At last [game] became so scarce that a choice had to be made: either move away from the lakes to keep abreast of the game or else remain there and permanently reorient subsistence so that fishing almost totally replaced hunting in providing protein. . . . As the few remaining animals in the vicinity were hunted out, they perforce ceased to be eaten; and not eating them because they were unavailable became transmuted into not eating them because “they were not fit to eat.” . . . Today game animals occur in appreciable numbers in the Upper Xingú, but the prohibition against eating them remains.⁵

Modern Xingú peoples belong to a number of cultural-linguistic families (Arawak, Carib, Tupi) but share a common cultural tradition, including similar food taboos. The origins of this cultural complex are attributed to ancient Arawak-speaking peoples (Heckenberger 2005). The Enawene-Nawe, an Arawak-speaking indigenous group currently living some 700 kilometers to the west of the Xingú, maintain similar dietary taboos (M. Heckenberger, personal communication; H. Ramirez, personal communication). The Enawene-Nawe speak a language in the Pareci-Salumã subfamily, related to the Arawakan tongues of the Xingú (Ramirez 2001). Linguist Henri Ramirez (personal communication) estimates a time separation of 1,500 to 2,000 years between the Xingú and Pareci-Salumã subfamilies of Arawak. Assuming that Enawene-Nawe and Xingú taboos against eating harvest-sensitive large mammals share a common Arawakan cultural origin, these prohibitions would have arisen roughly during the same time frame (first millennium C.E.) that ancient Xingú peoples were emerging as a sedentary civilization.⁶ (Note that the Matsigenka of Manu Park, discussed above, also belong to the Arawakan language

family but have no dietary taboos against these species, having separated culturally and linguistically far earlier.)

Contemporary Amazonian indigenous groups demonstrate culturally variable preferences and avoidances of various animal species (Cormier 2006; Milton 1991). However, modern Xingú peoples are unusual in the extent of their taboos regarding large, harvest-sensitive mammals like spider monkeys and tapir that top the list of preferred game animals for most indigenous populations (see Cormier 2006; Jerolimski and Peres 2003). Although it may be impossible to prove a causal relationship between modern Xingú food taboos and the hypothetical local depletion of game by their ancient predecessors shown by modeling, the coincidence is suggestive and supports Carneiro’s “conjectural reconstruction.” At any rate, large primates and other large game vertebrates abound in the vicinity of modern Xingú villages (Carneiro 1978), a clear reflection of how ideology can reshape ecology.

By contrast, large primate populations (notably spider and woolly monkeys) appear to be entirely absent from forest sites surveyed in the interfluvial peninsula between the Solimões River and the lower section of the Negro River, a pattern that remains enigmatic given the presence of other, medium-sized monkeys (Barnett et al. 2002). Our model suggests that the indigenous populations occupying this peninsula in the first millennium C.E. would have driven large primate populations to extinction even using bow-and-arrow technology. Wide rivers along the main Amazon channel would have hindered the ability of extirpated large primates to recolonize these forests.

CONCLUSION

Using traditional sustainability indices, conservationists and researchers have focused on population growth as the main factor leading to game-animal depletion throughout Amazonia (Alvard 1995; Redford 2000; Redford and Stearman 1993). Our model sheds light on both the overwhelming impact of gun-hunting technology and population distribution in the landscape. Except in geographically circumscribed areas or at extremely dense levels of occupation, the relatively low efficiency of bow hunting provides a built-in mechanism for sustainable hunting in Amazonian forests. When guns are introduced, however, even small human populations can eliminate vulnerable species throughout a wide area (Peres 2000). Thus, firearms, which have become widely available only in recent decades in many indigenous territories, have changed the fundamental nature of indigenous peoples’ relationship with the Amazonian fauna, a fact that cultural anthropologists working in Amazonia have not fully appreciated in their analyses of hunting ideology. This is not just a question of an incremental increase in hunting efficiency; it is a paradigmatic shift in the spatial and temporal impacts of hunting, analogous to the effects of steel axes on indigenous agriculture (Denevan 1992).

To date, the question of sustainable hunting in the Amazon has hinged on measuring actual game offtake levels (a time-consuming enterprise) and comparing these levels with estimated “maximum sustainable yields” calculated using an arbitrarily assigned catchment area. For example, Alvard and H. Kaplan (1991) concluded that the Matsigenka of Yomybato were already hunting large primate species at unsustainable levels in 1989, when the population was only about a hundred. Twenty years later, the human population of Yomybato had doubled, and monkeys were still being hunted at roughly the same levels (da Silva et al. 2005; Shepard 2002): in other words, “unsustainable” levels of hunting have been sustained over 20 years by a quickly growing human population. Such contradictions highlight the flaws in sustainability indices and call into question their utility as game management tools.

Our model allows us to apprehend the long-term, landscape-level impacts of hunting and address the question of sustainability at different temporal and spatial scales. One management recommendation that emerged from our study in Manu Park is that the park should maintain formal restrictions against firearm use. This technological limitation, which so far has been enforced with reasonable success, provides a long-term benefit both for animal populations and for indigenous groups who are still skilled at bow hunting. Adopting guns would bring a short-lived increase in hunting efficiency, resulting in severe local depletion, such that hunters would soon need to expend as much effort as they had with bow and arrow (cf. Alvard and Kaplan 1991). This dubious contribution to human welfare would be counter-balanced by a dramatic decrease in the welfare of nonhuman primate species: persistent shotgun hunting reduces woolly and spider monkey populations by 91 percent and 98 percent, respectively, compared to floristically similar nonhunted areas (Peres and Palacios 2007).

Manu is one of the few places (other than the dwindling territories of isolated groups) where indigenous hunters still hunt for game with bow and arrow. Although it would be a boon for game-animal conservation, and maybe even for indigenous livelihoods in the long term, it is hard to imagine indigenous groups in other regions going back to bow hunting and other traditional technologies. Unlike North America, Europe, South Africa, and other countries that have developed strictly enforced, scientifically based hunting regulations, Amazonian countries have proven largely incapable of enforcing existing hunting regulations even in national parks and other forest reserves designated (at least on paper) as strictly protected areas. The result has been the collapse of harvest-sensitive large vertebrate populations in virtually all accessible regions (Peres and Lake 2003). To promote sustainable hunting in the vast majority of indigenous territories and other rural Amazonian areas where guns are the weapon of choice, we suggest that governments, conservation groups, and indigenous organizations continue to invest in infrastructure improvements in exist-

ing settlements. Most indigenous groups are eager to obtain benefits such as schools, health clinics, water projects, and economic opportunities available in permanent communities. The more that population growth and hunting effort can be concentrated around existing settlements, the more “source” areas will continue to be available for game-animals to reproduce. Establishing strict “no-hunting” zones within indigenous reserves would be more difficult to enforce and be less of a benefit to indigenous hunters than simply restricting where permanent settlements can be established. Many indigenous groups already trek to seek game in remote, bountiful regions, taking advantage of such “source-sink” dynamics. Explicitly recognizing and protecting such source zones helps justify the maintenance of large, uninhabited areas in current reserves, which are typically viewed as “wasted space” by land-hungry agribusiness interests. Ultimately, the establishment of enforceable bag limits, hunting seasons, no-go zones, and so on may be desirable and even necessary for effective game management in Amazonia, but our model can be used in the interim to visualize current and projected hunting impacts under different scenarios, as well as to provide realistic management suggestions such as restricting the expansion of permanent settlements in source areas. In addition to being verifiable and enforceable, settlement restrictions also appear to balance human welfare with the welfare of nonhuman animal populations and the ecological services they provide.

Indigenous peoples’ territories present both tremendous opportunities and challenges for tropical biodiversity conservation worldwide, perhaps nowhere more so than in the Amazon basin, where fully 21 percent of the landscape is under the stewardship of indigenous peoples, constituting 54 percent of the total forest cover under some form of state protection (Peres 1993). In Amazonian Brazil, Peru, and Bolivia, indigenous reserves together total more than 130 million hectares of 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 are equally or more effective than strictly protected parks at preventing deforestation and forest fires (Nepstad et al. 2006). However, many indigenous-inhabited reserves are beset by internal threats to biodiversity, notably overhunting of vulnerable game-animal species associated with the adoption of firearms. The modeling framework that we present here, which is available as a plug-in for use with geographical information systems (Levi et al. 2011b), could be used by governments, conservationists, and indigenous organizations to study the long-term implications of different scenarios and make more-informed choices about the future management of their territories and resources. The same model, applied to archaeological contexts, can be used to simulate the effects of hunting in the past and better understand the impacts of ancient indigenous populations on Amazonian landscapes.

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NOTES

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1. Western birth-control methods are now available in the communities from the government health post. Currently only a handful of Matisgenka women use them, although interest appears to be growing. We make the conservative assumption of continued natural fertility at the current rates with no increased use of birth control.
2. The “spread” scenario plus hypothetical adoption of guns represents a situation of nongovernance in which current park norms and zoning are ignored. We view this scenario as unlikely but include it as a conservative “worst-case” (at least for conservationists and primates) scenario.
3. A census conducted after Alvard’s study (Mitchell and Luna 1991) found far-greater depletion of spider monkeys in the Piro settlement than at bow-hunted sites in Manu, confirming our conclusion.
4. Note that incremental population growth beyond a certain point does not greatly affect the outcome of the model (Figure 2; see also Levi et al. 2009).
5. “The one exception is the capuchin monkey,” notes Carneiro (1979:19). While appreciating Carneiro’s warning that “ecological explanations can be false as well as true” (1979:19), we note that the capuchin monkey is far more amenable to disturbed habitats and far less susceptible to hunting pressure than the highly vulnerable spider monkey.

6. Michael Heckenberger (personal communication) prefers the alternative explanation that ancient Arawakan peoples arrived in the Xingú with a fully formed fishing and sedentary agricultural lifestyle.

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APPENDIX 1: Location, occupation dates, mapped sizes, and population estimates for archaeological sites from the Central Amazon (confluence of the Solimões and Negro rivers) occupied continually from approximately 800 C.E. to 1100 C.E., comprising the overlapping Manacapuru (6th–9th century C.E.) and Paredão (7th–12th century C.E.) phases. Sites not yet mapped (site size = “?”) are given an average population estimate based on all but the exceptionally large Açutuba site. Asterisks indicate sites that may have not have been occupied during the simulation period (800–1100 C.E.) but which are included as additional data points to correct for possible underrepresentation of archaeological survey efforts. Dates in brackets are estimates based on pottery sequences, all other dates are based on radiocarbon dating (Lima et al. 2006).

Site name	UTM coordinates	Occupation dates (centuries C.E.)	Size (Ha)	Population estimate
Acajituba	20M 778500 E/9653900 N	[7 th –12 th]	?	(226?)
Açutuba	20M 792822 E/9657542 N	8 th –12 th	70	1,750
Antonio Galo	20M 0796183E–9646108N	8 th –11 th	28	700
Barroso	20M 0822662E–9639056N	[7 th –12 th]	5–10	125–250
Cachoeira*	20M 800750 E/9656200 N	[6 th –9 th]	2	50
Hatahara	20M 810687 E/9637621 N	10 th –11 th	16	400
Lago do Limão*	20M 0794962E–9647614N	Early 8 th	12	300
Lago Grande	20 M 803560E–964274N	Late 7 th –early 12 th	4	100
Lago Iranduba	20M 818482E–9636196N	[7 th –12 th]	4.5	112
Lago Sto. Antonio	20M 0811579E–9639237N	[7 th –12 th]	?	(226?)
Laguinho	20M 819083E–9636594N	10 th	19	475
Paricatuba*	20M 807250 E/9659000 N	[6 th –9 th]	10	250
Pilão	20M 0796190E–9645666N	10 th /11 th	7.5	188
São João	20M 0815547E–9635946N	[7 th –12 th]	?	(226?)
Zé Ricardo	20M 0802300E–964290N	[7 th –12 th]	1.5	38