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Humans as predators and prey in ecological systems

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HUMANS AS PREDATORS AND PREY IN ECOLOGICAL SYSTEMS

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by

Taal Levi

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ABSTRACT

HUMANS AS PREDATORS AND PREY IN ECOLOGICAL SYSTEMS

Taal Levi

The era in which we now live has been called the anthropocene (Steffen et al. 2007), suggesting that humans have become such a global force that we fundamentally alter global ecological interactions, the carbon and nitrogen cycles (Gruber and Galloway 2008), the ecology of infectious diseases (Daszak et al. 2000), and our own climate. Such anthropogenic disturbance is often seen as an external perturbation rather than as a part of ecological systems. I take the alternate view that humans are just another strongly interacting component within the larger community of species. By putting humans back into community ecology, I explore the impacts of human predation on wildlife, and the consequences of predator community restructuring on human disease.

In some cases, management actions informed by science can mitigate or reverse negative anthropogenic environmental impacts. For example, the scientific discovery of the ozone hole (Solomon 1988) led to international action to regulate ozone depleting chemicals. It is my goal as a scientist to provide fundamental ecological insight that can inform management. As a result, this work is broken into three policy-relevant research themes. The first research theme quantifies the impact of varying levels of human predation of pacific salmon on ecosystems. The second theme addresses how changes in predator communities influenced the emergence of Lyme disease and other tick-borne pathogens that ‘prey’ on humans. The third

research theme addresses the need to understand the impact of human predation on large primates in tropical forests.

ACKNOWLEDGEMENTS

I had not planned to go to graduate school, and for many years I had not considered becoming a biologist. Thankfully, my interest in ethnobotany led me to contact Glenn Shepard, an Anthropologist who has long studied shamanism (among other things) in Amazonia. Glenn introduced me to Douglas Yu and Carlos Peres, ecologists who were looking for someone to spend a year with an isolated Amazonian group, the Matsigenka, in order to assess the sustainability of subsistence hunting within Manu National Park, Peru. Doug was in charge of hiring. He was impressed with my background in physics, and because I was an avid backpacker and enjoyed the solitude of the forest, he thought that I might be a suitable candidate. But what really convinced Doug to hire me was that a year earlier I spent three weeks in Kalalau Valley, Kauai, where I packed in bows and arrows and successfully hunted a goat (from which I made goat pizza – an accomplishment in the backcountry). Since we were to work with bow hunters, it must have seemed like fate.

The resulting field experience in Manu was wildly full of long days hunting, and many nights drinking manioc beer (literally made with spit) and laughing with Matsigenka friends. Glenn Shepard joined me in the field at first and helped me learn the Matsigenka language. Together Doug and Glenn became fantastic mentors who above all taught me that the practice of science did not have to be buttoned-up, but could be spent answering important environmental questions while running around Amazonian forests looking for spider monkeys and making friends with interesting people from different cultures. Rejoining Carlos Peres in Brazil years later further affirmed the need for imagination and adventurous field projects in ecology and conservation. For teaching me that science is an adventurous endeavor and starting my career in science, I thank Douglas Yu, Carlos Peres, and Glenn Shepard.

I eventually made it to the PhD program in Environmental Studies where I found three fantastic mentors that greatly nurtured my career as a scientist. Whereas some graduate students complained of rarely seeing their advisor, I was placed into a world with two lab meetings a week. One of these meetings, called the megagroup meeting, consisted of labs led my Marm Kilpatrick, Marc Mangel, and my advisor, Chris Wilmers. These weekly meetings turned out to be exactly what I needed to be able to work on diverse new projects that satisfied multiple interests. That my dissertation combines elements of fisheries science, wildlife ecology, and disease ecology is no coincidence, but is due to the interdisciplinary mentoring environment fostered by the megagroup.

Chris mentored me in wildlife ecology-allowing me to get involved with wolf-elk research in Yellowstone and to experience mountain lion captures in the Santa Cruz mountains. He had the confidence in me to send me off to Alaska with 20 camera traps and a pat on the back, which ended up being a productive experience. Our research collaborations while drinking beer on his porch are exactly how writing papers should be done. One day this will be mandatory for graduate students in my lab (fingers crossed). I look forward to our continued collaborations.

Marc was an ideal mentor and teacher of the mathematics of ecology and conservation. His course in applied dynamical systems directly led to the Lyme disease research in this dissertation, and his course on stochastic modeling in biology produced additional published research on hunter behavior. Without the stream of fisheries scientists that he invited to megagroup, I would have never begun salmon research. Marc always made time to meet with me and mentored me like I was one of his students, for which I thank him greatly.

I asked Marm for help with my Lyme disease research, which might have been one of the best decisions of my career. Marm taught me to question every assumption and every inference made from every result-both in my research and in the research of others. Science should be done with a critical lens, and this constant questioning has greatly improved the quality of my work. Despite being exceptionally busy and not being my advisor or even on my committee, Marm made time to meet with me and closely read and edit my work. I hope that we are colleagues for years to come.

Others at UCSC greatly improved my experience and research. I thank Flora Lu, who was an excellent collaborator and a pleasure to work with. She was exceptionally kind to me. My lab mates, and especially Yiwei Wang of my cohort greatly impacted my success. Her friendship is important to me and her artwork graces the pages of this dissertation.

My family greatly improved this dissertation and my research productivity. My parents were always supportive even though they cannot conceive of what I have been doing all these years. I am grateful for them, and appreciate how proud they are of me. Most important to this dissertation are Jenn, my love, and Quark, my dog, who

had to deal with me every day as I wrote computer code in my bath robe. Living with them in Alaska was unforgettable. Having them with me in Santa Cruz was a blessing.

Finally I am very grateful to the National Science Foundation, the University of California Cota-Robles fellowship program, and dissertation fellowship program. I also thank the STEPS institute, the Leverhulme trust, and the UCSC Environmental Studies department for funding my research.

Introduction

Large-bodied vertebrates are vulnerable to the dual threats of habitat destruction and overexploitation. The continuing extinction and extirpation of large-bodied vertebrates is likely an ongoing consequence of the growth and spread of human populations. Beginning around 50,000 years ago, the Quaternary Megafauna Extinction claimed more than two-thirds of mammalian genera, and one-half of all species, larger than 44 kg. Extinction intensity varied by continent with Australia and the Americas losing 72-88% of mammalian megafauana genera (Barnosky 2008). These include iconic species such as the saber-toothed cat, woolly mammoth, woolly rhinoceros, American lions, dire wolves, giant polar bears, and the giant ground sloths that once covered the Americas from Alaska to Patagonia. In the wake of the continued global expansion of human populations, few ecosystems now contain the assemblage of large vertebrates of only 150 years ago. It was in this post industrial revolution era that overexploitation by humans contributed to the widespread extirpation of grizzly bears, mountain lions, bison, wolves (including red, gray, and Mexican species), white-tailed deer, elk, fisher, marten, lynx, bobcat, and moose from large expanses of the contiguous United States.

The problem of wildlife overexploitation continues to be a serious conservation threat worldwide to large-bodied vertebrates, many of which are now critically endangered. Notable examples include the large Felids in Asia, several species of apes, black and Javan rhinoceros, and Asian elephants. Concomitant habitat destruction has reduced the ranges of these species to smaller tracts of forest, which not only increases the vulnerability of wildlife populations to environmental stochasticity and inbreeding depression, but also increases the accessibility of these wildlands to hunters. The impact of overexploitation is not relegated to terrestrial systems. Several species of great whales were nearly driven to extinction before the International Whaling Commission banned commercial whaling in 1986. Northern elephant seals were so overexploited that they were thought to be extinct until a small remnant population was found on Guadalupe island in 1892. At the same time, once productive global fisheries have been in decline since the late 1980s despite increased technological efficiency (Pauly et al. 2002), and today it is estimated that large predatory fish biomass is only 10% of preindustrial levels (Myers and Worm 2003).

Although the role of the human predator in ecological systems is more immediately perceivable, there is growing recognition that changes in host community ecology and trophic interactions can contribute to the emergence of infectious diseases that 'prey' on humans (Jones et al. 1998, Ostfeld and Holt 2004, Keesing et al. 2010). For example, due to the widespread eradication of large carnivores (Pinheiro et al. 2011), top predators in many terrestrial ecosystems are now medium sized carnivores such as coyotes (Connell 1980). These medium-sized carnivores can indirectly increase the abundance and diversity of low trophic level species, such as rodents and songbirds, by suppressing populations of smaller carnivores such as foxes (Crooks and Soule 1999). Strong interactions among predators that lead to cascading effects on prey have been documented for over 60 systems worldwide (Ritchie and Johnson 2009). As top predators are extirpated in some parts of the world, and recolonize in others, it is important to understand the consequences for vertebrate community composition and for low-trophic-level species in particular. Because emerging zoonotic diseases overwhelmingly depend on vertebrate hosts that occupy low trophic levels, such restructuring of predator communities may have unintended consequences for human disease.

In this dissertation, I explore the role of humans as both predators and prey in ecological systems. First, I explore the predation of Pacific salmon, which are an economically, ecologically, and culturally important resource. This research strives to include ecosystem considerations in the management of Pacific salmon in order to balance the needs of fisheries and the ecosystem. Next, I explore the predation of large primates in the Neotropics, which contain some of the last remaining vast tracts of tropical forest in the world. Previous research has categorized Neotropical hunting as ‘sustainable’ or ‘not sustainable’. My research redefines sustainability as a spatial concept so that rather than ask whether hunting is sustainable, the goal is to estimate the spatial impact of hunting. This includes mapping the area over which large primates will be extirpated by hunting. In this dissertation, I switch to focus on humans as prey using Lyme disease as a case study. Lyme disease is a paradigmatic case of disease emergence that is thought to be driven by changes in the host community. Here I assess how the restructuring of predator communities due to the colonization of coyotes in the absence of gray wolves has influenced the emergence of this disease.

Chapter 1

Using Grizzly Bears to Assess Harvest-Ecosystem Tradeoffs in Salmon Fisheries

Abstract

Implementation of Ecosystem-based Fisheries Management (EBFM) requires a clear conceptual and quantitative framework for assessing how different harvest options can modify benefits to ecosystem and human beneficiaries. We address this social-ecological need for Pacific salmon fisheries, which are economically valuable but intercept much of the annual pulse of nutrient subsidies that salmon provide to terrestrial and aquatic food webs. We used grizzly bears, vectors of salmon nutrients and animals with densities strongly coupled to salmon abundance, as surrogates for 'salmon ecosystem' function. Combining salmon biomass and stock-recruitment data with stable isotope analysis, we assess potential tradeoffs between fishery yields and bear population densities for six sockeye salmon stocks in Bristol Bay, Alaska and British Columbia (BC), Canada. For the coastal stocks, we find that both bear densities and fishery yields would increase substantially if ecosystem allocations of salmon increase from currently applied lower to upper goals and beyond. This aligning of benefits comes at a potential cost, however, with the possibility of forgoing harvests in low productivity years. In contrast, we detect acute tradeoffs between bear densities and fishery yields in interior stocks within the Fraser River, BC, where biomass from other salmon species is low. There, increasing salmon allocations to ecosystems would benefit threatened bear populations at the cost of reduced long-term yields. To resolve this conflict, we propose

an EBFM management goal, which values fisheries and bears (and by extension, the ecosystem) equally. At such targets, ecosystem benefits are unexpectedly large compared with losses in fishery yields. To explore other management options, we generate tradeoff curves that provide stock-specific accounting of the expected loss to fishers and gain to bears as more salmon escape the fishery. Our approach, modified to suit multiple scenarios, provides a generalizable method to resolve conflicts over shared resources in other systems.

Introduction

Due to the impacts of fisheries on non-target species and ecological processes, there is growing pressure to apply ecosystem-based fisheries management (EBFM) (Pikitch et al. 2004, Fowler 2009, Link 2010, Belgrano and Fowler 2011). Guiding principles exist, but EBFM cannot be implemented without quantitative methods that can guide policy. Additionally, designing EBFM approaches requires an assessment of the tradeoffs inherent to balancing ecosystem protection and economic costs. This is because any EBFM plan, however technically robust, requires political will. Confronting these challenges requires a new focus on case studies that account for the unique biology of each fishery from which general guidance might emerge for other systems.

Pacific Salmon (*Oncorhynchus* spp.) are economically, socio-culturally, and ecologically important. Alaskan landings alone surpass 300,000 metric tons and ex-vessel values exceed $260 million annually (Woodby et al. 2005). Many cultures, aboriginal and otherwise, are also tied to salmon (Quinn 2005). Transcending value to humans, adult wild salmon are critical to aquatic, terrestrial and marine ecosystem function. They are the dominant prey of a number of marine and terrestrial predators such as orcas (Ford et al. 1998), salmon sharks (Nagasawa 1998), pinnipeds (Roffe and Mate 1984) and grizzly bears (Hilderbrand et al. 1999b). Salmon carcasses, distributed primarily by bears during spawning events, contribute annual pulses of marine-derived nutrients to freshwater systems that propagate through food-webs and influence primary producers, invertebrates, fish and wildlife (Willson and Halupka 1995).

The inherent conflict between the socio-economic value of salmon and their critical role in ecosystem function has led to calls for a change from current single-species management to EBFM (Piccolo et al. 2009). However, such challenges have yet to lead to scientifically grounded and quantitative policy recommendations that can inform managers and fishery certifiers such as the Marine Stewardship Council (MSC). One of the MSC's guiding principle is that fisheries must minimize ecosystem impacts, but it remains unclear how to quantify: i) the impact that competition with fisheries has on wildlife, ii) the influence of modifying harvest levels on the ecosystem, iii) or the economic costs of various management options.

Selecting which organisms to monitor is also a consistent problem in the implementation of EBFM because knowledge of the relationships between biomass availability of the central resource and population responses of non-human consumers are often limited (Browman et al. 2004, LInk 2005, Richerson et al. 2010). Here we cross ecosystem boundaries to use a terrestrial animal, the grizzly bear (*Ursus arctos horribilis*), as a focal species to develop a quantitative framework that evaluates the tradeoffs between fisheries yields and an ecosystem response to salmon (*i.e.* grizzly bear densities).

We chose grizzly bears, which are also called brown bears in coastal systems, as a surrogate of salmon-influenced ecosystem function because: 1) bear population dynamics are strongly linked to salmon abundance (Hilderbrand et al. 1999b); 2) bears are the *terminal* predator, consuming salmon in their final life history phase; thus, if there are enough salmon to sustain healthy bear densities, we reason that there should be sufficient salmon numbers to sustain populations of earlier salmon-life-history predators such as seabirds, pinnipeds and sharks (Fig. 1A-B), and; 3) bears are the dominant species mediating the flow of salmon-derived nutrients from the ocean to the terrestrial ecosystem (Fig. 1B)(Hilderbrand et al. 1999a). After capturing salmon in estuaries and streams, grizzly bears typically move to land to consume each fish, distributing carcass remains to vertebrate and invertebrate scavengers up to several hundred meters from waterways (Gende et al. 2001, Gende and Quinn 2004). Carcass remains (nutrients and energy) can influence all trophic levels from primary producers to large carnivores in both terrestrial and aquatic ecosystems (Hilderbrand et al. 1999a, Helfield and Naiman 2006, Hocking and Reynolds 2011). Described as a 'keystone interaction', this coupled grizzly-salmon association (at high bear densities) can provide up to a quarter of the nitrogen budget to plant communities in riparian areas adjacent to spawning grounds (Helfield and Naiman 2006). Additional benefits provided by a focus on grizzly bears are their charismatic appeal to the public and their status as a large carnivore commonly of conservation concern.

The fundamental challenge with implementing EBFM in this bear-salmon-human system (and others) is to determine how much of the fished resource to allocate to fisheries versus the ecosystem. Currently, under single-species management, fisheries commonly intercept more than 50% of inbound salmon that would otherwise be available to bears and the terrestrial and aquatic ecosystems they support (Quinn 2005). Managers, typically focused exclusively on prioritizing allocation to fisheries, determine an optimum number of the total salmon run to allocate to spawning, or "escapement". The goal is generally to achieve maximum sustainable yield (MSY), but the political process, uncertainty in the relationship between spawning stock (escapement) and recruitment, and multiple management objectives can result in escapement goals below an estimated MSY level (see below). For fisheries like this, managed below MSY, both yield and bear density would increase with greater escapement, but the potential responses have not been explored quantitatively. For those managed at MSY, increased escapement would benefit grizzly bears (and the ecosystem) but costs would be borne by fishers via losses in yield. The precise tradeoffs, however, require a detailed quantitative assessment over a range of managed escapements to be of maximum value to decision-makers faced with this potentially contentious change to salmon management.

To evaluate the effects of different management options, we modeled how bear population densities and fisheries yields would respond to increased escapement. This involved first estimating a relationship between salmon biomass availability and salmon consumption by bears from eighteen grizzly bear populations across British Columbia (BC), Canada (Fig. 1C & D). We linked this relationship to a known positive relationship between meat (*i.e.* salmon) consumption by grizzlies and grizzly densities (Hilderbrand et al. 1999b, Hilderbrand et al. 2004). We then used stock-recruitment models, specific to sockeye salmon (*O. nerka*) stocks that spawn in Bristol Bay, Alaska, and BC (Fig. 2) to estimate fisheries yields as a function of escapement, and the expected abundance of salmon in the absence of the fishery (Fig. 3). For stocks managed below a MSY escapement, we assessed how departures from *status quo* management would increase bear densities and fisheries yields. For stocks managed at MSY, we scaled bear density and fishery yield by their system-specific maxima to create dimensionless and commensurate values that could be compared. In all assessments, we focused on sockeye while holding other salmonids at their management escapement targets, or mean escapement levels, because sockeye: i) are often dominant runs, ii) migrate deep into interior regions, iii) are the most commercially valuable species (Quinn 2005) and iv) are species for which high quality stock-recruitment data exist.

While this work aims to develop a new conceptual and quantitative framework applicable to other resource management contexts, we also seek to inform contemporary bear and salmon management in BC and Alaska. First, we model potential population responses by grizzly bears in the Fraser River watershed, where bears are provincially threatened in the Chilko and partially extirpated in the Quesnel system (Fig. 2). Second, we assess whether competition with the salmon fishery has the potential to significantly constrain grizzly bear productivity. This is particularly relevant because both the Fraser River and Bristol Bay stocks are certified by the MSC, having satisfied the minimal ecosystem impact principle.

Results

In all systems, bear diets would respond considerably to increases in salmon abundance (*i.e.* escapement). Despite the myriad potential errors in estimating both variables across such large spatial scales we found that salmon biomass availability alone explained nearly 50% of the variation in bear diets (% salmon in diet), which followed a saturating trend (Fig. 1C). The relative accessibility of salmon that spawn in varied habitats, from small streams to rivers to lakeshores, likely explains some of the additional variability. Statistically fitting this relationship to 18 grizzly bear populations accounted for errors to produce a robust estimate of the relationship between salmon availability and salmon in bear diets. We estimated that the salmon biomass density necessary for salmon to constitute roughly 45% of bear diets (half of the recorded maximum salmon consumption by bears; *see* Materials and Methods) is 80.08 kg/km^2, with a 95%

confidence interval from 50.9 to 128.4 kg/km^2. This population scale model was robust at other scales, accurately predicting bear diets at the watershed scale for three systems with known salmon biomass (Fig. 1D; Table 1). This model, which predicts how percent salmon in bear diet responds to increased salmon escapements, helps explain corresponding increases in bear densities (*see* below; Materials & Methods).

Increased escapements relative to current management levels would also affect long term fisheries yields, though patterns differ among systems. By fitting stock-recruitment relationships for each fishery, we identified three qualitatively distinct types of sockeye management dynamics (Fig. 3). The Chilko and Quesnel stocks (Fraser River) exhibit clear overcompensating density dependence (when recruitment declines as the number of spawners increases). For these stocks, both the escapement that produces MSY, E_{MSY}, and the escapement in the absence of a fishery, E_m, could be reasonably estimated. These fisheries are currently managed at MSY (Fig. 3). The Ugashik and Nushagak stocks are data poor in the upper regions of escapement making E_m difficult to estimate, but reasonable estimates of E_{MSY} are possible. These systems are managed for lower and upper escapement goals, which are both below an estimated E_{MSY}. Finally the Egegik and Rivers Inlet stocks have the highest uncertainty because it is unclear if the stock recruitment relationship is even appropriate to characterize the data. Recruitment in the Egegik stock does not saturate over the observed range of escapement, which is strong evidence that escapement goals could increase to reach E_{MSY}. Similarly, management here occurs with lower and upper escapement goals, both below predicted E_{MSY}. Rivers Inlet is uncertain because after a period of high productivity the stock has collapsed and is slowly rebuilding, which raises the possibility that unobserved factors (*e.g.* changing productivity due to a regime shift) are driving recruitment dynamics (Cox-Rogers and Sturhahn 2005). Rather than consider upper and lower escapement goals for this stock in our analyses, we consider the escapement above which fishing is currently allowed and the optimal (and higher) escapement target estimated from a lake productivity model (Cox-Rogers and Sturhahn 2005). Although fishery yields are difficult to assess when there is high uncertainty in the stock-recruitment relationship, the impact of increasing escapement on bears densities can still be assessed.

We found that the presence and degree of conflict between fisheries yields and bear densities is stock-specific. Increasing escapement from lower to upper management targets in Rivers Inlet and the Alaskan systems would increase not only bear densities but also fisheries yields (Figure 4A-B). Compared with the lower goals, the upper escapement goals of Ugashik, Egegik, Nushagak, and Rivers Inlet are expected to provide for roughly 22%, 8%, 8% and 28% increases in bear density; if escapements were to increase from the lower goals to the estimated E_{MSY} levels, bear density would increase by roughly 34%, 19%, 8% and 44% (Fig. 4B). Notably, expected increases in yield are proportionately much greater than increases in bear densities (Figure 4B)

For stocks with predictable stock-recruitment relationships and overcompensating density dependence (Chilko and Quesnel), we detect conflict between benefits to bears and benefits to fisheries. Across a range of escapements, expected fishery yields increase until escapements produce MSY and decline thereafter ("Relative Fisheries Yield" [RFY] line in Fig. 5A). In contrast, predicted bear densities increase monotonically and saturate as escapements increase ("Relative Bear Density" [RBD] line in Figure 5A). In these interior systems of the Fraser River, where species other than sockeye contribute relatively little to total available salmon biomass, realizable bear densities are highly dependent on sockeye escapement (y-intercept of RBD in Figure 5A). Increasing escapement beyond E_{MSY} leads to conflict between fishery yields and bear density, with the former decreasing and the latter increasing.

To aid in resolving such conflict in these systems and others, we provide here a straightforward EBFM decision-making framework. By scaling yields and bear densities relative to their maxima (that occur at E_{MSY} and in the absence of fishing respectively), we compare the dimensionless and commensurate values of *RFY* (Richerson et al. 2010) and *RBD*. When *RFY* and *RBD* are equal, which is visualized at the intersection of *RFY* and *RBD* when plotted together (Fig 5A), equal relative costs are imposed on bears and fishers. We propose that this escapement level, which places equal social value to fisheries and the ecosystem, be termed "ecosystem-based management escapement", or E_{EBM}.

Managing at E_{EBM}, rather than at E_{MSY} would impose considerable costs to fisheries. Losses in long-term yield are about 12% and 23% in the Quesnel and Chilko systems, respectively (Fig. 5B-C). Based on 10 year average ex-vessel prices, lost revenues would be approximately \$680,000 and \$480,000 annually. These losses in yield would correspond to proportionally greater increases in escapement, however, nearing 50% in the Quesnel system and 80% in the Chilko run (Fig. 5C).

These E_{EBM} escapement levels, however, represents only one option within a continuum of ecosystem-harvest tradeoffs. We quantified these tradeoffs to assess losses in yield associated with increased bear densities as escapement varies above E_{MSY} (Figure 5B). Costs to fisheries for increasing bear densities accrue slowly at first (low initial slope) and then accelerate.

Discussion

Our goal here was to assess quantitatively the expected impact to fisheries and grizzly bears - a surrogate for salmon ecosystem function - if *status quo* management was adjusted to increase escapement across a range of contexts. We present a general framework that is flexible enough to address salmon management in systems that vary in escapement targets that themselves vary as a function of certainty in stock recruitment relationships. In low certainty systems, managed at targets below estimated E_{MSY}, the benefits to bears (and fisheries) of increased escapements can be assessed, but fishery yields are too uncertain beyond this level to assess accurately the tradeoffs. In relatively high certainty systems managed for MSY, we were able to evaluate the system-specific tradeoffs between the costs to humans in lost yield and the benefits of salmon escapement to bears (and the ecosystem) if escapements were to increase.

Any departure from current management would necessarily involve conflict between multiple competing objectives. Whereas forgoing yield for increased bear densities with escapements beyond E_{MSY} in the Chilko and Quesnel systems represents obvious tradeoffs, others are more complex. For example, the expected increase in both bear density and fishery yield in the other four systems results in an apparent win-win situation where both the ecosystem and fisheries benefit from increasing escapement. However, high annual variability in recruitment could sometimes lead to a fishery closure if higher escapement targets committed to cannot be met. One way to avoid this is to increase upper escapement goals while retaining lower goals, which would continue to allow some fishing in low return years (as long as lower escapement goals are met) while allowing for increased escapement in other years. Retaining lower escapement goals may benefit subsistence fishers, who must harvest some fish each year but face restrictions if escapements are perceived to be too low. Finally, although we argue that the grizzly bear offers a sensible and attractive surrogate for salmon ecosystem function, additional ecosystem responses to different management options might instead be considered. For example, increasing net nutrient input into systems (*e.g.* (Moore et al. 2007)) or trophic (egg) subsidies to resident fishes (*e.g*. (Moore et al. 2008)) might also form reasonable and important ecosystem objectives. Similarly, minimizing the probability of years without harvests might form a desirable management objective; a quantitative evaluation of these tradeoffs might lead to very different escapement targets. In our system and others, multiple competing objectives like these increase complexity for managers, though relevant methods have been developed for decision-making (*e.g*. (McDaniels 1995, Robb and Peterman 2005)).

One utility of our approach is that it offers a quantitative method to evaluate how well various harvest options satisfy the MSC ecosystem criterion while accounting simultaneously for the potential economic costs to fishers. Our results suggest that low sockeye escapement is most detrimental to bears in systems where there is little biomass available from other salmon species. For example, because Nushagak has large runs of all five Pacific salmon species, salmon are expected to represent roughly 63% of bear diets even in the absence of sockeye (Figure 4A). In contrast, nearly no salmon other than sockeye is available in the Quesnel run. This makes consideration of ecosystem needs in salmon management particularly important for inland stocks, where abundant runs of pink (*O. gorbuscha*) and chum (*O. keta*) salmon are absent. Moreover, in all six systems, which have received MSC certification, the observation that bear densities can increase substantially with increased escapement from current management levels implies that fisheries compete with bears and other ecosystem recipients. This suggests that the "minimal ecosystem impact" criterion, currently satisfied with certification, might in fact require increased scrutiny. This might be particularly the case with the newly certified Fraser River sockeye; grizzly bears are provincially threatened in the Chilko and partially extirpated in the Quesnel system (Figure 2;(Austin et al. 2004)). Thus, the significant restrictions to bear population productivity we document as a result of conflict with fisheries are relevant to bear conservation.

Another utility of our approach, particularly when applied to systems with high certainty managed at MSY, is that it offers a novel conceptual and philosophical framework of conservation value. Although arbitrary, the escapement that imposes equal costs on bears and fisheries, E_{EBM}, can serve as a starting point to guide likely contentious management decisions. Although provocative, we highlight that this target would provide greater benefit than expected; the additional sockeye escapement to bears (and the ecosystem) at E_{EBM} relative to E_{MSY} is greater than the penalty to fishers might suggest (Fig. 5C). Such unexpectedly large contributions of salmon carcasses to broader ecosystem beneficiaries might form a good conservation investment. Compelling support for an "abundance matters" hypothesis is now emerging (Darimont et al. 2010); that is, while often site-specific, evidence is accumulating that suggests increased spawning density is associated with positive ecological responses across a broad array of taxa, including aquatic primary productivity (Schindler et al. 2005), terrestrial vegetation growth (Helfield and Naiman 2001, Hocking et al. 2009), invertebrate density (Hocking et al. 2009), songbird density (Gende and Willson 2001), growth rates of resident fish, including juvenile salmon (Scheuerell et al. 2007) as well as other aquatic and terrestrial ecological processes (Janetski et al. 2009). Higher salmon escapement might also provide increased opportunities for salmon-based eco-tourism (Darimont et al. 2010).

Adopting E_{EBM} escapement goals using bears as an ecosystem surrogate has several additional desirable properties. First, implementing E_{EBM} might be more politically robust than increasing escapements above E_{MSY} by some arbitrary amount. Due to the saturating relationship between salmon biomass and bear density, harvests are not sacrificed in systems where bears can maintain high densities. Second, E_{EBM} is environmentally robust. In systems with lower relative bear densities, moderate reductions in yield can translate to substantial gains for bears and ecosystems (Fig. 5C). Third, this model, which makes tractable the complex cross-boundary interactions between salmon nutrients and multiple beneficiaries, reflects a quantifiable ecosystem approach to management. Implementation of this method by managers can be refined with a site-specific approach relating bear diets to salmon availability across years from focal populations, rather than across populations as we have done. Finally, recognizing that E_{EBM} might not be socio-politically possible, our tradeoff curve approach (Fig. 5B) allows estimation of costs and benefits associated with adjustments to escapement in either direction.

Applying our framework to other fisheries requires the following consideration. First, critical knowledge sets for focal non-target species should include not only their estimated population responses across a range of fish biomass, but also some distinguishing role the candidate species serves in the ecosystem (*e.g.* keystone function).

Additionally, estimates of the costs to fisheries across a range of management options that depart from the status quo are critical. Moreover, selecting focal species of conservation concern to resource managers and the public might extend greater political will to any EBFM recommendation (see also (Williams et al. 2011)). Finally, we note that the principles of single-species fisheries management and EBFM depart conceptually and practically. The former focuses narrowly and almost exclusively on the exploitation of natural resources for humans, whereas EBFM is inclusive of all biodiversity, including humans. Our proposed EBFM targets, in which costs are equally born by fisheries and bears (and by extension, the ecosystem), closely match the spirit of EBFM.

Materials and Methods

We used a multi-stage analysis to predict how bear population density would respond to variation in spawning salmon abundance as influenced by harvest management. This involved first estimating a relationship between salmon abundance and salmon consumption by bears, and then linking this result to a known positive relationship between salmon consumption by bears and bear density.

Salmon abundance and salmon consumption by bears

We used estimates of the proportion of salmon (including Kokanee) in the diet of bears from 18 grizzly bear populations units (GBPUs) in British Columbia, Canada that were derived from stable isotope analysis (Mowat and Heard 2006). These estimates were derived from hair, which grows throughout most of the annual activity period of bears. For these same GBPUs across the same period (1995-2003), we estimated the mean annual salmon biomass potentially available to bears (after interception by fisheries; the "escapement"). This involved using spatially explicit escapement data for all five species (pink, chum, coho, sockeye, and Chinook) to estimate the salmon returns in each of the watersheds captured by GBPUs (Fig. 2C). We assigned a portion of these estimates to GBPUs based on the fraction of each watershed that intersects each GBPU. We converted salmon numbers to biomass, using average masses of each species and sex (Groot and Margolis 1991), assuming a 50:50 ratio between sexes.

To determine how the availability of salmon biomass, S (kg/km^2), influenced the proportion of salmon in grizzly bear diets, $D(S)$, we fit a saturation curve using nonlinear least squares (Eq. 1). Stable isotope data from grizzly bear hair sampled in the Columbia River Basin, USA, during the late 1800s, when salmon were much more abundant, indicate that salmon can represent up to 90% of bear diets (Hilderbrand et al. 1996). Several current bear populations consume more than 80% salmon (Mowat and Heard 2006), but – logically – we constrained consumption to values less than 100%. Accordingly, we fixed the asymptotic maximum consumption (*i.e.* the consumption when there are infinite salmon on the landscape) at 90% and used the data to fit the half-saturation parameter of the saturation curve. Robust estimation of the half-saturation parameter, and its confidence interval, is key because the 90% assumption will cancel in our analysis.

Percent salmon in diet, $D(S)$, as a function of salmon biomass density, S (*kg/km^2*), is given by,

$$D(S) = \frac{90S}{h + S} \tag{1}$$

where h is the half saturation parameter that determines how quickly bear diets respond to salmon availability. We tested the derived relationship (Eq. 1) at the watershed level (as opposed to population [*i.e.* GBPU] level) using escapement data from Rivers Inlet and Quesnel (BC) (Cox-Rogers and Sturhahn 2005) and Ugashik and Egegik (Alaska) (Baker et al. 2009, Morstad et al. 2009) to estimate salmon consumption by bears (see Tables S1-2). The Rivers Inlet escapement and stable isotope data are from 1998 and 1999, when salmon were relatively rare due to an extremely poor sockeye run (Table 1). Note that we estimated biomass density by summing over escapements of all salmon species. We grouped Egegik and Ugashik watersheds (Fig. 2) and compared predicted dietary salmon (Ugashik: 67.2%, Egegik: 76.6%, Average: 71.9%) with the average estimates from stable isotope data, also from hair, collected in the associated Alaska Game Management Units 9B, 9C, and 9D (71%, 73%, and 73% dietary salmon respectively, average of 72.3%) (Mowat and Heard 2006). Because the Quesnel sockeye run is cyclic, we used the median, rather than mean, escapement since it is a more robust approximation of inter-annual biomass availability.

Fishery yields

We determined the expected salmon harvest (run size minus escapement) using standard Ricker stock-recruitment models (Fig. 3), which are well suited to characterize overcompensating density dependence (Baker et al. 2009). They are also conservative in favor of fisheries because yields decline more quickly with increased escapement than if Beaverton-Holt dynamics are assumed.

The size of the recruited salmon population *R*, when the spawning population is *E*, is given by

$$R(E) = \alpha E e^{-\beta E} \tag{2}$$

and yield is simply recruitment minus escapement.

The escapement that maximizes long term "sustainable yield" is E_{MSY}, which we determined graphically based on the best-fit parameters . However, it is often difficult to estimate E_{MSY} because many stock recruitment relationships are fraught with uncertainty in parameter estimates and even uncertainty over whether the stock-recruitment relationship is appropriate to describe the dynamics of the fishery. As a result, fisheries with adequate stock-recruitment data can be managed by targeting a biologically-based escapement of E_{MSY} (called a 'biological escapement goal'). Other fisheries are managed between lower and upper target escapements that have provided adequate yield in the past (called a 'sustainable escapement goal'), but this escapement range is not necessarily optimal (*i.e*. maximizing long term yield). Because our goal was to determine how departures from *status quo* management impact bears and ecosystems, we conducted distinct analyses for stocks managed at E_{MSY} and those managed for a range of target escapements that were generally below estimates of E_{MSY} as determined by stock-recruitment relationships.

For fisheries managed at E_{MSY}, the relative fishery yield (*RFY*) achieved with escapement *E* relative to the maximum yield is

$$RFY = \frac{\alpha E e^{-\beta E} - E}{\alpha E_{MSY} e^{-\beta E_{MSY}} - E_{MSY}} \tag{3}$$

which is a measure of the proportion of yield achieved by the fishery when escapement is *E* compared with when yields are maximized at E_{MSY}. For fisheries managed for a range of target escapements, we used the same functional form but with the lower target escapement as our management baseline rather than E_{MSY} (Fig. 4B).

Linking salmon consumption by bears to bear density

We consider the bear density at a particular escapement relative to the bear density at the stock-specific maximum escapement (*i.e.* no fishery). The escapement in the absence of the fishery, E_m, is the escapement at the steady state (*i.e.* where recruitment and escapement are equal) of the Ricker stock-recruitment model,

$$E_m = \frac{\ln(\alpha)}{\beta} \tag{4}$$

However, for fisheries without adequate certainty in stock recruitment data to estimate E_m, we use the maximum observed escapement (Fig. 3) instead. The maximum observed escapement in these stocks is well-below estimates of E_m from stock-recruitment relationships, which suggests that our projections of impacts of fisheries on bear populations are conservative. We estimated the expected bear density for a given level of escapement relative to the expected bear density with the maximum escapement (E_m; Eq. 4 or maximum observed escapement). Bear density, B, was estimated by linking Eq. 1 with a known linear relationship between percent meat in diet and bear density (Hilderbrand et al. 1999b), but we assumed a zero intercept, which is conservative in favour of fisheries because some meat is likely necessary to sustain even the smallest bear density. Note that we assumed all meat consumed in coastal populations was derived from salmon, a reasonable assumption based on data from multiple populations (Mowat and Heard 2006). The bear density for a given escapement is thus,

$$B(E) = b_0 D(E) \tag{5}$$

where b_0 determines how quickly bear densities increase with dietary salmon. Because bear densities increase linearly, b_0 cancels when determining relative bear density so that our results depend only on the assumption of linearity and are not dependent on any particular slope from Eq. 5. Although in practice bear densities are limited by bottom-up (*i.e.* salmon) and top-down (*i.e.* hunting) forces, bottom-up forces influence population productivity and potential bear densities in the absence of killing by humans (Mowat et al. 2005).

Percent salmon in diet (Eq. 1) saturates with salmon availability,

$$D(E) = \frac{90\,\frac{E\cdot m_s + M}{A}}{h + \frac{E\cdot m_s + M}{A}} \tag{6}$$

where m_s is the mean mass (kg) of an individual sockeye, M is an estimate of the biomass of all other salmon species present in each system, and A is the area of the watersheds that contains each salmon stock (Table 2). To estimate M, we used target escapement goals when they existed (mean of lower and upper goal) (Baker et al. 2009); if not, we used average escapements from 1999-2008. For runs with neither escapement targets nor data, we used harvest to approximate escapement by assuming a 50% harvest rate (Morstad et al. 2009) (see Table 2 for stock and species-specific data sources).

The *relative* bear density, *RBD*, can be written by combining Eqs. 5 and 6 as

$$RBD = \frac{B(E)}{B(E_m)} = \frac{D(E)}{D(E_m)}\,. \tag{7}$$

Plugging Eq. 6 into Eq. 7 and simplifying, *RBD* becomes

$$RBD = \frac{E\cdot m_s + M}{E_m\cdot m_s + M}\cdot\frac{Ah + E_m\cdot m_s + M}{Ah + E\cdot m_s + M}\,. \tag{8}$$

The Relative Fisheries Yield, *RFY*, and the Relative Bear Density, *RBD*, are now both dimensionless and commensurate values that can be directly compared.

Percent change in yields and bear densities in systems with high uncertainty in stock-recruitment relationships

For stocks with high uncertainty, E_{MSY} and E_m could not be reliably estimated. Moreover, current management practice in these systems target a range of escapements, bounded by lower and upper goals, rather than E_{MSY} level escapements. For these stocks we calculated percent changes in bear densities and fisheries yields when increasing from lower escapement goals to upper goals and to E_{MSY} (Figure 4B). To do this, we followed the same functional form as for *RFY* and *RBD* (Eqs. 3 and 8), but used the lower escapement goal as our baseline rather than E_m and E_{MSY}. Thus, rather than assess how bear densities and fishery yields compare to their system-specific maxima, we assessed how they are expected to respond to variation in the current management regime (*i.e.* from current lower to upper escapement goals), as well as how they are expected to respond when moving from lower escapement goals to predicted E_{MSY}.

Acknowledgements

We thank Yiwei Wang for original artwork in Figure 1. We thank the Alaska Department of Fish and Game and the Pacific Salmon Foundation for supplying stock-recruitment data. Two anonymous reviewers greatly improved this manuscript.

Table 1.1. The biomass density (kg/km^2) of each salmon species used to compare predicted to actual percent salmon in bear diets. For Rivers Inlet, pink and chum escapements were higher during the years when sockeye were not being fished. We used the median, rather than mean, sockeye escapement when calculating biomass for Quesnel because this stock is cyclic and the median is a more robust estimate of biomass availability. All other biomass density estimates are consistent with Table 2.

Stock	**Years**	**Pink**	**Chum**	**Chinook**	**Coho**	**Sockeye**
Rivers Inlet Collapse	**1998-1999**	**67.33**	21.74	0.00	0.00	27.24
Quesnel	**1995-2003**	0.00	0.00	8.18	0.06	34.84
Ugashik	**1995-2003**	0.00	0.00	1.19	0.28	205.70
Egegik	**1995-2003**	0.00	28.11	1.52	0.72	199.03

Table 1.2. The biomass density (kg/km^2) of each non-sockeye salmon species and escapements (in thousands) for the six sockeye stocks we consider. Biomass data come from the [A]mean of lower and upper escapement goal from the 2009 Bristol Bay Escapement Review (Baker et al. 2009), [B] mean 1999-2008 harvests from the 2009 Bristol Bay Management Report, assuming 50% harvest rate (Morstad et al. 2009), [C]mean escapement 1999-2008 from Department of Fisheries and Oceans Canada spawning escapement database (unpublished data), [D]MSY escapements calculated with stock recruitment models (MacDuffee 2009).

	Area (km^2)	**Pink**	**Chum**	**Chinook**	**Coho**	**Sockeye Elow**	**Sockeye Eup**	**Sockeye E_{MSY}**	**Sockeye E_m**	**Sockeye E_{EBM}**
Rivers Inlet	**8910**	41.85[D]	9.77[D]	0.00	1.9[D]	**200**	**610**	**1150**	**2460**	**1445**
Chilko	**19548**	0.00	0.00	8.18[C]	0.06[C]	**---**	**---**	**224**	**742**	**400**
Quesnel	**12009**	0.00	0.00	1.19[C]	0.28[C]	**---**	**---**	**763**	**2380**	**1155**
Ugashik	**11157**	0.00[B]	28.11[B]	1.52[B]	0.72[B]	**500**	**1200**	**2145**	**5140**	**2715**
Egegik	**7185**	0.06[B]	37.56[B]	0.85[A]	6.90[B]	**800**	**1400**	**6305**	**16405**	**7285**
Nushagak	**20794**	53.14[A]	32.89	39.24[A]	11.54[A]	**340**	**760**	**749**	**1930**	**1005**

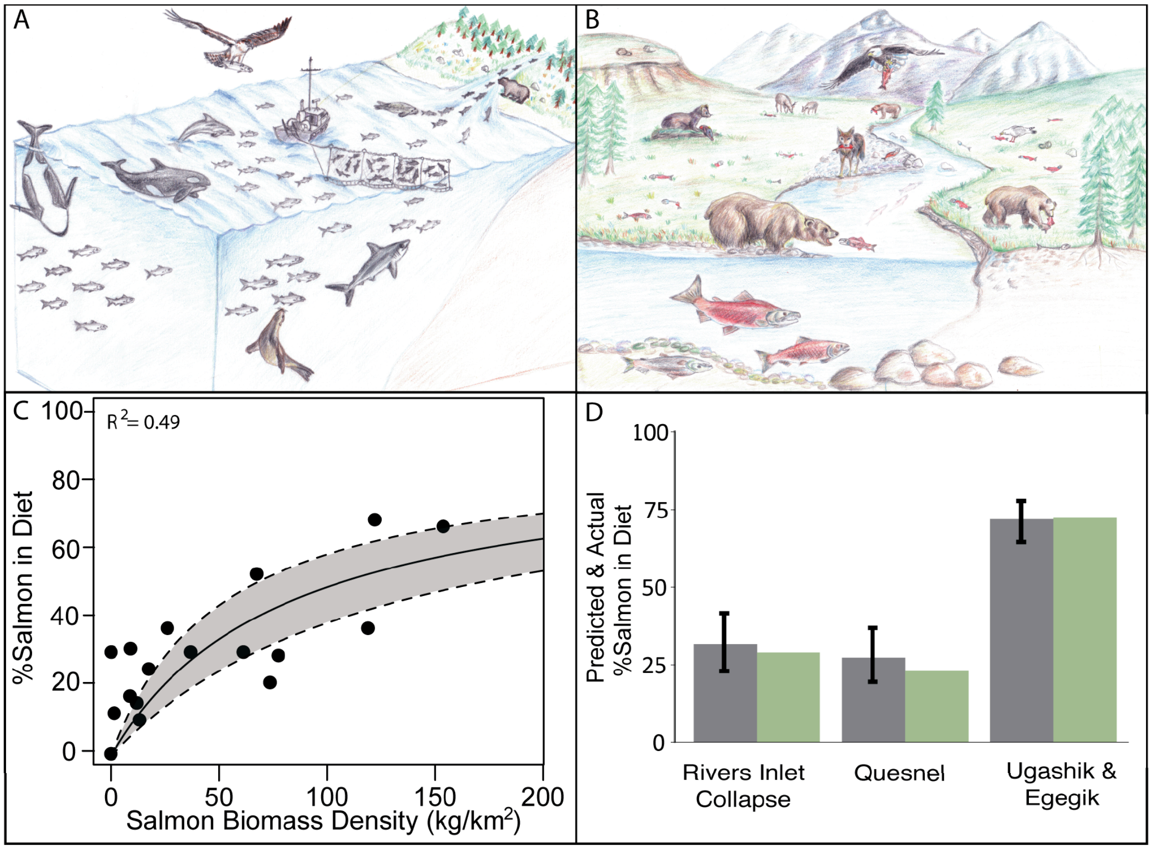

Figure 1.1 Using bears to quantify the importance of salmon to wildlife. Mature salmon are (A) important prey to orcas, pinnipeds, salmon sharks, humans and other predators in the marine domain before they (B) reach terrestrial and aquatic systems where they supply annual pulses of marine-derived nutrients and are the dominant prey of grizzly bears. By leaving uneaten carcass remains in riparian areas, bears serve as vectors of salmon to terrestrial and aquatic systems, supplying nutrients and food to riparian vegetation, invertebrates, and vertebrate scavengers including canids, gulls, eagles, and mustelids. The importance of salmon to bears can be quantified with (C) the relationship between salmon density and salmon consumption by bears as determined by stable isotope analysis of 18 grizzly bear populations from British Columbia (BC) (Mowat and Heard 2006). (D) Predicted salmon consumption by bears (gray bars with 95% confidence intervals) closely matches measured salmon consumption (green bars) as estimated by stable isotope analysis in bears from Rivers Inlet and Quesnel Lake in interior BC, and for the Ugashik and Egegik stocks combined in Bristol Bay, Alaska.

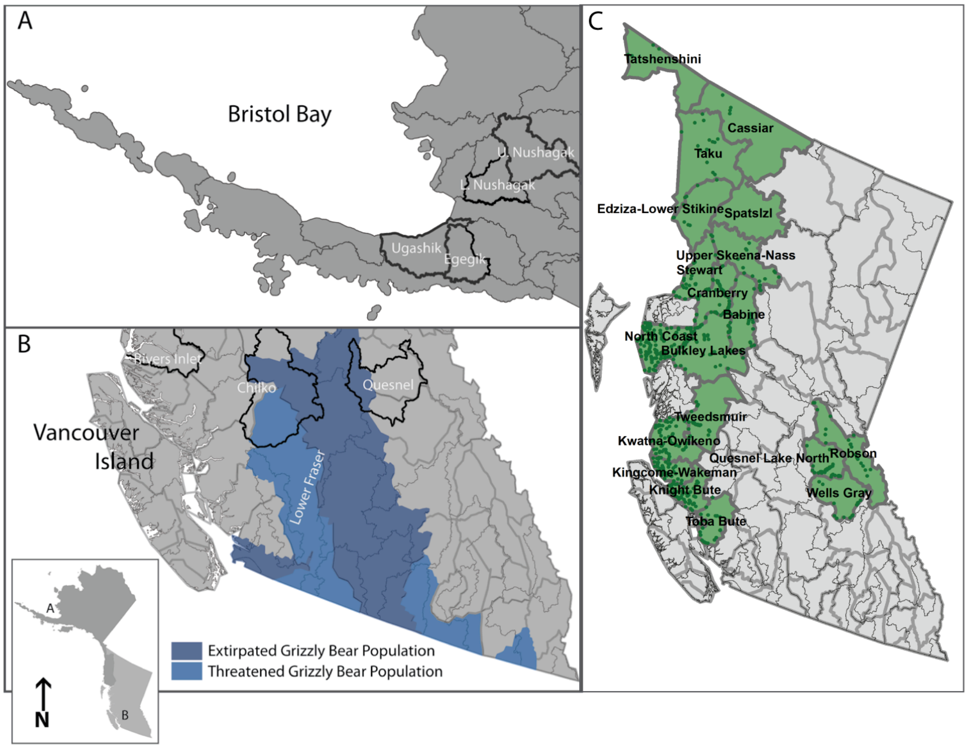

Figure 1.2 We consider three sockeye salmon stocks from (A) Bristol Bay, Alaska, and (B) two stocks from the Fraser River, British Columbia (BC), Canada, and one from the mid-coast of BC (Rivers Inlet). Watersheds are outlined by thin gray lines and focal watersheds are outlined in black. In BC, thick gray lines denote designated 'grizzly bear population units' (GBPUs) from which isotope data were derived. The Chilko and Quesnel stocks are in a region of bear conservation concern. (C) Percent salmon in grizzly bear diet as a function of salmon availability across 18 GBPUs in BC. Stable isotope data were collected from 1995-2003 in green-filled GBPUs. We first allocated mean salmon biomass measured at points from 1995-2003 to watersheds (thin lines). We then allocated salmon biomass to grizzly GBPUs (thick lines) based on the area of intersection between watersheds and GBPUs.

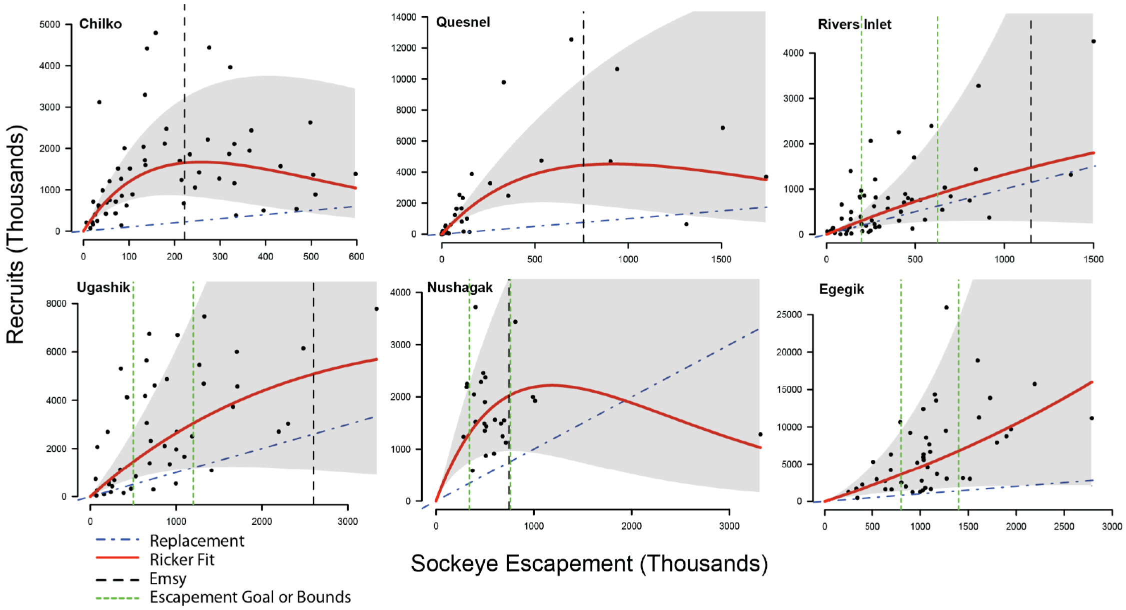

Figure 1.3 Stock recruitment relationships for study systems, fit with the Ricker stock-recruitment model. The difference between recruitment and the replacement line is considered surplus production that can be sustainably harvested. This difference is maximized at E_{MSY} but the lower and upper target escapements are often well below estimates of E_{MSY}. The escapement in the absence of the fishery, E_m, is estimated at the steady state of the Ricker model, which is best visualized at the intersection of the Ricker and replacement lines.

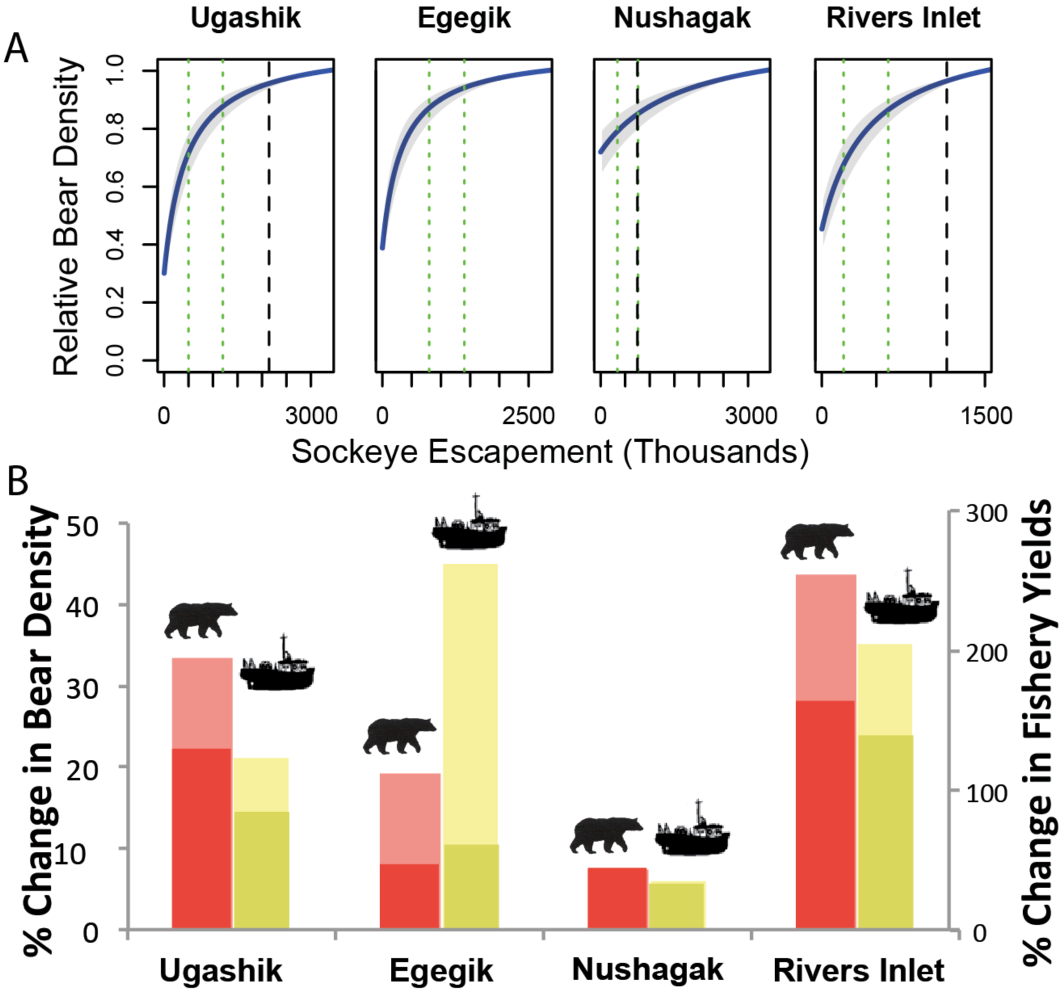

Figure 1.4 Accounting for bears when setting escapement goals in Bristol Bay and Rivers Inlet. (A) Bear density as a function of sockeye salmon escapement relative to the expected bear density at the maximum observed escapement (solid blue line). Vertical black dashed lines indicate E_{MSY}. The lower and upper escapement goals are highlighted by green dotted lines. (B) Increasing escapements from the lower to upper goals can substantially increase bear density (lower dark-red bar). Further increases in escapement to E_{MSY} continue to increase bear density (upper light-red bar), but the benefit is somewhat less due to the saturating relationship between escapement and percent salmon in diet. Importantly, there is no expected tradeoff to increasing escapement; yields are expected to be higher at upper escapement goals (lower dark-yellow bar) and increase further until E_{MSY} (upper light-yellow bar). Although E_{MSY} and the response in fisheries yields are uncertain, especially for the Egegik stock, bear success can still be assessed at the tangible lower and upper escapement goals and beyond.

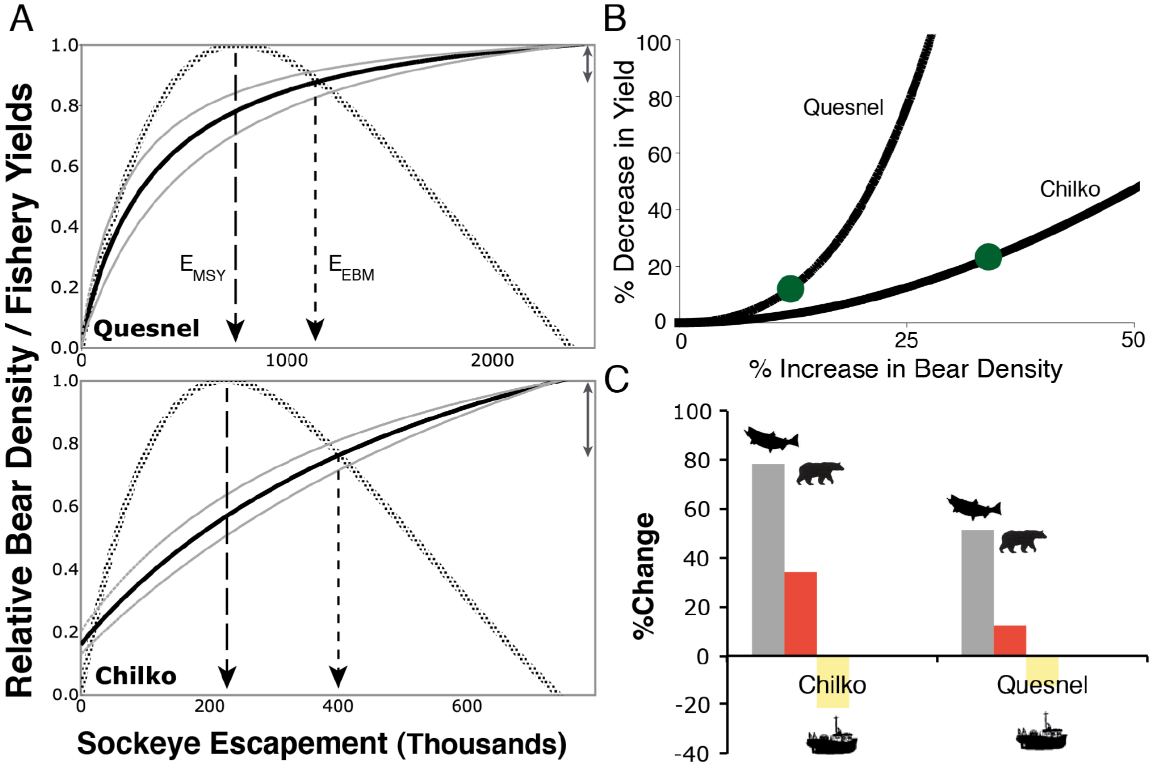

Figure 1.5 Using bears for ecosystem-based management in Chilko and Quesnel. (A) The Relative Bear Density (solid) and Relative Fisheries Yield (hatched) across a range of sockeye salmon escapements in Chilko and Quesnel (Fraser River) systems from British Columbia (BC), Canada. Ecosystem-based escapement goals, E_{EBM}, occur where the curves meet, indicating that bears and fishery yields are equally reduced from their maxima (double-sided arrows). Increases in escapement from E_{MSY} (Maximum Sustainable Yield escapements; dashed arrows) to E_{EBM} (dotted arrows) reduce harvests to some fraction of *MSY*. (B) Tradeoffs between loss in fisheries yield and increase in grizzly bear densities for escapements greater than those corresponding to Maximum Sustainable Yield. Green dots indicate proposed Ecosystem-based Management escapements (E_{EBM}) for each system. Reduction in fishery yields can result in substantial increases in bear density. (C) However, increased salmon allocations to bears (gray) under E_{EBM} provide much higher nutrient subsidies to terrestrial and aquatic systems than either the percent increase in bear densities (red) or decrease in fishery yields (yellow) suggest due to the shape of the stock-recruitment relationships.

Chapter 2

Deer, Predators, and the Emergence of Lyme Disease

Abstract

Lyme disease is the most prevalent vector-borne disease in North America and both the annual incidence and geographic range are still increasing. The emergence of Lyme disease has been attributed to a century-long recovery of deer, an important reproductive host for adult ticks, but an incompetent host for the bacterial pathogen. However, a growing body of evidence suggests that Lyme disease risk may now be more dynamically linked to fluctuations in the abundance of small mammals hosts that are thought to infect the majority of ticks. The rapid increase in Lyme disease over the last decade, long after the recolonization of deer, suggests that changes in the ecology of small mammal hosts may be responsible for the continuing emergence of Lyme disease. We present a theoretical model that illustrates how reductions in small mammal predators can sharply increase Lyme disease risk. We then show that increases in Lyme disease in the northeastern and midwestern USA over the past three decades coincide with a range-wide decline of a key small mammal predator, the red fox, likely due to expansion of coyote populations. Further, we find that coyote abundance and fox rarity predict the spatial distribution of Lyme disease in New York, while deer density is uncorrelated with Lyme disease incidence across four states. These results suggest that changes in predator communities have cascading impacts that may facilitate the emergence of zoonotic diseases, the vast majority of which rely on hosts that occupy low trophic levels.

Introduction

There is growing recognition that changes in host community ecology and trophic interactions can contribute to the emergence of infectious diseases (Jones et al. 1998, Ostfeld and Holt 2004, Keesing et al. 2010). In particular, the transmission of vector-borne zoonotic diseases to humans depends on multiple species interactions that influence host and vector abundance and infection prevalence. Because most zoonotic pathogens are harbored by wildlife that occupy low trophic levels (Ostfeld and Holt 2004), the extirpation of top predators and the consequent restructuring of predator communities (Connell 1980, Pinheiro et al. 2011) may increase the risk of contracting zoonotic infectious diseases if predation of reservoir hosts plays a key role in disease suppression. A paradigmatic case of disease emergence that is thought to be driven by changes in the host community is Lyme disease.

Lyme disease is the most prevalent vector-borne disease in North America and both the annual incidence and geographic range are still increasing (Bacon et al. 2008). It is caused by the bacteria *Borrelia burgdorferi,* which is transmitted to humans in the eastern USA primarily by the nymphal stage of *Ixodes scapularis* ticks (Barbour and Fish 1993). The emergence of Lyme disease has been attributed to the century-long population recovery of deer, which are not competent hosts for transmitting *B. burgdorferi* to ticks but are nonetheless important reproductive hosts for adult ticks (Spielman et al. 1985, Barbour and Fish 1993). Support for this hypothesis comes partly from studies of experimental removal or exclusion of deer, which has often reduced tick densities (Wilson et al. 1988). However, substantial research indicates that experimental or natural increases of deer density above a low threshold often have little effect on nymphal tick abundance (and also see Wilson et al. 1984, Ostfeld et al. 2006, Jordan et al. 2007, Table S1, reviewed in Ostfeld 2011). This suggests that when deer are sufficiently abundant, other factors, such as hosts for immature ticks, may become limiting. Decades after the recolonization of deer, and despite a shift in management objectives from increasing deer populations to stabilizing or reducing them (Ellis 2007), Lyme disease cases have increased enormously (380% increase in Minnesota, 280% in Wisconsin, and 1300% in Virginia from 1997-2007). This suggests that other unidentified ecological changes may now be facilitating the emergence of Lyme disease.

A growing body of evidence implicates small mammal abundance as a key determinant of the density of infected nymphs, the primary measure of entomological risk for Lyme disease (Ostfeld et al. 2001, Ostfeld et al. 2006). Molecular evidence suggests that four species of small mammals, (the white-footed mouse *Peromyscus leucopus,* Eastern chipmunk *Tamias striatus*, short-tailed shrew *Sorex brevicauda*, and masked shrew *Sorex cinereus*), are responsible for infecting 80-90% of ticks (Brisson et al. 2007). Thus it is possible that changes in the ecology of small mammals played a role in the continuing increase of Lyme disease. Small mammal populations are influenced both by resource availability, which has been correlated with the subsequent density of infected nymphs (Ostfeld et al. 2001, Ostfeld et al. 2006), and by predation (Hanski et al. 2001). The latter finding has led to the suggestion that predation may play a key role in suppressing Lyme disease (Ostfeld and Holt 2004).

A major change in predator-prey interactions in North America over the last half-century has resulted from the range expansion and population growth of a new top predator - the coyote, *Canis latrans*, which has spread across the continent following the extirpation of gray wolves, *Canis lupus* (Gompper 2002b). The expansion of coyotes may have suppressed the abundance of several small mammal predators, but reduction of foxes by interference competition with coyotes is the best documented (Sargeant et al. 1987, Crooks and Soule 1999, Ritchie and Johnson 2009). The replacement of foxes by coyotes would likely reduce predation rates on small mammal prey (i.e. the reverse of mesopredator release) because red fox, *Vulpes vulpes*, densities are typically an order of magnitude higher than coyote densities (Tremblay et al. 1998, Patterson and Messier 2001, Way et al. 2002) and small mammals make up a larger fraction of their diets, particularly in the east where coyotes rely far more on deer (Major and Sherburne 1987, Gompper 2002a). Further, red fox cache prey for later consumption and are thus capable of killing large quantities of prey when prey are abundant (e.g. after an acorn mast). The high abundance of foxes , their ability to kill large quantities of small mammals due to both dietary preference and prey caching behavior, and their adaptability to human-dominated landscapes makes them potentially highly important to suppressing Lyme disease hosts in areas around human habitation. Thus, somewhat paradoxically, the expansion of coyotes likely decreased predation rates on small mammals by suppressing more efficient predators (foxes).

Here we test the hypothesis that changes in predation have contributed to the continuing emergence of Lyme disease by analyzing disease models that explicitly incorporate predation intensity, and by examining spatial and temporal correlations on multiple scales between Lyme disease, coyote, fox, and deer abundance.

Results

Host-Vector Dynamical Model

We built a host-vector model to determine how changes in predation might impact Lyme disease risk. Using plausible assumptions and parameter values (Fig.1, see Methods), we find that predation can have a strong nonlinear influence on both the density and infection prevalence of nymphs (Fig. 1, Fig. S1). At intermediate predator densities small changes in predator abundance can cause large changes in Lyme disease risk (a 20% reduction in predation at the inflection point in Fig. 1B more than doubles the density of infected nymphs). This nonlinearity is due to the interaction of predation with the quadratic shape of logistic population growth. Host densities near carrying capacity are by definition unproductive. Increasing the predation rate reduces host density, which increases population productivity. When the host population is maximally productive near intermediate host densities, further increases in predation cannot be compensated for with more reproduction, which allows small increases in predation to cause greater reductions in host density. Additionally, at these intermediate densities the host turnover rate is highest (maximal steady-state birth and death rates) which reduces host infection prevalence because hosts are born uninfected.

In this model, increasing deer abundance can also increase the density of infected nymphs by increasing the tick birth rate (Fig. 1B). However, the relationship between deer abundance and the tick birth rate is highly uncertain because adult ticks may be able to increasingly concentrate bloodmeals on fewer deer (Deblinger et al. 1993) or alternate hosts as deer abundance declines. On islands or other geographically isolated regions without alternate reproductive hosts, deer are likely to have a larger impact than on mainland sites, where other species (i.e. medium/large mammals) can satisfy the need for reproductive hosts.

In contrast, the model suggests that nymphal infection prevalence is only weakly influenced by the tick birth rate (Fig. 1C) because the fraction of ticks that are infected depends primarily on the composition of the host community and only weakly on the abundance of ticks. This is consistent with observations that nymphal infection prevalence does not decline inside deer exclosures (Daneils et al. 1993), but does increase with small mammal abundance (Ostfeld et al. 2001, Tsao et al. 2004).

Temporal Correlations

We examined drivers of Lyme incidence in four states with large canid harvests (on the order of thousands or tens of thousands of animals), and with data on proxies of coyote and fox abundance. Harvests varied up to ten-fold as coyotes increased and foxes declined during the emergence of Lyme disease (Fig. 2). In Minnesota, fox hunter-harvest decreased 95% from a high of 78,000 in 1991 to a low of 4000 in 2008, while coyote harvest increased 2200% from a low of 2000 in 1982 to 46,000 in recent years. In Wisconsin coyote hunter-harvests increased 660% from a low of 6847 in 1984 to over 52,000 in 2009, while fox harvests decreased 80% from over 25,000 to under 5000 over that time. In Pennsylvania only 1810 coyotes were harvested in 1990, but harvests increased nearly 1600% to a high of over 30,000 in 2009. In Virginia, where Lyme disease cases have only recently increased (more than 300% increase from 2005 to 2007), coyotes have also increased only recently – averaging about 3000 in the 1990s, reaching nearly 10,000 in 2004, and increasing to a recent high of nearly 25,000 (Fig. S2).

Strong correlations between predator abundance and Lyme disease cases over the past 30 years were present in all four states (Fig. 2). In contrast, correlations between deer and Lyme disease were not significant or mixed in direction (Fig. 2) regardless of whether we scaled antlered-deer harvest by hunting license sales (Table S3-4). The best models, using a model selection approach based on an information theoretic criterion (Burnham and Anderson 2002), included measures of predator abundance for all four states whereas deer abundance was present in the best fitting model only in Virginia (Fig 2D).

Spatial Correlations

To test whether the spatial distribution of Lyme disease is correlated with the spatial distribution of deer or small mammal predators, we examined Lyme disease incidence in Wisconsin, Pennsylvania, Virginia, and New York. Across space, Lyme disease incidence did not consistently increase with deer abundance. Deer and Lyme incidence were negatively correlated in Wisconsin and Pennsylvania, positively correlated in Virginia, and uncorrelated in New York (Fig. 3C-F). In contrast, the spatial distribution of Lyme disease incidence in New York (the only state for which we had spatial data on predator abundance) is positively correlated with coyotes and negatively correlated with foxes (Fig. 4), which suggests a more important role for variation in the abundance of canids than deer (Fig. 4). Lyme disease is notably rare in western New York, where fox are abundant, despite having among the highest deer abundance in the state. It is worth noting that the nonlinear relationship between foxes and Lyme in Fig. 4 closely resembles model predictions (Fig. 1). Previously compiled data on catch-per-unit-effort of red fox by trappers and buck harvest density also corroborate this spatial relationship derived from harvest-independent data (Roberts 2008).

Temporal Correlations at Smaller Spatial Scales

Harvest-independent data from multiple regions of Wisconsin also suggest that Lyme incidence is more tightly linked to predator abundance than deer abundance. In Wisconsin, where Lyme disease incidence has increased greatly over the past decade, landowner wildlife surveys indicate that a fox decline and coyote increase occurred throughout the state (Fig. 5), which corroborates the statewide trends from hunter harvest data. Deer observations have been stable or declining over this period (Fig. 5), although due to high deer abundance, these surveys may be a less sensitive index for deer. However, on a fine spatial scale, deer density in management units with the highest Lyme incidence did not change over the last decade while Lyme disease cases increased 300% (Fig. S3). Deer densities have increased at most sites since the early 1980s (particularly until the mid 1990s), which possibly caused the initial emergence of Lyme disease. However, this increase has been patchy with one quarter of units showing no increase and several others increasing only a small percentage (Fig. S3).

Discussion

The increase in deer during the early twentieth century is thought to have allowed tick populations to grow and spread from small remnant populations. This likely contributed significantly to the initial rise in Lyme disease cases. However, in recent decades Lyme disease has continued to increase substantially in many places where deer populations have stabilized (Fig. 2, Fig 5, Fig. S3). Further, we detected no relationship between the spatial distribution of Lyme disease and deer abundance (Fig. 2). The poor correlation between changes in relatively abundant deer and Lyme disease incidence would be expected if the probability that an adult tick finds a host (e.g. deer) is a saturating function of host density (as it must be). To explore the hypothesis that the relationship between deer and Lyme disease risk (density of infected nymphs) saturates (i.e. further increases in already abundant deer have little impact on nymph abundance), we reanalyzed data from deer removal studies that recorded deer abundance and the response of nymphs (Deblinger et al. 1993). Deer abundance was a poor predictor of tick abundance (measured as nymphs per mouse) two years later (Fig. 3A), which did not decline despite great reduction in deer abundance. Similarly, reducing deer density from >90 km^{-2} to 10 km^{-2} at Bluff Point coastal reserve in Groton, CT only reduced tick density below 20 deer per km^{2} (Fig. 3B) (Stafford et al. 2003). Additionally, recent work from New York found no relationship between three-fold variation in deer abundance and the density of infected nymphs over 13 years (Ostfeld et al. 2006), and there was no response in nymph abundance to a recent deer culling program in New Jersey (Jordan et al. 2007). Thus, while there is convincing evidence linking deer to high nymph densities from deer exclosure studies, and from the complete or near complete deer removal on islands, linking variable deer abundance to ticks has been less successful, particularly at mainland sites where there are many other potential reproductive hosts for *Ixodes* ticks and where most Lyme disease cases are contracted (reviewed in Table S1).

At the same time, over the past three decades there has been a regional red fox decline coincident with an expanding coyote population. Both spatial and temporal evidence across multiple states suggest that these changes in predator abundance are more closely linked with increases in Lyme disease than are changes in deer abundance.

Our theoretical model suggested that changes in predation can in fact lead to the observed increases in Lyme risk, in that both the density and infection prevalence of nymphal ticks are sensitive to reduced predation (Fig. 1). Taken together with the empirical data on spatial and temporal patterns of Lyme incidence, deer and predator abundance, these results suggest that the red fox declines resulted in increased Lyme disease risk due to the loss of predation as an ecosystem service. Controlling Lyme disease might be accomplished by reducing deer densities to a sufficiently low level, but otherwise predator manipulation may be more effective.

More broadly, these results suggest a need to explore the role of predation in the community ecology of other emerging zoonotic diseases, which overwhelmingly rely on hosts that occupy low trophic levels (Ostfeld and Holt 2004). Due to the widespread eradication of large carnivores (Pinheiro et al. 2011), top predators in many terrestrial ecosystems are now medium sized carnivores such as coyotes (Connell 1980). These medium-sized carnivores can indirectly increase the abundance and diversity of low trophic level species, such as rodents and songbirds, by suppressing populations of smaller carnivores such as foxes (Crooks and Soule 1999). Strong interactions among predators that lead to cascading effects on prey have been documented for over 60 systems worldwide (Ritchie and Johnson 2009). As top predators are extirpated in some parts of the world, and recolonize in others, it will be important to understand the consequences for community composition and for low-trophic-level species in particular. Such restructuring of predator communities may have unintended consequences for human disease.

Methods

Host-Vector-Disease Model

We use a vector-borne, Susceptible-Infected (Kermack and McKendrick 1927) modeling framework that describes the dynamics of ticks, small mammal hosts, and includes parameters to account for the density of alternate hosts and deer. We group multiple species into a functional group of small mammal hosts with density, N_m. The small-mammal host population growth rate, $G(N_m)$, is logistic with maximum intrinsic growth rate r, and carrying capacity K. The mortality rate, $M(N_m)$, follows a Holling type III functional response, which is characteristic of generalist predation, with maximum predation rate, a, half-saturation parameter, c, and predator density, P (Murdoch 1969, Erlinge et al. 1983, Turchin 2003). The differential equation for the total host population is,

$$\begin{aligned}\frac{dN_m}{dt} &= G(N_m) - M(N_m) \\ &= rN_m\left(1 - \frac{N_m}{K}\right) - \frac{aPN_m{}^2}{c^2 + N_m{}^2}\end{aligned} \qquad (1)$$

The small-mammal host population consists of susceptible, S_m, and infected, I_m, classes. Susceptible hosts become infected with probability T_{mt} when bitten by an infected nymph, I_t. The tick bite rate, $\beta(N_m + F)$, follows a type II functional response with half saturation parameter, b_0, because ticks are expected to bite hosts as they encounter them rather than behaviorally switching their foraging strategies. A fraction of tick bites occur on incompetent “dilution” hosts, F, so that these hosts divert bloodmeals away from small mammals but also increase total host abundance. Each tick life stage only requires a single blood meal so that the functional response saturates at 1 as the abundance of hosts increases (i.e. if there are infinite hosts, all ticks can feed). Thus the tick bite rate can be interpreted as the fraction of ticks that successfully feed given the total hosts population, N_m+F. The small-mammal host population differential equations are,

$$\begin{aligned}\frac{dS_m}{dt} &= G(N_m) - T_{mt} I_t \frac{S_m}{N_m + F}\beta(N_m + F) - \frac{S_m}{N_m} M(N_m) \\ &= rN_m\left(1 - \frac{N_m}{K}\right) - \frac{T_{mt} I_t S_m}{b_0 + N_m + F} - S_m \frac{aPN_m}{c^2 + N_m{}^2}\end{aligned} \tag{2}$$

$$\begin{aligned}\frac{dI_m}{dt} &= T_{mt} I_t \frac{S_m}{N_m + F}\beta(N_m + F) - \frac{I_m}{N_m} M(N_m) \\ &= \frac{T_{mt} I_t S_m}{b_0 + N_m + F} - I_m \frac{aPN_m}{c^2 + N_m{}^2}\end{aligned} \tag{3}$$

,

Larval ticks, S_t, which are all susceptible, have birth rate ν and per-capita death rate μ_l. We use a constant birth rate than can be varied independently because it is unknown how vertebrate biomass and community composition influence the tick birth rate. Any larval tick that successfully feeds leaves this class so that the differential equation for larva is,

$$\begin{aligned}\frac{dS_t}{dt} &= \nu - \beta(N_m + F)S_t - \mu_l S_t \\ &= \nu - \frac{N_m + F}{b_0 + N_m + F} S_t - \mu_l S_t\end{aligned} \tag{4}$$

Nymphs die at rate, μ_n, and also leave their class by successfully feeding. Nymphs become infected when larva successfully contract *Borrelia* from an infected host (i.e. this depends on the frequency of infected hosts) with probability T_{tm}. Thus, the differential equation for infected nymphs, I_t, is,

$$\begin{aligned}\frac{dI_t}{dt} &= \frac{I_m}{N_m + F}\beta(N_m + F)T_{tm} S_t - \beta(N_m + F)I_t - \mu_n I_t \\ &= \frac{T_{tm} I_m S_t}{b_0 + N_m + F} - \frac{N_m + F}{b_0 + N_m + F} I_t - \mu_n I_t\end{aligned} \tag{5}$$

Uninfected nymphs, J_t, can either be uninfected because a larval tick fed on a susceptible or dilution host or because a larval tick fed on an infected host but did not contract *Borrelia*. The equation for uninfected nymphs thus has an additional term to account for the probability that feeding on an infected host did not cause infection, but can be simplified to,

$$\frac{dJ_t}{dt} = \frac{S_m + F}{N_m + F}\beta(N_m + F)S_t + (1 - T_{tm})\frac{I_m}{N_m + F}\beta(N_m + F)S_t - \beta(N_m + F)J_t - \mu_n J_t$$

$$= \frac{S_m + F + I_m(1 - T_{tm})}{b_0 + N_m + F}S_t - \frac{N_m + F}{b_0 + N_m + F}J_t - \mu_n J_t \tag{6}$$

We solved for the steady states as a function of the steady-state small mammal density $\overline{N_m}$. Therefore, the steady state solution to Eq. 1 provides the steady states of the epidemiologically relevant variables. The closed form solutions, which are presented in Supporting Information S2, explicitly demonstrate the strength of the known multiple drivers of Lyme disease.

Methods for Data Analysis

Spatial analysis in New York

Bow hunters spend many hours or days silently waiting for deer while perched in a tree. New York enlists them to survey wildlife and records their observation rates in wildlife management unit groupings. We averaged the observation rates of each species from 2005 to 2007 in each management unit to compare to Lyme disease incidence from 2006-2008. Lyme disease incidence is recorded at a county scale, so we allocated incidence to management units as a weighted average based on the relative area of each county in each wildlife management unit groupings.

Spatial analysis in Virginia, Wisconsin and Pennsylvania

In Virginia we used buck harvest per square mile reported in the Virginia deer management plan (Ellis 2007) as a proxy for deer density. Both the harvest data and Lyme disease data are on the county spatial scale. Wisconsin and Pennsylvania produce deer density estimates using the sex-age-kill model (Skalski et al. 2005), which estimates density in management units using data on harvest, age and sex structure, and fawn to doe ratios. Lyme disease incidence is recorded at a county scale. In Pennsylvania, wildlife management units are larger than counties so we allocated Lyme incidence to management units as above. In Wisconsin, wildlife management units are smaller than counties, so we allocated deer density to counties based on the relative area of each wildlife management unit in each county. For Wisconsin, we additionally analyze changes in deer densities since 1981 in twenty-five randomly chosen management units intersecting counties with the highest incidence (Fig. S3).

Time Series Methods

We use harvest-based proxies for white-tailed deer, coyote, and red fox abundance. To compare the populations of coyotes and foxes (hereafter grouped as canids) with annual Lyme disease cases, we use hunter-harvest (and hunter-harvest scaled by deer/big-game license sales) as a proxy for abundance. Any longitudinal changes in hunting effort are unlikely to be biased in favor of one of these species over another, suggesting that a decline in fox harvests and an increase in coyote harvests represent real population changes. Data on trapper harvest is more widely available but is not reliable because it is influenced by exogenous factors such as pelt prices and changes in trapping regulations designed to prevent incidental catch of high value or endangered species.

Many states, including the four we consider, have liberal coyote and fox hunting regulations including very long or continuous seasons and no bag limits. We therefore conduct our analysis on the subset of large states from which we could obtain hunter-harvest time series data: Wisconsin, Minnesota, Pennsylvania, and Virginia (New York does not collect hunter harvest data). The exception is Pennsylvania for which we have only total harvest (hunter + trapper) data, which are not as reliable an index for foxes but are likely representative of the population expansion of coyotes as they colonized the state.

As a proxy for deer abundance, we use antlered deer harvest, which is routinely used by wildlife management agencies to monitor trends in deer abundance. Antlered deer harvest is a robust estimate of the statewide deer population due to the large number of hunters that sample the deer population with success rates dependent on the abundance of deer. We scale antlered deer harvest by hunting license sales to capture changes in hunter participation (Fig. S4). Analysis of the hunter functional response from ten datasets supports a type I functional response (VanDeelen and Etter 2003), which suggests that hunter success rates are expected to increase linearly, rather than simply monotonically, with deer density. Longitudinal hunter-harvest data has been shown to correlate well with trends in deer density and has been used in the literature not only for crude population trends but also for more sophisticated time-series analysis (Picton 1984, Sand et al. 1996, Forchhammer et al. 1998, Mysterud et al. 2000).

Combining the available wildlife harvest time series, we evaluate the relative support of the predation and deer hypotheses. While there is reliable data on the number of deer hunters, there is no such data for fox and coyote hunters because small game hunters may focus on a variety of species, and individuals may only report that they are coyote hunters if they opportunistically kill a coyote, which often occurs incidental to other activities (Krause et al. 1969). However, using raw harvest data for canids is reasonable because there is no reason to suspect a directional bias that would force coyote harvests up and fox harvests down. We additionally analyze antlered-deer harvest data not corrected for license sales (Table S3) and harvests of deer, coyotes, and foxes all scaled by hunting license sales (Table S4) to ensure that our results are statistically robust to changes in hunter participation (Fig. S4). The strength of each candidate model was evaluated using corrected Akaike Information Criterion (Hurvich and Tsai 1989, Burnham and Anderson 2002).

Acknowledgements

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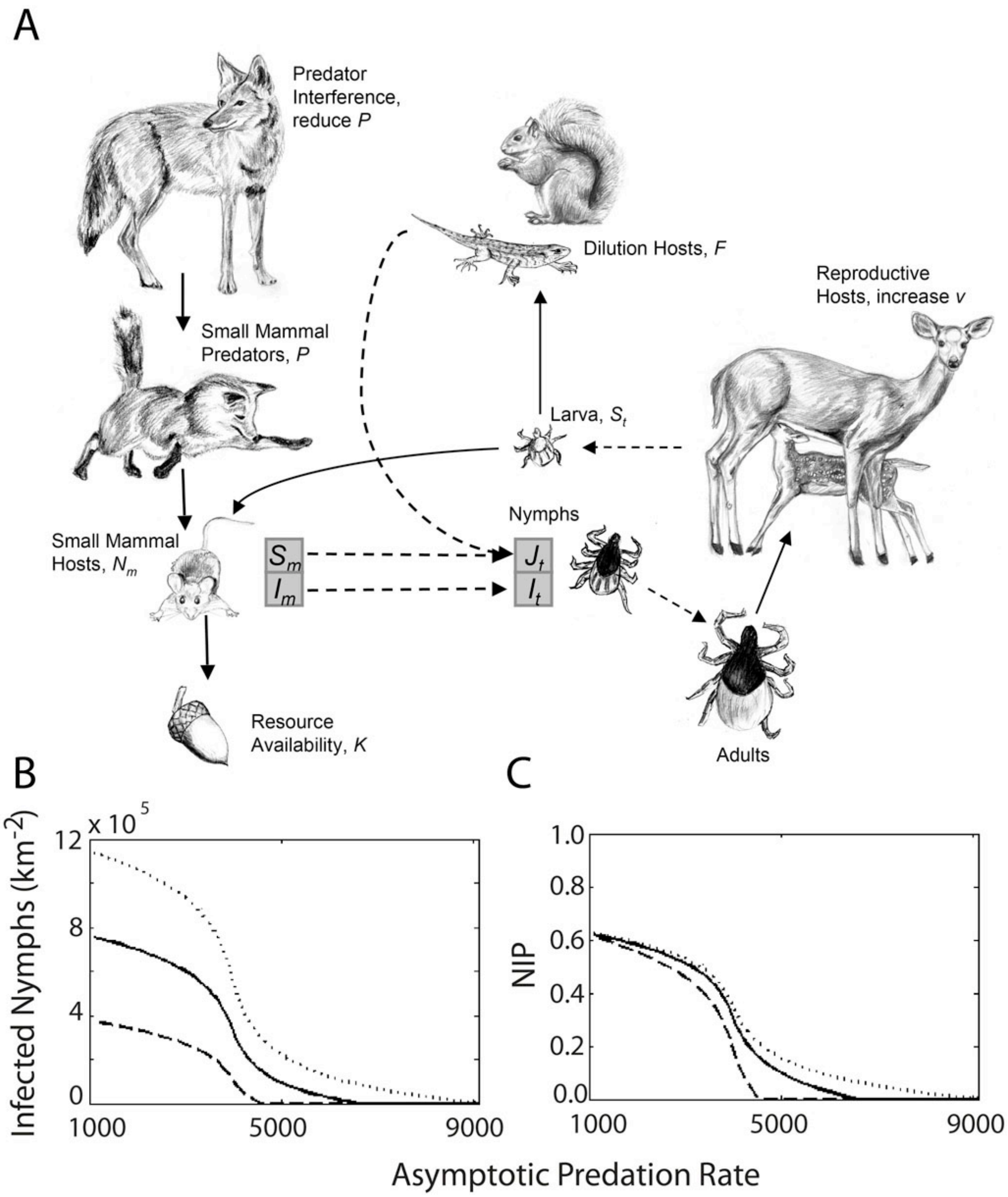
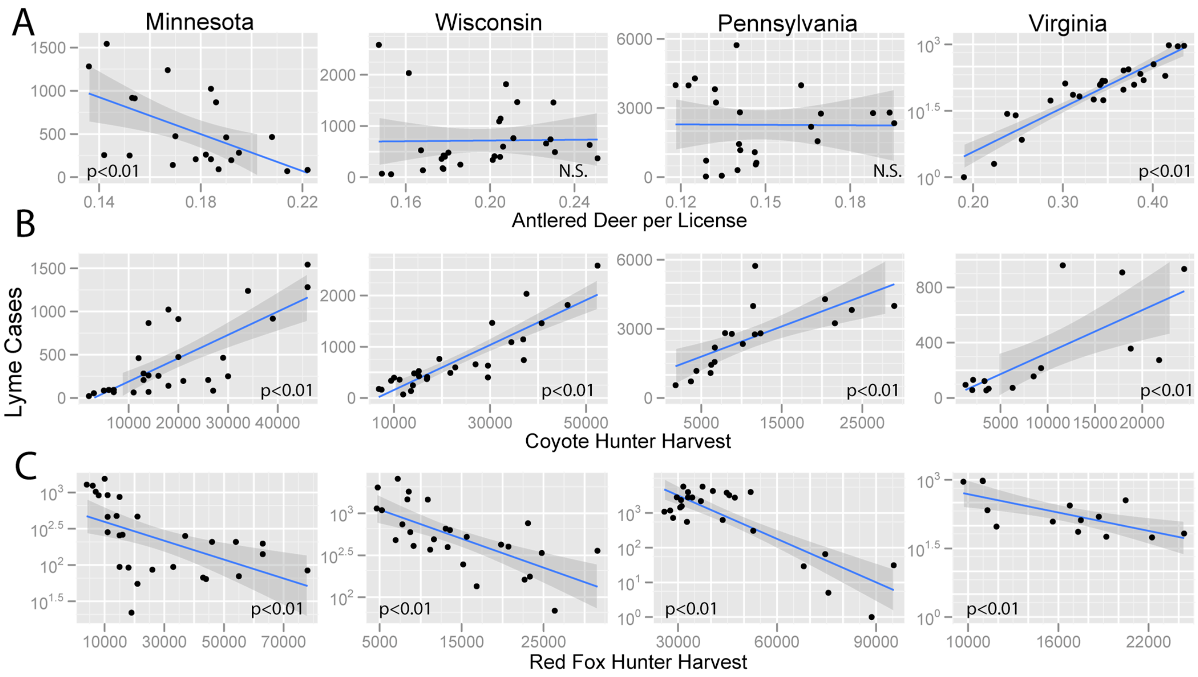


Figure 2.1 (A) A simplified web of interactions involved in the ecology of Lyme disease. Solid lines indicate negative interactions such as predation or parasitism. Dotted lines indicate resulting state transitions of ticks. Susceptible larva, S_t , infected nymphs, I_t , uninfected nymphs, J_t , and small-mammal hosts, N_m , broken into susceptible, S_m , and infected I_m , classes are dynamically modeled. The density of dilution hosts, *F*, and predators, *P*, are incorporated into the model with parameters. Reproductive hosts are included with a parameter for the birth rate of ticks ν. Our model uses ecologically realistic assumptions such as logistic population growth, a type II functional response for ticks, and a type III functional response for generalist predators. (B) The model reveals a sharp nonlinear increase in the density of infected nymphs (*DIN*) and (C) nymphal infection prevalence (*NIP*) as the maximum predation rate (predator density * their consumption rate as prey increase to infinity) declines.



D

Variable	R-2	ΔAICc	w
Coy+Fox	0.79	0.00	0.85
Deer +Coy+Fox	0.79	3.49	0.15
Fox	0.58	11.03	0.00
Deer+Fox	0.64	11.23	0.00
Deer+Coy	0.44	20.17	0.00
Deer	0.34	20.58	0.00
Coy	0.32	21.21	0.00

Variable	R-2	ΔAICc	w
Coy	0.73	0.00	0.37
Coy+Fox	0.75	0.11	0.35
Deer+Coy	0.74	1.55	0.17
Deer +Coy+Fox	0.76	2.60	0.10
Fox	0.47	17.94	0.00
Deer+Fox	0.47	20.59	0.00
Deer	0.07	33.19	0.00

Variable	R-2	ΔAICc	w
Deer+Coy	0.61	0.00	0.43
Coy	0.53	0.34	0.36
Deer+Coy+Fox	0.64	2.78	0.11
Coy+Fox	0.54	3.01	0.09
Fox	0.28	7.77	0.01
Deer+Fox	0.31	10.45	0.00
Deer	0.00	13.78	0.00

Variable	R-2	ΔAICc	w
Coy+Fox	0.83	0.00	0.39
Deer	0.76	1.14	0.22
Deer+Coy	0.81	1.77	0.16
Deer +Coy+Fox	0.87	2.00	0.14
Deer+Fox	0.79	3.22	0.08
Coy	0.66	6.01	0.02
Fox	0.47	12.07	0.00

Figure 2.2 Trends between Lyme cases and (A) deer harvest per license, the hunter-harvest of (B) coyotes, and (C) foxes are consistent with the predation hypothesis. As predicted by the model, the relationship between foxes and Lyme is nonlinear (Lyme cases are on a log-scale). (D) Statistical models were compared with AIC$_c$. Pennsylvania model selection is suspect because we only use data since 1990, the first year that coyote data were collected, and we use total harvest (hunter+trapper) rather than hunter harvest data.

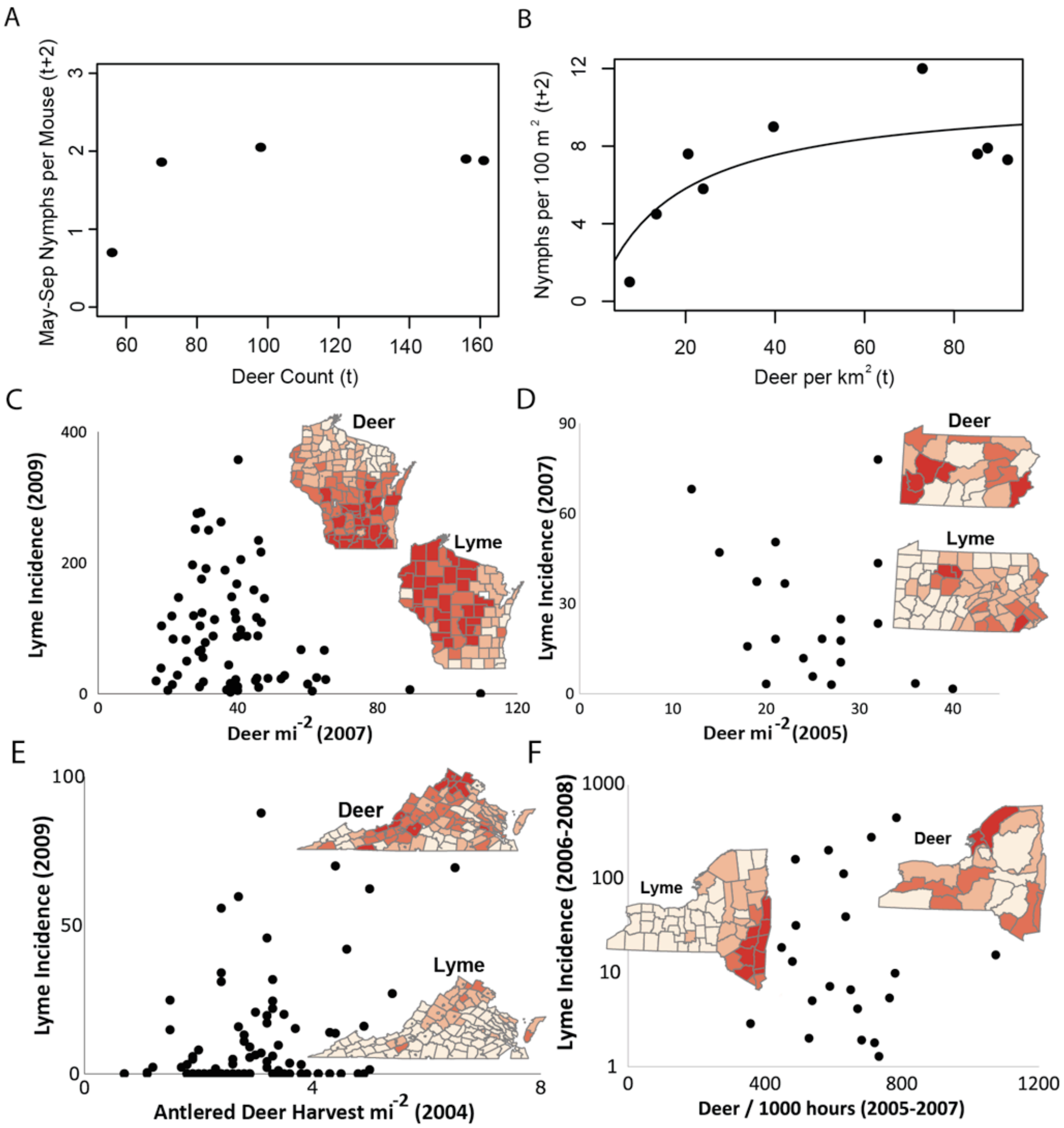


Figure 2.3 Relationships between deer and Lyme disease. (A) Response of *I. scapularis* nymphs, measured as nymphs per mouse, in response to deer removal experiment in Deblinger et al. 1993 (B) Nymph density (100 m^{-2}) as a function of deer density (per km^2) from Stafford et al. 2003. When all data are included there is a saturating relationship, but there is no significant relationship when one data point is removed (right panel) despite nearly ten-fold variation in deer density. (C) Deer as estimated by the buck harvest density are (A) positively correlated with Lyme disease incidence in Virginia counties (R^2=0.1, p=0.001), but (B) deer density estimates (from Sex-Age-Kill models) are negatively correlated with Lyme in Wisconsin counties (R^2=0.06, p=0.05, but driven by few data points-not significant when removed) and (C) negatively correlated in Pennsylvania deer management units (R^2=0.14, p=0.09), where the unit with the lowest deer density has the second highest Lyme incidence. In all states hyperabundant deer do not guarantee Lyme.

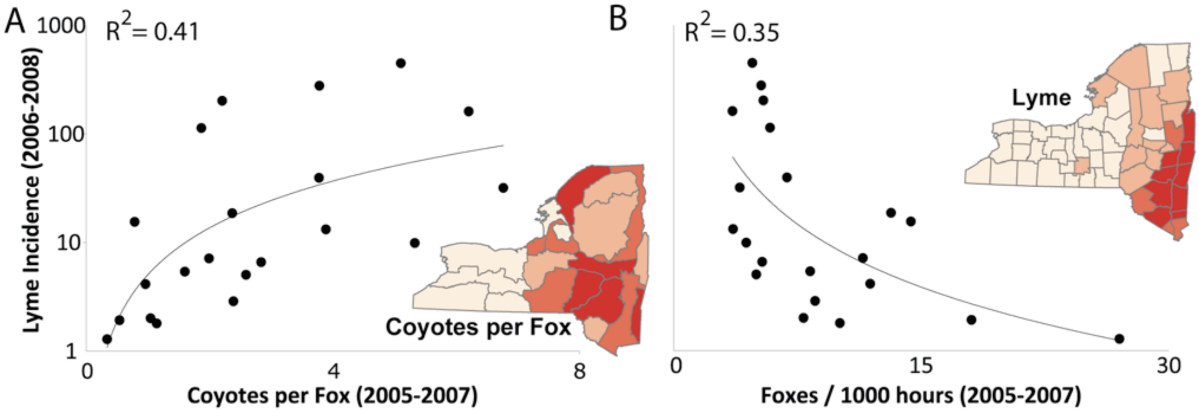


Figure 2.4 In New York, observation rates from the bow hunter wildlife survey indicate that Lyme disease incidence (cases per 100,000) is (A) positively correlated with coyotes, (B) negatively correlated with foxes, and (C) unrelated to deer. Coyote observations are scaled by foxes to highlight the transition in the canid community and its impact on Lyme. Darker red on inset maps indicates more abundant wildlife populations and higher Lyme incidence (in four classes: 0-10, 10-50, 50-100, >100 cases per 100,000).

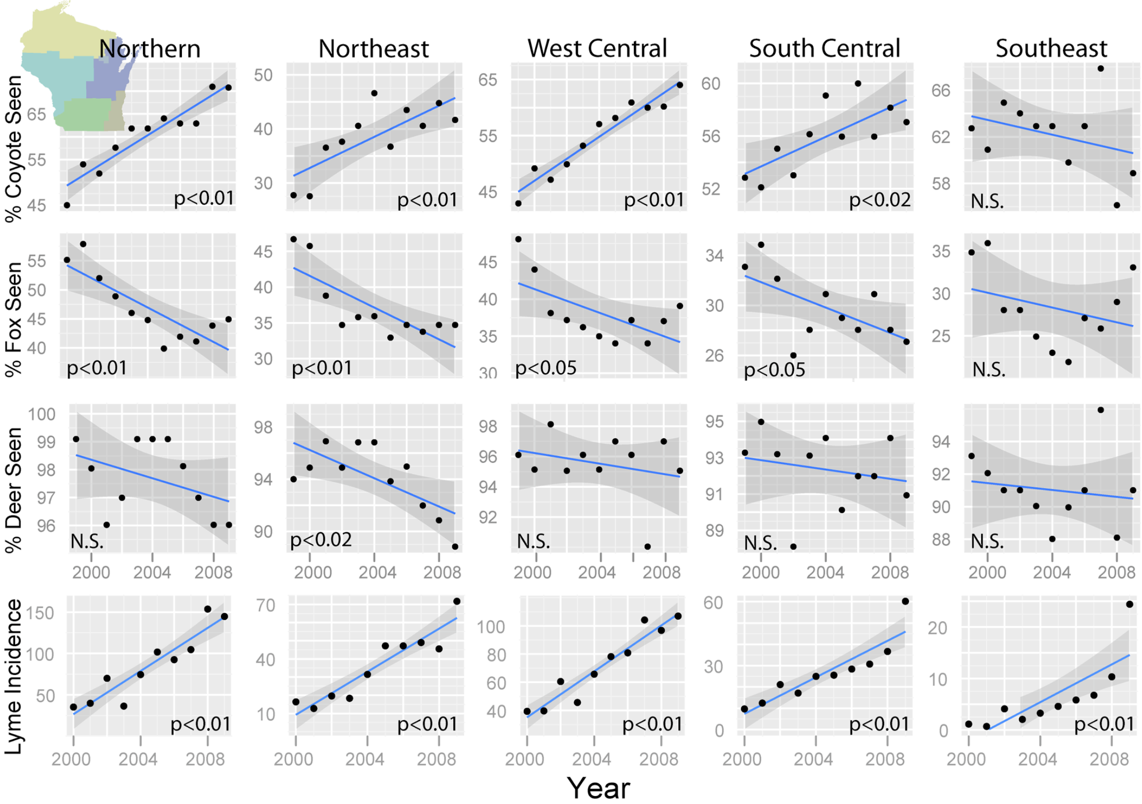


Figure 2.5 The percent of surveyed rural landowners who saw coyotes, foxes, and deer in five geographic regions of Wisconsin from 1999 to 2009 according to the annual *Summer Wildlife Inquiry* run by the Department of Natural Resources. Lyme incidence in each region is the weighted average (by area) of county-level incidence.

Chapter 2: Supplementary Information

S1. Parameters and Derivations

Although our analysis is qualitative and we produce closed form solutions, we nevertheless find plausible parameter values to see if reasonable levels of predation can influence Lyme disease.

F: We estimate the density of noncompetent dilution hosts following LoGuidice et al. (1). We sum the density estimates of dilution hosts to obtain $F \sim 4120$. We ignore the fact that dilution hosts are somewhat reservoir competent because of evidence that 80-90% of ticks are infected by a few small mammal species (2). We thus consider a class of dilution hosts rather than considering the variability among hosts. The nonzero infectiousness of dilution hosts can prevent complete *Borrelia* extinction even when small mammals are rare, but this does not impact the qualitative relationship between predation and Lyme disease risk.

***b_0*:** We use tick densities estimated with mark-recapture techniques (3) to estimate the half saturation parameter of the tick functional response, b_0.

Daniels and colleagues (3) found larval densities of roughly 11,500,000 km^{-2} and nymph densities of 1,200,000 km^{-2}. The nymph population was approximately 10% of the larva population. We reason that at least 10% of larva successfully fed, allowing us to estimate b_0.

$$\beta(N_m + F) = \frac{N_m + F}{b_0 + N_m + F} = 0.10$$

Following LoGuidice and colleagues (1), the reservoir competent small mammal density (N_m) ranges from 5000 km^{-2} to 200000 km^{-2} . To estimate b_0, we use an intermediate (non-resource pulse) value of 10000 km^{-2}. Substituting in F and solving for b_0, a reasonable estimate of b_0 is approximately 80000, meaning that half of ticks are expected feed if the total host population ($N_m + F$) is 80000 km^{-2}.

aP and *c*:

One classic study (4) quantified the impact of generalist predators on two species of small mammals over 40km^2 in Southern Sweden. This study found that generalist predators were responsible for far more predation on voles and wood mice than specialist predators. We use predation rate data from this study to fit the parameters *aP* and *c*. A precise estimate of *aP* is not necessary because we explore the steady states of the differential equations as a function of a variable maximum predation rate, *aP* (Fig. 1B-C, Fig. S3). We thus only need a reasonable half-saturation parameter. Although this study comes from Sweden, the predator community is similar to that of the Northeastern United States with red foxes being the dominant predator of small mammals.

We fit the per capita predation rate $\frac{aP \cdot N}{c^2 + N^2}$ (a type III functional response divided by N) to the data with and without two potential outliers. These data come from monthly predation rates that should show considerably more variation than annual predation rates because annual measures smooth over seasonal and stochastic variability. The best estimate of *aP* is 241,391 per 40 km^2 which is equivalent to 6,034 annual kills per km^2.

S2. Steady State Solutions

The steady states are given by,

$$\overline{S_t} = \frac{\nu\left(b_0 + \overline{N_m} + F\right)}{\overline{N_m} + F + \mu_l\left(b_0 + \overline{N_m} + F\right)} \tag{S1}$$

$$\overline{I_t} = \overline{N_m}\left(b_0 + \overline{N_m} + F\right)\left(\frac{T_{tm}\nu}{\left(\overline{N_m} + F + \mu_l\left(b_0 + \overline{N_m} + F\right)\right)\left(\overline{N_m} + F + \mu_n\left(b_0 + \overline{N_m} + F\right)\right)} - \frac{aP}{T_{mt}\left(c^2 + \overline{N_m}^2\right)}\right) \tag{S2}$$

$$\overline{J_t} = \overline{N_m}\left(b_0 + \overline{N_m} + F\right)\left(\frac{\nu\left(1 - T_{tm} + \frac{F}{\overline{N_m}}\right)}{\left(\overline{N_m} + F + \mu_l\left(b_0 + \overline{N_m} + F\right)\right)\left(\overline{N_m} + F + \mu_n\left(b_0 + \overline{N_m} + F\right)\right)} + \frac{aP}{T_{mt}\left(c^2 + \overline{N_m}^2\right)}\right) \tag{S3}$$

$$\overline{S_m} = \frac{\left(\overline{N_m} + F + \mu_l\left(b_0 + \overline{N_m} + F\right)\right)\left(\overline{N_m} + F + \mu_n\left(b_0 + \overline{N_m} + F\right)\right)aP\,\overline{N_m}}{\left(c^2 + \overline{N_m}^2\right)T_{mt}T_{tm}\nu} \tag{S4}$$

$$\overline{I_m} = \overline{N_m}\left[1 - \frac{aP\left(\overline{N_m} + F + \mu_l\left(b_0 + \overline{N_m}\right)\right)\left(\overline{N_m} + F + \mu_n\left(b_0 + \overline{N_m}\right)\right)}{\left(c^2 + \overline{N_m}^2\right)T_{mt}T_{tm}\nu}\right] \tag{S5}$$

All quantities are restricted to be nonnegative, and the abundance of any one class of either hosts or ticks is restricted to be less than the total abundance of hosts or ticks.

The infection prevalence of hosts (*HIP*) and nymphs (*NIP*) both decrease with predation and alternate hosts, but increase with the tick birth rate:

$$HIP = 1 - \frac{aP\left(\overline{N_m} + F + \mu_l\left(b_0 + \overline{N_m} + F\right)\right)\left(\overline{N_m} + F + \mu_n\left(b_0 + \overline{N_m} + F\right)\right)}{\left(c^2 + \overline{N_m}^2\right)T_{mt}T_{tm}\nu} \tag{S6}$$

$$NIP = \frac{\overline{I_t}}{\overline{I_t} + \overline{J_t}} = T_{tm} \frac{\overline{N_m}}{\overline{N_m} + F} \left(1 - \frac{aP\left(\overline{N_m} + F + \mu_l \left(b_0 + \overline{N_m} + F\right)\right)\left(\overline{N_m} + F + \mu_n \left(b_0 + \overline{N_m} + F\right)\right)}{\left(c^2 + \overline{N_m}^2\right) T_{mt} T_{tm} \nu} \right) \tag{S7}$$

Combining equations S6 and S7, we recover the intuitive result that relates the nymphal infection prevalence to the infection prevalence of hosts,

$$NIP = \frac{\overline{I_t}}{\overline{I_t} + \overline{J_t}} = T_{tm} \frac{\overline{N_m}}{\overline{N_m} + F} HIP \tag{S8}$$

The fraction of hosts that are reservoir competent determines the relationship between host infection prevalence and nymphal infection prevalence.

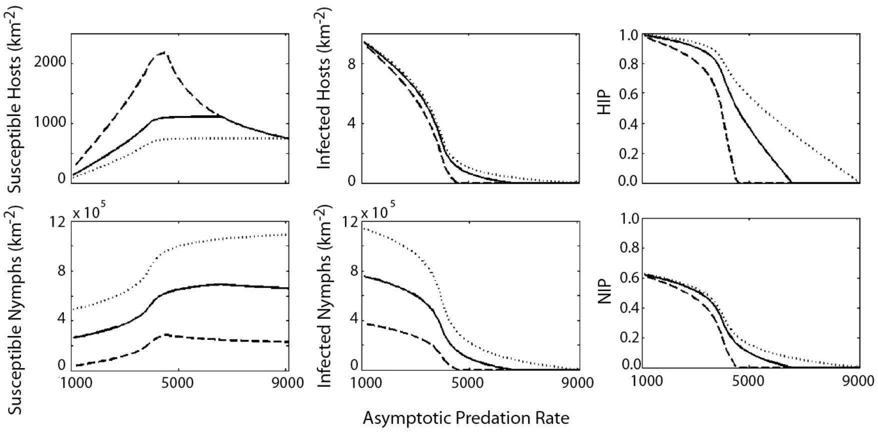


Figure 2.S1. Steady states of the different equations, and steady state host and nymph infection prevalence (HIP and NIP), as a function of the asymptotic maximum predation rate.

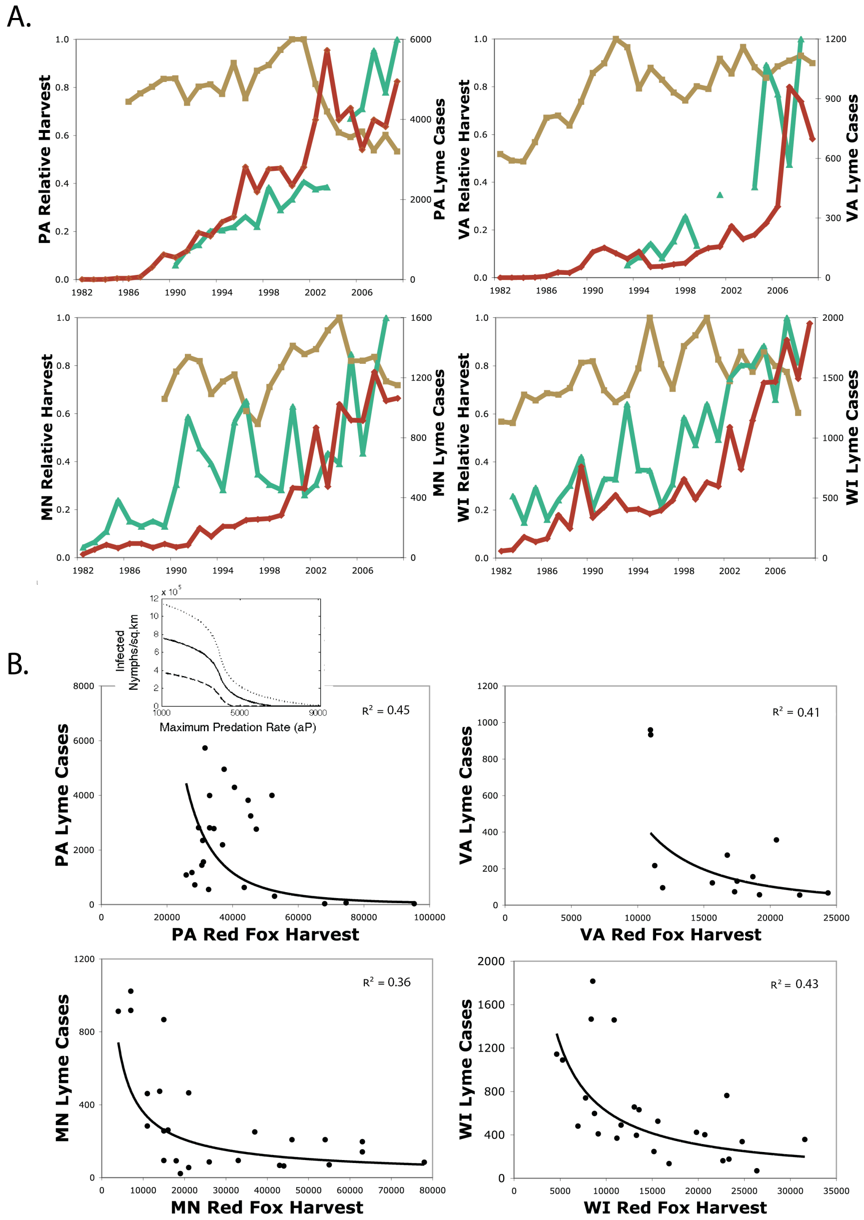


Figure 2.S2. (A) Annual Lyme disease cases (red diamonds) and the hunter-harvests of coyotes (green diamonds) and antlered deer (brown squares) scaled to the fraction of maximum harvest in Pennsylvania (PA), Virginia (VA), Minnesota (MN), and Wisconsin (WI) (PA data includes trapper harvest). The maximum coyote harvest exceeds 20,000 in PA and VA, and 40,000 in WI and MN, and the maximum buck harvest exceeds 100,000 in all four states and 200,000 in PA. (B) Lyme disease incidence vs. red fox abundance, fit with a power function, follows the relationship predicted by our theoretical model (inset). The inset shows the steady state density of infected nymphs as a function of the predation rate for low, medium and high tick birth rates.

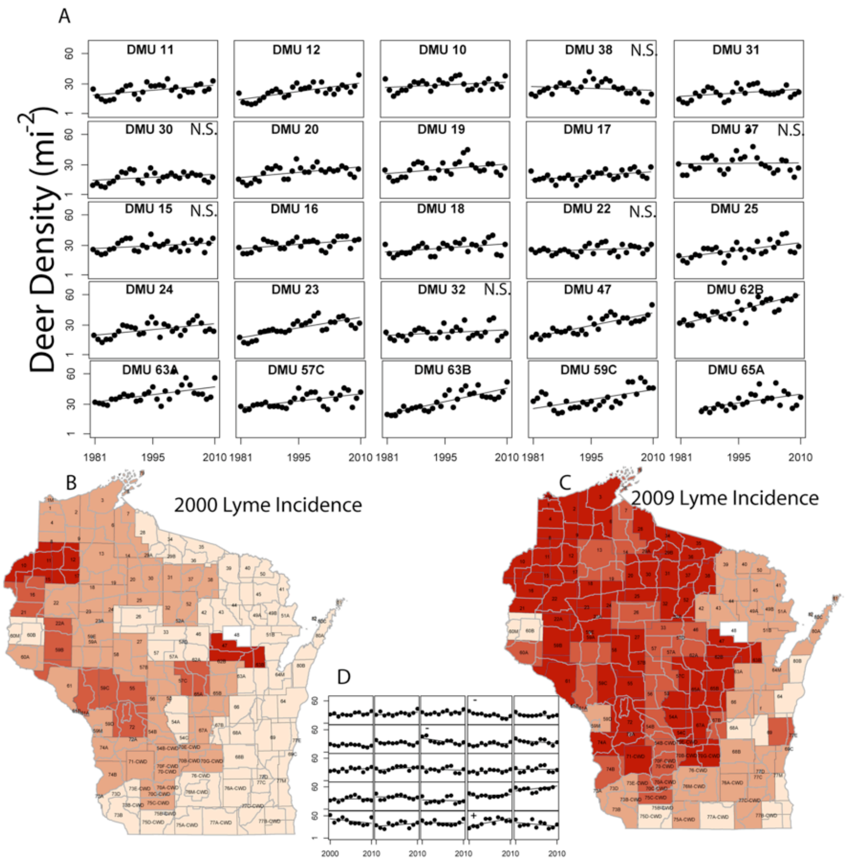


Figure 2.S3. (A) Deer Density in a sample of 25 management units where Lyme disease incidence is highest in Wisconsin. Deer density has increased substantially in some cases, but deer have been abundant since the early 1980s, and in many units deer populations have been stable or only slightly increasing despite a great increase in incidence since 2000. The six units that have shown no significant increase since 1981 are labeled "N.S." (B-C) Shades of red indicate Lyme incidence from 0-10, 10-50, 50-100, and > 100 cases per 100,000. (D) In the same management units, there has been no change in deer densities over the past decade in twenty-two of the twenty five units, a decrease in two and an increase in one. Significant changes are labeled "+" and "-".

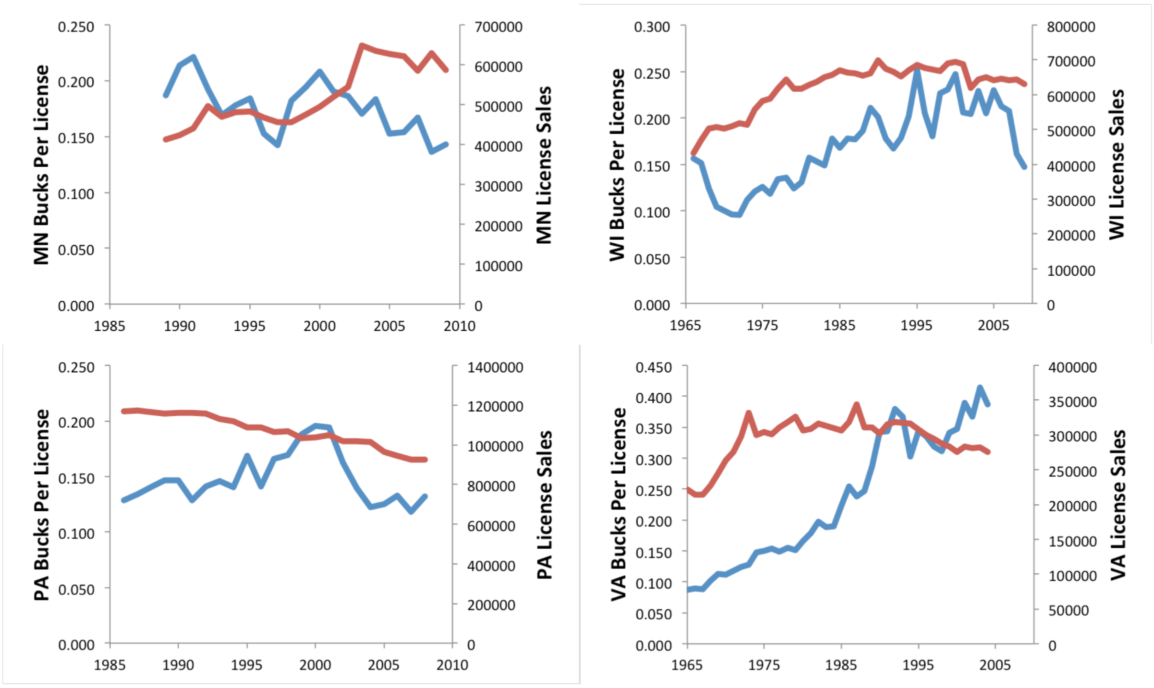


Figure 2.S4. Buck harvest per license (blue) and license sales (red) in MN, WI, PA, and VA. We have included data farther into the past from VA and WI so that the long period of deer population increase (particularly in VA) can be seen in the harvest data.

Chapter 3

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

Abstract

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

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. Our study area in the rainforests of southeastern Peru, Manu National Park, is inhabited by Matsigenka indigenous people.

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

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 modeling 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 response is to negotiate limits on the establishment of new settlements in return for development aid (e.g., schools) in existing settlements. The latter's advantages is that settlement numbers are more easily monitored than is hunting effort or technology. Similar policies could help reduce landscape-scale depletion of prey species in human-occupied reserves and protected areas throughout the Amazon.

Introduction

Most of the Amazon Basin is accessible to hunting (Peres and Lake 2003), and almost all Amazonian protected areas, from indigenous territories and extractive reserves to national parks, are occupied by human populations (Brandon et al. 1998b, Terborgh and Peres 2002). Hunting threatens the persistence of large vertebrates and the loss of their ecological functions (Peres and Palacios 2007a). Large primates—keystone seed dispersers upon which much plant diversity depends (Terborgh et al. 2008b)–are especially threatened (Peres 1990).

Conversely, game species are themselves an ecological benefit, providing protein and income for millions of forest-dwelling humans. In the Brazilian Amazon, the annual wild-meat harvest is estimated to exceed 89,000 tons (Peres 2000a). Moreover, under some conditions, forest dwellers can prevent forest conversion to industrial agriculture and logging, especially in indigenous territories (Schwartzman and 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 localized depletion around a settlement and defaunation on a large spatial scale. With regards to ecosystem collapse, it is the latter that we are concerned about, but empirical hunting studies are typically small-scale, limited to ≈300 km^2 hunting zones and one or two years (Alvard et al. 1997, Bodmer et al. 1997, Sirén et al. 2004, Peres and Nascimento 2006, Ohl-Schacherer et al. 2007a, Smith 2008). The problem with local studies is that if we want to explore the effect of human population growth, we cannot just increase offtake in a linear fashion and recalculate the sustainability index. Aside from the errors that plague such indices (Milner-Gulland and Akçakaya 2001b), the relationship of offtake to hunter number is not straightforward. For instance, adding more hunters to a village increases pseudointerference, reducing per-hunter offtake.

Thus, if we wish to explore the long-term effects of different management options on hunting sustainability, we must 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 southeastern 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 manioc 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 Matsigenka reside in isolated settlements in the Manu headwaters, and there are unknown numbers of additional uncontacted hunter-gatherers.

Almost all Matsigenka 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 shotgun use, despite contravening park regulations. Moreover, improved health care and immigration from isolated 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. 2007a, Shepard et al. in press). Suggesting that "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 1999a). In this context, we carried out an empirical study to assess the impacts of subsistence hunting on Manu's wildlife (Ohl-Schacherer et al. 2007a), and we here develop a model to evaluate future scenarios of faunal depletion.

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 et al. 2005), and are keystone dispersers of many tree species (Terborgh et al. 2008b). Several studies demonstrate that spider monkeys can serve as an indicator species, since forests containing viable populations will generally contain other large vertebrates (see Peres 2000 for a survey of Amazon forest sites over 10 years; see also Ohl-Schacherer *et al.* 2007; Smith *et al.* 2008; Bodmer and Lozano 2001; 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 timescale than the time necessary for spider monkey populations to become depleted. Hunting studies in Amazonia covering the range of technological and demographic change that we consider in our model reveal similar maximum hunting distances (~10km radius), regardless of the state of spider monkey populations [e.g., compare gun hunters in Alvard *et al.* (1997) and Smith (2008) to 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 use four information sources: (1) a game-offtake dataset from four Matsigenka settlements (Oct 2004 – Oct 2005; 102,397 consumer days: (Ohl-Schacherer et al. 2007a)), (2) a hunting foray dataset in which hunters recorded observed and pursued animals in addition to those killed (Nov 2004 – Dec 2005; 619 forays across 56 hunters: (Ohl-Schacherer et al. 2007a)), (3) a terrestrial-vertebrate density dataset in which linear "Distance sampling" transects (Buckland et al. 1993b) were run in five unhunted sites in Manu and within the hunting zones of the Tayakome and Yomybato settlements using Matsigenka hunters as spotters (Jan 2006 – Aug 2006, authors' unpublished data, Supplementary Material S1), and (4) a demographic dataset of the studied Matsigenka communities (authors' unpublished data, Supplementary Material 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 modeled as a Gaussian centered on the settlement, reflecting the decline of 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. 2007a) and so do not focus exclusively on spider monkeys, but since spider monkey is highly desired, they are nearly always pursued when encountered (authors' personal observations; see Shepard 2002). Fission-fusion groups of spider monkeys exhibit territoriality and site fidelity over large "community" home ranges, so their dispersal into hunting zones can be modeled as a diffusion process. The result is that hunting creates depletion zones, and our objective is to project the growth and spatial arrangement of those zones as a function of the growth and spread of Matsigenka settlements, which are determined exogenously.

Using the model outputs, we explore realistic 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 et al. 2005b).

The Model

We construct a 2-dimensional 140 x 95 km (13,300 km^2) array of bins (Fig. 1), where each bin represents 1 km^2, holding a value for the density of spider monkeys, N. The array is smaller than the actual park size 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, $N_{x,y,t}$ (for clarity, dependence of N on x,y is suppressed.). N_{t+1} is a function of population growth $R(N_t)$, migration $M(N_t)$, and offtake, which is itself a function of both spider monkey and human populations $O(N_t,p_t)$.

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

Prey population growth

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

$$R(N_t) = rN_t(1 - \frac{N_t}{K}) \tag{2}$$

where $r = 0.07$ is the maximum intrinsic growth rate (Robinson & Redford 1991), and $K = 25$ 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), where spider monkeys have been studied (Symington 1988), and densities regularly 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 $O(N_t, p_t)$, 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,

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

The encounter rate term, $E_{x,y,t}$, is determined by spider-monkey density. To estimate $E_{x,y,t}$, we effectively run a linear transect in reverse. Normally, in "Distance sampling" transects, the "cluster"-encounter rate, $E_{x,y,t}$, of terrestrial vertebrates at each (x,y,t) is converted to a group density and then multiplied by the average cluster size *CSz* to get individual density, $N_{x,y,t}$,

$$N_{x,y,t} = \frac{E_{x,y,t} \times CSz}{2\left(ESW + \frac{CSp}{3}\right)} \tag{4}$$

where *ESW* is the effective strip width on one side of a census trail, calculated using the distribution of observation distances perpendicular to the trail (Buckland et al. 1993b), and *CSp* is an estimate of social cluster areal "spread," routinely used in primate censuses to correct for density overestimates of large, uncohesive group-living primates (Peres 1999). We use clusters as our detection unit because spider monkeys forage in subgroups. *ESW*, *CSz*, and *CSp* are estimated empirically from transects, with Matsigenka hunters as spotters (Table 1, Supplementary Material S1). We solve Eqn. 6 for $E_{x,y,t}$, from each bin's density $N_{x,y,t}$, meaning that we convert each local density into an expected hunter-encounter-rate of clusters.

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 Supplementary Material 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). As noted above, empirical studies tell us that the set of walking distances (from the settlement centre to the return point) is normally distributed. Thus, hunting effort (km walked) is modeled as a two-dimensional Gaussian centered on each settlement.

This is not a trivial task, because our Cartesian (*x*-*y*) coordinate system does not lend itself to modeling hunter trajectories that emanate from a single starting point. Consider a bin at location (x, y) and a community at $(x_{0,i}, y_{0,i})$. The distance *s* from the community to the bin is $s = \sqrt{(x_{0,i} - x)^2 + (y_{0,i} - y)^2}$.

We use a polar coordinate system (radius *r*, angle θ) to find the probability that a hunt is walked past *s* distance units. To do this, we first convert the area integral of the bivariate normal distribution (with $\sigma = \sigma_x = \sigma_y$) into polar coordinates.

$$\iint \frac{1}{2\pi\sigma^2} \exp\left[-\frac{1}{2\sigma^2}\left(x^2 + y^2\right)\right] dxdy = \iint \frac{r}{2\pi\sigma^2} \exp\left[-\frac{r^2}{2\sigma^2}\right] drd\theta \tag{5}$$

The probability 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, 2π).

$$\begin{aligned} &\int_0^{2\pi}\int_s^{\infty} \frac{r}{2\pi\sigma^2} \exp\left[-\frac{r^2}{2\sigma^2}\right] drd\theta \\ &= \exp\left(\frac{-1}{2\sigma^2} s^2\right) \end{aligned} \tag{6}$$

We treat the above term as the fraction of hunts that walk at least *s* distance units. However, 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 center so that no more than the total number of hunts go through the settlement center. This scaling method is, however, an approximation, but it gives estimates close to the true value without requiring numerical integration (Supplementary Material S3, authors' unpublished data). Using the approximation, total annual effort at (*x,y,t*) is

$$h_{x,y,t} = hphy \sum_{i=1}^{settlements} p_{i,t} \cdot \exp(\frac{-1}{2\sigma^2}((x_{0,i} - x)^2 + (y_{0,i} - y)^2)) \frac{1}{2\pi\sqrt{(x_{0,i} - x)^2 + (y_{0,i} - y)^2} + 1} \quad (7)$$

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) in settlement *i* at time *t*. σ 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, since the trajectories are 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 neighboring bins and that the rate of doing so is faster the greater the density difference between bins. Thus, migration is given by

$$M(N) = D \times \nabla^2 N \quad (8)$$

where D is the diffusivity constant (distance^2/time), which must be estimated, and ∇^2 is the Laplace operator, which gives the density gradient, and which in two dimensions is

$$\nabla^2 N = \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \qquad (9)$$

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 2-dimensions. The values of the four nearest neighbors (up, down, left, right) are used to approximate derivatives on a grid. For bins 1-km across, and for a one-year time step, the approximation is

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

At the boundaries of our array, we set the perimeter bins equal to K (a Dirichlet boundary condition).

Parameter estimation

We explore the future dynamics of hunting by generating possible scenarios along which the Matsigenka may develop. Wildlife populations are affected by five factors: the range of distances walked by hunters (σ), human population growth (i.e., the male population at hunting age, 14-49), human population spread (new settlements), hunting effort (hunts/hunter/year, *hphy*), and hunting technology (shotguns vs. arrows, d_r) (Table 1). The estimation process is described in Supplementary Material S4.

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 without respect to current park zoning. Note that the latter assumes total non-governance in Manu Park such that indigenous communities are allowed to occupy portions of the middle and lower Manu River currently zoned for tourism and scientific investigation and off-limits for indigenous settlements. This scenario overestimates the long-term spread of Manu's indigenous inhabitants.

Both scenarios are initialized by following the historical trajectory of population growth and settlement spread from 1960 to 2008 (Shepard et al. in press), hunting only with bow-and-arrow. Demographic data were compiled and analyzed using *Community Express* software V.2.0 (www.communityexpress.info). The Matsigenka population in Manu Park and adjacent tributaries was contacted by missionaries and settled at the single-family settlement of Tayakome in the early 1960s. The hunting model therefore starts with the original family at Tayakome surrounded by an unhunted spider monkey population. The settlement population is increased to simulate the arrival of missionary-contacted families, followed by natural population growth using the actual demographic data. About half the Matsigenka population of Tayakome left when the missionaries were expelled upon the park's establishment in 1973 (Shepard et al. in press). Another settlement, Yomybato, was established in the late 1970s. Other settlements have since fissioned from the main communities, and immigrants have arrived from outside the park and from isolated settlements in the Andean foothills, which we exclude from our model because of the distinctive environmental conditions (Fig. 1). Year-to-year population growth in these settlements was simulated using actual birth, death, and life history records from the demographic database. Immigrants from the isolated settlements to our study communities were added as new migrants from outside the system.

Our demographic dataset allows us to track the number of hunters (male, ages 14-49) 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 the number of hunters (Supplementary Material S2). In the SEDENTARY scenario, the 2009 population (131 hunters) is immediately distributed evenly amongst the 6 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 (6 existing plus 7 hypothetical settlements) throughout Manu Park. Both scenarios then grow at the current rate for 50 more years, to 770 hunters ($n_{tot} = 3560$). 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 also gauge 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. Following the model into the future, 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 timescale over which this occurs, we calculate the catch-per-unit-effort (CPUE) through time for a gun-only scenario vs. an arrow-only scenario, where effort is measured as total km walked. In both scenarios, runs are initialized as above and grown according to the same age-structured matrix until 2059. Average yearly hunting effort (*hphy*) is varied between 40 and 80, and the diffusivity of monkeys, *D,* ranges from 0.2 to 1.0 (Supplementary Material S4).

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 color 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 km^{-2}) 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*). In contrast, if hunting technology is 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 the number of settlements 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 to the SEDENTARY scenario (corresponding upper-left panels in Figs 2a vs 2b, Fig. 3); because 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 population viability in Manu Park over the next 50 years, but does produce localized areas of depletion.

In contrast, spreading shotgun hunters across the park does increase the proportion of defaunated landscape (corresponding mid and lower panels in Figs 2a vs 2b, Fig. 3). Even small numbers of hunters wielding shotguns can deplete local populations. Thus, spreading the population across more settlements simply increases the number of areas emptied by hunting. Furthermore, where communities are sufficiently close so that their hunting zones begin to overlap (~ < 20 km apart), contiguous regions of local extinction are created (mid and lower panels in Fig. 2ab), which decreases the perimeter available for monkey immigration. Since 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 (*hphy*) increases depletion in all scenarios (compare left to right panels in Figs 2 & 3). Total hunts per year is the product of *hphy* and the number of hunters. Using a higher value of *hphy* thus provides a more conservative scenario, correcting for a number of potential underestimates in the model, e.g., not counting kills made on return trajectories of hunting forays or underestimating the human population growth rate (Supplementary Material S2).

It is also important to understand that shotgun hunting would be expected to reduce the considerable observed variation in hunting skill observed among Matsigenka bow hunters (Supplementary Material S4). Less skilled bow hunters hunt less effectively and less frequently, and many hunters killing no spider monkeys. We therefore expect that the introduction of guns should make all Matsigenka men more effective *and* more frequent hunters. Thus, to get a realistic sense of the long-term impact of a switch to shotguns, the more relevant comparisons are between low-*hphy* bow-and-arrow and high-*hphy* gun scenarios (Fig. 3). In summary, gun use should increase not only the killing rate d_r but also hunting effort *hphy*, leading to much greater depletion.

Catch-per-unit-effort and source-sink dynamics

During 50 years of human population growth in each settlement, the catch per unit effort (CPUE) in the gun-hunting scenario starts high and decreases steeply as spider monkey populations are "mined." CPUE then stabilizes at a level at or below that modeled in the bow-hunting scenario (Fig. 4). CPUE for bow hunters is also projected to decline over time, but not nearly as steeply. The larger the settlement, the more transient the advantage of using guns (Fig. 4); in the two main settlements of Tayakome and Yomybato, with populations of ~200 people, the harvest advantage (CPUE) of guns is predicted to disappear in <10 years, with most of the advantage disappearing in the first few years. This has an important implication. Although we assumed a wholesale switch to guns in the first year of our simulations (2009), the more realistic scenario is gradual adoption. However, even gradual adoption will still cause rapid reduction in CPUE because a small numbers of gun hunters in a large settlement is similar to wholesale gun adoption in a small settlement, the latter of which causes rapid depletion.

We also present the estimated historical CPUE trajectory for Yomybato from 1988 to 2006 (Fig. 5), during which time the hunter population more than doubled from 21 to 54. Despite the fact that spider-monkey offtake is thought to have exceeded the maximum sustainable yield in the hunting zone since at least 1988 (Alvard et al. 1997, Ohl-Schacherer et al. 2007a), the estimated CPUE trajectory 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 80% (Ohl-Schacherer et al. 2007a), 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 modeling framework allows us to incorporate and grow multiple human settlements, allow overlapping hunting zones, and project game offtake and depletion over a landscape through time. This method converts assessments of sustainability from a yes-or-no question for fixed amounts of habitat and offtake, which is the approach taken when using a sustainability index, (e.g., Robinson and Redford 1991) to quantified levels of depletion that can be projected over time and space and visualized on spatially explicit landscapes.

Over the next half 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 by the Matsigenka is unlikely to threaten other large vertebrate species over most of Manu in the next half century (Figs 2 & 3), with the possible exceptions of some rare and patchily distributed species such as giant river otter *Pteronura brasiliensis* Gmelin and Orinoco Goose *Neochen jubata* Spix. However, we note that 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 predictors since 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 floodplain forests vs. upland *terra firme*. Instead, we use a conservative estimate of spider monkey density, and the model therefore provides a quantitatively conservative approximation of depletion over space. Also, due to both 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 modeling with this approach. For example, the large 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 populations, which makes it difficult to map and project their populations within our framework. A similar caveat applies to large carnivores.

We also caution that our models do not anticipate the effects of climate change on forest fires and, thus, on the persistence of vertebrate populations (Barlow and Peres 2008), nor can they address the potential for a major policy change in Peru 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 (Naughton-Treves et al. 2003). Substitutes, by definition, reduce hunting effort, and therefore reduce the impact of hunting on game populations (Bulte and Horan 2002, Damania et al. 2005b, Ling and Milner-Gulland 2006). Additionally, we do not consider the effect of mechanized transport along rivers or roads (Souza-Mazurek 2000; Peres and 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 modeling framework. We also refer readers to Ohl *et al.* (Ohl et al. 2007a) for a complementary analysis of swidden agriculture by the Matsigenka, which we project will have a small impact on forest cover. Even if forest clearance is limited to just a 500-m radius of the two main settlements of Yomybato and Tayakome and even if gardens are given multi-decadal fallow periods, swidden agriculture can support between 2100 to 2800 Matsigenka indefinitely.

Weapons technology versus human population size

The greatest increase in game depletion results from increasing the kill rate (d_r) from values typical of bow hunting to those associated with guns (Figs 2 & 3). This effect far outstrips that produced by doubling hunting effort (*hphy*), which is equivalent to doubling the number of hunters. The decline of game animal species and other kinds of environmental damage are typically blamed on human population increase *per se* (Alvard et al. 1997, Redford 2000, Terborgh 2000). However, the more important proximate reason for game species decline has been the adoption of shotguns among Amazonian hunters, thereby increasing hunting efficiency by an order of magnitude or more (Table 1, Supplementary Material S4).

Our results also suggest that when shotguns are introduced into areas with high game densities, hunters will enjoy a transient period of high offtake (Fig. 4). For example, Peres (Peres 1990) reported that a single family of rubber tappers with just three hunters in a newly exploited hunting zone was able to kill more than 200 woolly monkeys, 100 spider monkeys, and 80 howler monkeys between early 1985 and late 1986. Eventually, overhunted spider monkey populations become so depleted in our gun scenarios (Peres and Palacios 2007a) that offtake is limited to stray migrants (Sirén et al. 2004) or kills on the edges of hunting zones (Smith 2008).

Our results contradict Alvard's (1995) conclusion that hunting technology is less relevant than consumer population in producing prey depletion. In a field study comparing return rates for bow-hunting Matsigenka in Manu Park and shotgun-hunting Piro in a community along the park's border, Alvard suggested that

> "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 Machiguenga [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."

Our analyses suggest exactly the opposite. The introduction of guns to Manu will result in a period of high exploitation, followed by a decline of CPUE to levels associated with bow hunting, as spider monkeys are severely depleted (Fig. 4). Our model suggests that just 15 years of continuous gun hunting (1974-1989, from the Piro community's inception to Alvard's fieldwork), was capable of causing hunters' return rates to drop to levels similar to those of bow hunters. 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 and 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, despite continued, locally unsustainable, hunting. 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 fully depleted the zones (Fig. 5). On the other hand, the correspondence between the observed continued high levels of large-primate offtake (Ohl-Schacherer *et al.* 2007) and the predicted slow decline in model-estimated CPUE over the same time period (Fig. 5) provides 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 (Fig. 2b & 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 km^{-2}. 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 (albeit transient) hunting advantage of shotgun use, and the widespread adoption of firearms by most indigenous Amazonian hunters (Hames 1979), it seems prudent to consider worst-case scenarios. When shotguns are used, we expect a substantial portion of floodplain forest to become depleted of large primates (Figs 2b & 3b), which should strangle the recruitment success of large-monkey-dispersed tree species restricted to floodplain habitats (Terborgh et al. 2008b).

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-CDF-lines between Figs 2a & 2b, Fig. 3). This is because gun hunters pseudointerfere with each other (Free *et al.* 1977), so fewer settlements with more hunters results in less total offtake than more settlements each with fewer hunters. Since 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 and 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 health care professionals present. Additionally, improvements in educational, economic and health care opportunities might contribute to decreasing population growth rates through increased adoption of family planning (Bertrand et al. 1999). Because settlement limitation eventually reduces per-capita game 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 analyzing 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 databases and satellite imagery. These data can be combined with literature parameter values for hunter behavior (e.g., Supplementary Information S4), 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, which will bias parameter estimates. Improved estimates of these parameters will influence the model output, but the qualitative dynamics and our policy conclusions are unlikely to change.

Acknowledgments. We thank the Matsigenka of Manu, and particularly Merino and Maura Matsipanko, Julian and Elias Mendoza, Cesar and Jesus Avanti, Abel Nontsotega, and Hilario, Carlitos, and Manuelito Kemari for participating in the study and allowing the researchers to accompany them on hunts and stay at their homes. We thank John Burton, Chris Wilmers, Sitabhra Sinha, and Marc Mangel for comments and important help with the modeling. This work was funded by a Leverhulme Trust grant and a National Geographic Society grant to DWY and CAP and an NSF Graduate Research Fellowship to TL.

Supplementary Material

The following are available as part of the on-line article from http://www.blackwell-synergy.com/ : detailed protocols for the terrestrial vertebrate censuses (Appendix S1) and the demographic dataset (Appendix S2), a non-mathematical explanation of the effort function (Appendix S3), and details and justifications for parameter estimates (Appendix S4).

Table 3.1 Parameter values and meanings

Parameters	**Values**	**Interpretation**
r	0.07	Maximum growth rate
K	25 km^{-2}	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
ESW	28.3 m	Effective strip width of linear transects
Gsp	301 m	Primate social group "areal spread" (width)
Gsz	5.1	Mean group size of spider monkeys
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 ith settlement
$p_{i,t}$		Population of ith settlement at time *t*

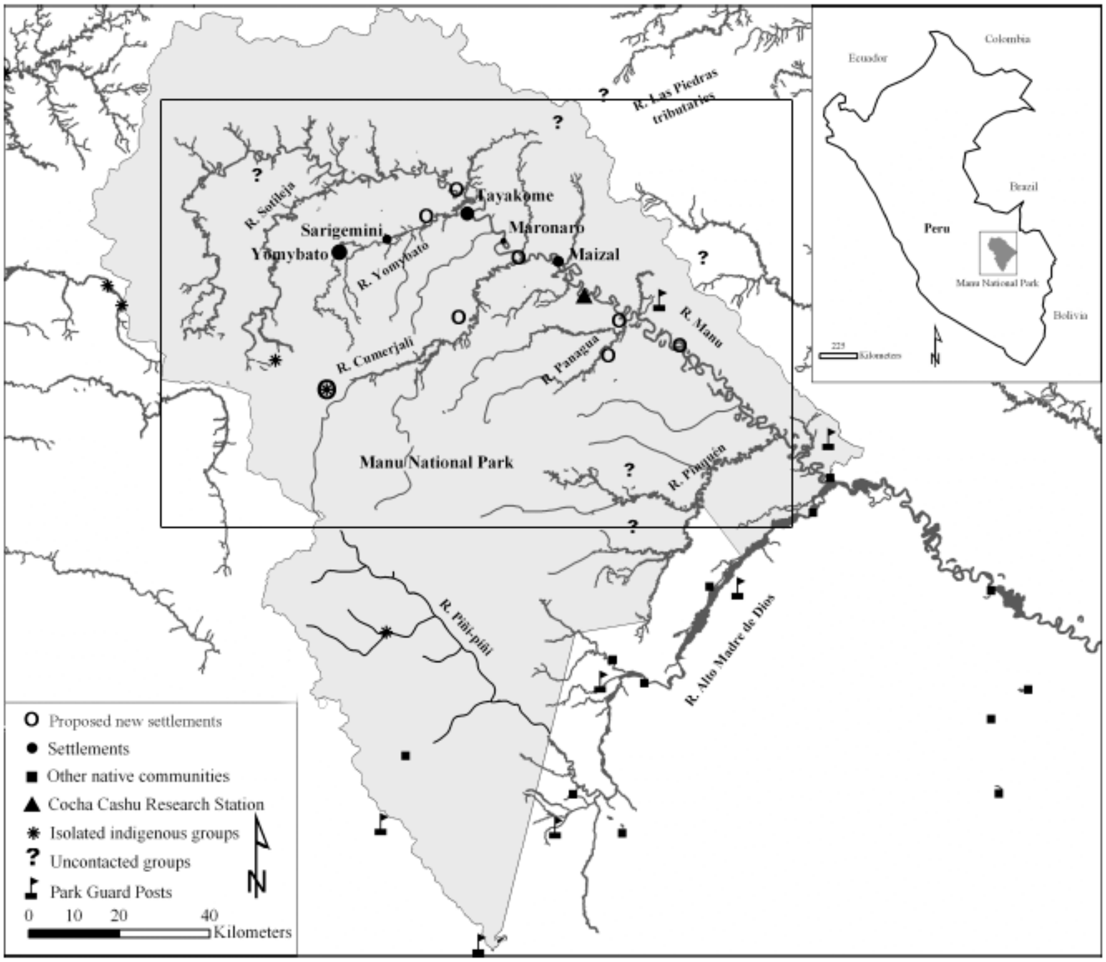
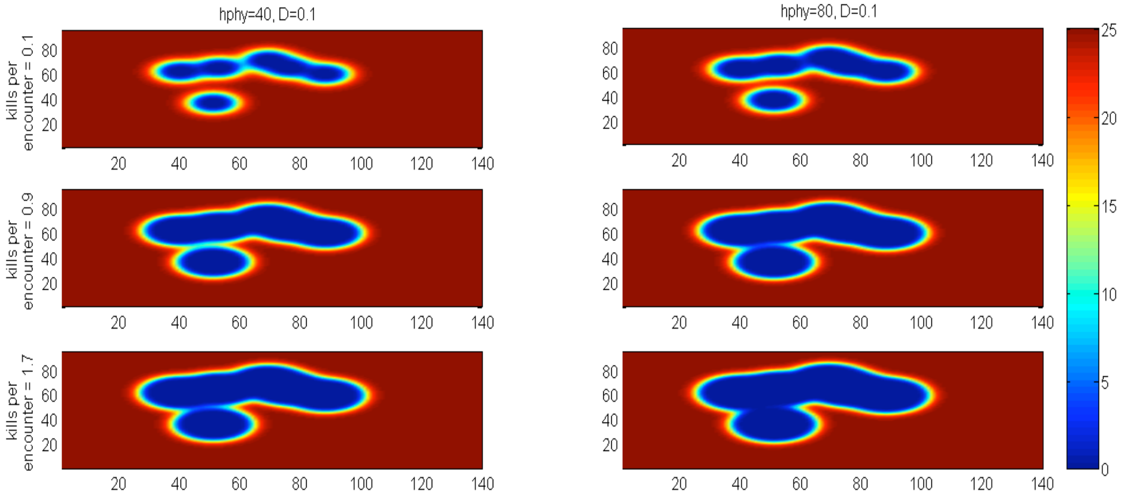


Figure 3.1 Map of Manu National Park. The two-dimensional array used in the model covers the area encompassed by the rectangle. Open circles represent projected new settlements for the SPREAD scenario, placed in areas likely to be colonized based on their current use as fishing and hunting grounds, their location near Manu River tributaries, and/or their proximity to other settlements or the 'Casa Machiguenga' lodge.

a) SEDENTARY scenarios



b) SPREAD scenarios

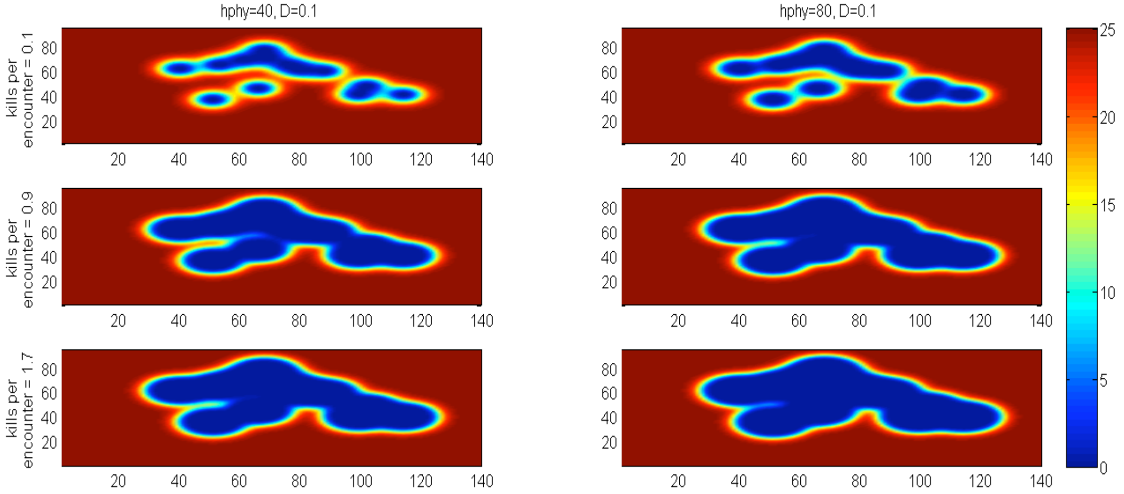
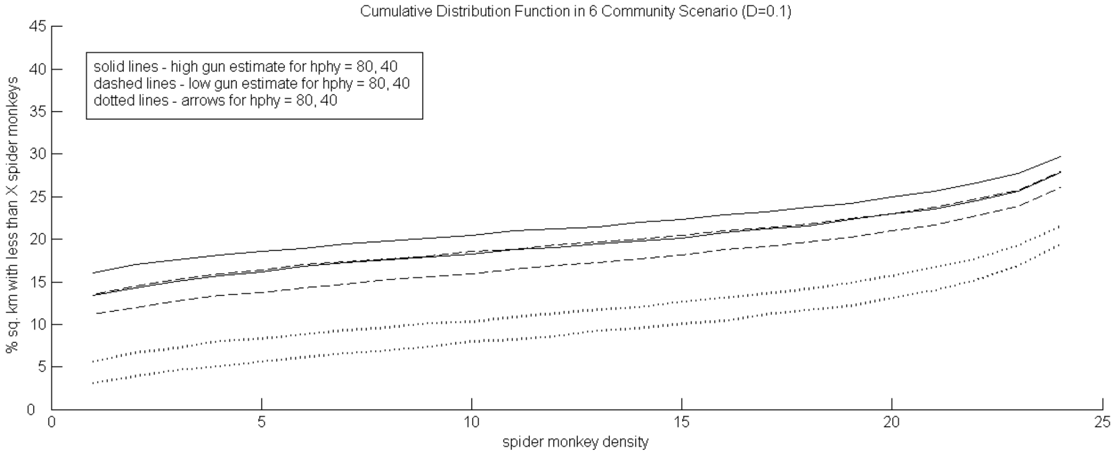


Figure 3.2 Density maps of spider monkey populations after 50 years over different scenarios and parameter combinations. Settlement locations are as depicted in Figure 1. (a) The SEDENTARY scenario, in which the human population is evenly distributed among six settlements in 2009. (b) The SPREAD scenario, 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.

a) SEDENTARY scenario



b) SPREAD scenario

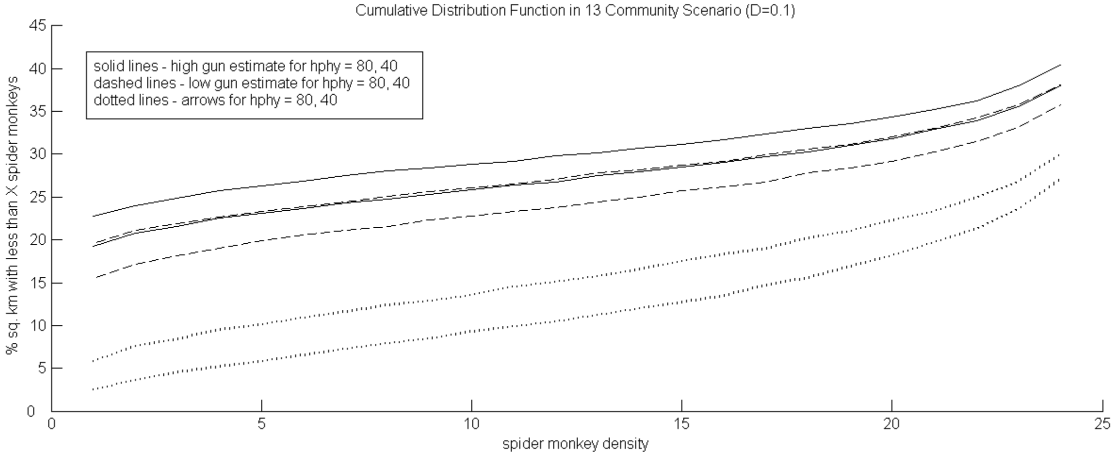


Figure 3.3 Cumulative distribution functions (CDFs) of spider monkey densities calculated from the density maps in Figure 2. (a) The SEDENTARY scenario. (b) The SPREAD scenario. The y-axis is truncated at 24 spider monkeys km^{-2} in order to zoom in on depletion, since in all scenarios, the CDFs reach 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.

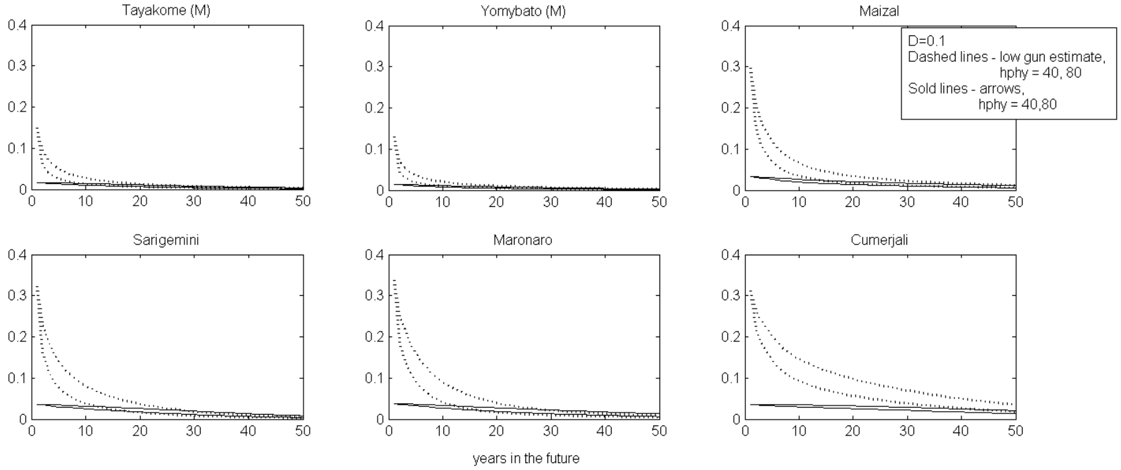


Figure 3.4 Catch-per-unit-effort over the next 50 years in the six existing settlements, with different hunting technologies. Here we use the low estimate for the gun kill rate of d_r=0.9. Convergence of CPUEs for guns and arrows is more rapid with the high gun kill rate of d_r=1.7. The two main settlements are marked with (M); the other settlements consist of a few isolated households. In each category, upper lines are for *hphy*=40, and lower lines for *hphy*=80. Diffusivity *D* is set to 0.1.

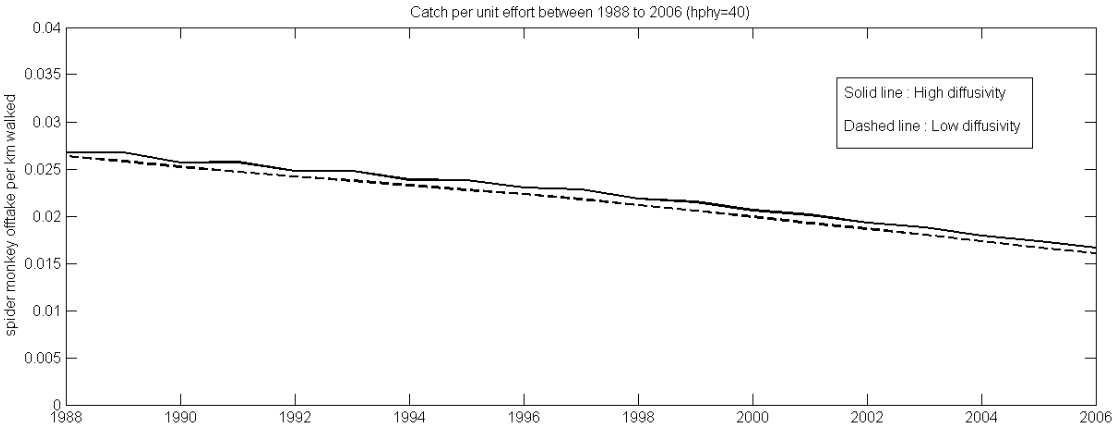


Figure 3.5 Estimated historical trajectory of catch-per-unit-effort from 1988 to 2006 in the Yomybato main settlement. Diffusion maintains populations via source-sink dynamics to some degree, but even with low diffusion the fall in catch-per-unit-effort is not extreme and may go unnoticed in prey profiles.

Chapter 3: Supplementary Information

S1. Terrestrial vertebrate density censuses

These results are in preparation for publication (W. Endo, E. Salas, S. Mori, C.A. Peres, V. Pacheco, & D.W. Yu, unpublished results), and we summarize the protocol here.

Study sites. – Line transect censuses were conducted at seven locations inside Manu Park, including five non-hunted locations, plus the two major Matsigenka settlements, Tayakome and Yomybato, which are located on upland terraces, between 10-50 m above the average river level (Fig. 1, Shepard *et al.* 2001). About 200 people live in each of these two villages. The five non-hunted census sites are 15 to 70 km from any Matsigenka settlement.

Line-transect surveys. - Our line-transects were focused on medium- to large-bodied diurnal vertebrates because these species can be detected visually, are the preferred game species among indigenous hunters (Ohl-Schacherer *et al.* 2007), and represent a disproportionate fraction of the total vertebrate biomass in tropical forests (Terborgh 1983, Peres 1999). For each animal sighting, we recorded species, perpendicular distance (PD) from the trail, group size, detection mode (e.g., visual or acoustic), diameters of large, uncohesive subgroups (‘clusters’) of the larger primate social group, which forage semi-independently, distance along the transect, and time. Detection rates decline with perpendicular distance from the trail, and with sufficient observations, the distribution of these distances can be used to calculate an “effective strip width” (ESW) using the program DISTANCE v. 4.1 (Buckland *et al.* 1993), which is then multiplied against the number of encounters to generate a density estimate.

Censuses were conducted from January to July 2006, thus, in the late rainy and early dry season. No census was conducted in May, the month with the highest frequency of cold fronts (*friajes*), when animal activity is typically low. Trails were walked on rainless days during the morning (0630 - 1030h) and in the afternoon (1230 -1700h) by two observers (a wildlife biologist and a local Matsigenka hunter) at a mean velocity of 1.2 km/h. All census walks started >200 m from campsites and >400 from any human settlement (Matsigenka houses). Transects in five of our seven sites were surveyed for c. 10 days, usually within a 21-day period (for a detailed description of our line-transect census procedure, see Peres 1999). However, two sites, Cocha Cashu Biological Station and Pakitza guard station were censused over multiple days interspersed between February and July, making comparisons with historical abundance estimates at these sites more reliable. Seasonal change may affect the detectability or even the spatial distribution of some species (Haugaasen and Peres 2007), so to control for this effect with respect to the non-hunted versus hunted comparison, one Matsigenka settlement was censused in the rainy season (Yomybato), and one in the dry season (Tayakome).

S2. Matsigenka demography

We use the historical population data as an input in our model and derive the demographic parameters to project the Matsigenka populations using an age-structured matrix model.

Detailed genealogical interviews were carried out in the Matsigenka language by anthropologist Glenn H. Shepard with all Matsigenka nuclear families of Tayakome and Yomybato during several stints of fieldwork from 1995 through 2007. Names, birth order, approximate year or date of birth, and (where applicable) approximate date and attributed cause of death were recorded for as many individuals as possible. Fairly accurate birth records have been kept since 1984 (when bilingual school teachers arrived in both communities) and especially since 1994, when government-funded health clinics were installed. For genealogical information prior to this time, we relied on women's reproductive histories, apparent birth order, and apparent age of the woman and her children at the time of interview to estimate birth dates. We also recorded as accurately as possible information regarding population emigration and immigration events that have occurred since the early 1960s, when the settlement of Tayakome was first established by Protestant missionaries. A total of 1039 total individuals were recorded in all interviews, with 1019 births and 341 deaths documented at least to an approximate year. Genealogical and demographic data were organized and analyzed using the software program *Community Express* v. 2.1 To generate a life table, we used the cohort survivorship method available in *Community Express*, which takes a user-defined cut-off date (1 December 2007, the date of our last interviews) and calculates life-history parameters from the percentage survivors for each five-year cohort.

Of course, the projection of any small population is fraught with error, especially since the medical environment has varied over the censused time period. For instance, the dominant eigenvalue of our life table is 1.037, giving a 3.7% growth rate, which is less than the measured population growth rate from the last fifteen years (4.5%, Ohl-Schacherer *et al.* 2007), because our method includes an era of high infant mortality in the late 1970s to early 1980s, when Western healthcare was mostly unavailable. Thus, we are likely underestimating future population growth if access to healthcare continues or improves. We deal with this error in two ways. Firstly, all our scenarios use the same population growth projection, so differences among scenarios can be discerned. Secondly, we vary hunting effort (hunts/hunter/year) in all scenarios. The annual number of hunts is the product of population size and effort, so by increasing effort, we correct for underestimating population growth.

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

The true effort function for (x,y) is the integral over each square grid cell of

The probability that the hunter walks past the outer border of the square × *The distance walked in the square* + *The probability the hunter ends up in the square* × *The expected distance walked in the square on that trajectory*.

The true contribution to effort of each angle θ is thus:

$$H(\theta) = \Pr\{r(\theta) > r_{\max}(\theta)\} \cdot (r_{\max}(\theta) - r_{\min}(\theta)) + \Pr\{r_{\min}(\theta) \le r(\theta) \le r_{\max}(\theta)\} \cdot E[r(\theta) \mid r_{\min}(\theta) \le r(\theta) \le r_{\max}(\theta)]$$

However, this method requires extensive numerical integration, and we have found our approximation (Eqn. 7) to be more accurate than our uncertainty about parameter estimates (Table 1). In a 100 km^2 grid cell area, the mean ratio of our approximation of hunting effort to the results from numerical integration of the above equation is 0.954 (T. Levi, D. Yu, in manuscript).

To understand the method used in this paper, imagine spinning a classic bell-curve in a circle to create a three-dimensional, upside-down bowl (with broad, flattish rim such as one might find on a decorative display piece), which we place on an *x*-*y* grid paper, centered over a settlement. We call each 1-km^2 grid square a “bin,” which holds some number of spider monkeys, *N*.

The distribution of air under the bowl represents the distribution of hunting effort exerted by a settlement’s hunters. We can see that most of the air is near the center, meaning that hunters walk mostly near the settlement, as they must. For any given walking distance *s* from the center, we can “cut out” and remove a circular section of radius *s* from the middle of the bowl, leaving us with only the bowl’s circular rim, now looking something like an upside-down football stadium (if the stadium were circular and had its playing field punched out). The volume of air remaining under the circular rim represents the proportion of total hunting (walking) effort that takes place beyond distance *s* from the settlement. To calculate that proportion, we therefore calculate the volume under the circular rim as a fraction of the original total volume under the entire bowl, which is the purpose of Eqn. 6. Intuitively, the greater the distance *s*, the more we cut out from the middle of the bowl, and the less edge (less remaining hunting effort) remains. In other words, most hunting is near the settlement, and a smaller and smaller fraction of total hunting effort takes place further and further away.

Finally, we want to divide up and allocate that remaining hunting effort to each of the bins that lies under the circular rim. More specifically, we want to allocate that remaining hunting effort to the *first ring of bins* that lies just past distance *s*, i.e., just where the circular rim starts. This will give us an approximation of the proportion of hunting effort *that occurs at distance s* from a settlement. We do this by first realizing that all the walks that manage to reach somewhere under the circular rim (and therefore contribute to the volume of hunting effort that is covered by that rim) must pass through or at least end in that first ring of bins. So the simplest thing to do, though not exact, is to take the total volume under the circular rim, which is the proportion of hunting effort that has been exerted beyond distance s, and divide it by the number of bins in just that first ring. That gives us an approximation of the fraction of total effort that was exerted in each bin at distance *s* from the settlement. We have elsewhere calculated this amount exactly, and it is very close to this approximation.

Finally, note that the absolute amount of hunting effort exerted by a settlement is calculated by multiplying the number of hunters ($p_{i,t}$) by the number of hunts per hunter per year (*hphy*). We can see these terms at the beginning of Eqn. (7), and they are multiplied by the larger term that apportions that effort across bins, as we have explained above.

To sum up, we have taken a settlement and calculated the number of hunters that walk through a 1-km^2 bin a distance *s* from the settlement. This is our hunting effort in any particular year, which is then allowed to interact with the density of spider monkeys in that bin and that year ($N_{x,y,t}$) and the killing rate per encounter, which is dependent on technology (d_r), to calculate the number of spider monkeys killed in a particular bin in a particular year at a particular distance from the settlement (Eqn. 3). For multiple settlements, we do the calculations for each of the settlements around any given bin and add up their effects to get the total kills.

S4 Parameter estimation

In our scenarios, wildlife populations are affected by five factors: the range of distances walked by hunters (σ), human population growth (males aged 14-49), human population spread (new settlements), hunting effort (hunts/hunter/year, *hphy*), and hunting technology (shotguns vs arrows, d_r). The first three can be determined via direct observation (Ohl-Schacherer *et al.* 2007 and see below), but the second two are likely to interact.

Estimating the offtake advantage of guns over arrows is not easy because guns increase kills, which deplete game populations, which decreases kills. Thus, offtake observations made even a few years after the introduction of guns will underestimate their effectiveness due to low encounter rates. In fact, we infer that guns should sharply increase offtake in the short run for three reasons: an increase in the rate of kills per encounter, an increase in hunting effort due to the recruitment of poor hunters, and an increase in solitary hunts.

In our previous study (Ohl-Schacherer *et al.* 2007), the modal number of large-primate (*Ateles chamek* and *Lagothrix cana)* kills per hunter in one year was zero, and 66% of hunters killed five or fewer (Supplementary Material). Using arrows to kill monkeys in tree canopies requires great skill, and most Matsigenka men cannot do so regularly, despite the high esteem accorded to those who can (Shepard 2002). In contrast, anyone can shoot a monkey with a gun. Alvard (Alvard 1995) reported a mean of 1.3 gun shots per kill (of all game) in a Piro settlement located just outside Manu against a mean of 30 arrow shots per kill in an early study of Matsigenka hunters in Manu. This 23-fold advantage is caused by a greater shooting range and by a higher hit rate, since pellets spread (Hames 1979).

We estimate mean spider-monkeys killed per encounter, d_r, using our offtake and density census datasets for spider monkeys. In 2006, three 5-km transects each were run in Yomybato and Tayakome, radiating out from the edge of the settlements, and spider-monkey group encounters per km recorded (Supplementary Material). The linear transects replicate what a hunter sees as he walks outward from a settlement center on a 6-km hunt (~1 km to settlement edge + 5 km hunt). We let the mean encounters per hunt, *eph*, be equal to the product of the transect encounter rate (km^{-1}) and the distance from the settlement center, 6 km ($eph=1.29_{\text{Tayakome}}$, 0.26_{Yomybato}). Spider-monkey offtake per hunter-year (*ophy*) is estimated from our offtake dataset (1.88_{Tayakome}, 1.78_{Yomybato}, Ohl-Schacherer *et al.* 2007), and we estimate that there are 40 hunts per hunter-year (*hphy*, see below). We can calculate d_r, the mean kill rate for the two communities as

$$d_r = \frac{ophy}{eph \times hphy} \tag{11}$$

Thus, $d_{r,Tayakome} = 0.036$, and $d_{r,\ Yomybato} = 0.173$. Accordingly, we set the expected number of kills per encounter for bow hunters to the mean, d_r=0.1. This might be an overestimate because some fraction of hunts takes place beyond the 6 km radius (particularly true in Yomybato where families maintain occasional second homes at some distance from the settlement, Ohl-Schacherer *et al.* 2007) where the encounter rate is greater, due to less depletion. Of course, many hunters have a higher kill rate, but the challenge is finding a mean kill rate, given the high variability amongst bow hunters.

To estimate d_r for gun hunters, we turn to the anthropological literature. While accompanying Piro shotgun hunters, who live on the edge of Manu, Alvard (1991) observed four kills in three spider monkey hunts, leaving us with an estimate of d_r = 1.33 kills per encounter. Because of the small sample size, we set d_r = 0.9 to 1.7 as a reasonable range for gun hunters, since gun hunters have a high success rate and can make multiple kills per encounter.

We could use the same process to estimate d_r for arrow hunters. However, of 12 observed spider and woolly monkey hunts (an equally desirable species) in Yomybato, no kills were observed (Alvard and Kaplan 1991a). An estimate of zero is not helpful, but if we consider the probability of making a kill, given an encounter, to be a Poisson process, then the probability of 12 encounters resulting in zero kills can be written as the joint probability distribution:

$$P(X_1,\ldots,X_{12}\,|\,\mathrm{d_r}) = \prod_{i}^{12} \frac{{d_r}^{x} e^{-d_r}}{x_i!} = e^{-12d_r}$$

If d_r were indeed 0.1 as estimated above, then we would expect to observe no kills in 12 tries 30% of the time ($e^{-12*0.1} = 0.3$). Thus 0.1 is taken to be a reasonable number, but, again, likely an overestimate, given the low kill rate of poor hunters (see below).

Guns should also increase offtake by increasing effort. Thirty-one of 176 hunters in our dataset killed no large primates, and we have observed that some of these hunters rarely go on long-distance forays, instead concentrating on fish or small game near the settlements. The availability of guns would likely induce these marginal hunters to increase their number of long-distance forays, as opposed to being limited to opportunistic shots when in the forest for other reasons.

Finally, guns should increase effort by inducing more solitary hunts. Bow hunters often pursue monkeys in groups because they get off more shots and because hunters can cooperatively flush and shoot monkeys trying to hide in trees. In our offtake dataset (Ohl-Schacherer *et al.* 2007), 68.6% (n = 382) of the successful kills of a woolly or spider monkey involved two or more hunters (mean 2.0). Kaplan observed a mean of 2.12 hunters per hunt in Yomybato, whereas Alvard observed only 1.4 hunters per hunt for shotgun using Piro hunters (Alvard and Kaplan 1991a). This has the effect of reducing the hunter population size: two hunters on a foray effectively go on half a hunt each. In contrast, shotgun hunters are more likely to be successful on their own (e.g., Sirén *et al.* 2004).

Thus, we set hunts per hunter-year (*hphy*) to range from 40 to 80. The lower end is calculated from our hunter foray dataset. For each of the six extended-family groups ('residence groups') for which we had at least 9 months of hunter foray data, the number of forays (n_{tot} = 589) was annualized and then divided by the number of hunters (males aged 14-49) in the group (n_{tot} = 24), so *hphy* ranges from 13.7 to 39.5. We conservatively use the high end of this range, in part to account for the possibility of foray underreporting, such as might occur when the main recorder in each residence group did not participate in a foray. The top end of the *hphy* range, 80, is used to incorporate the expected recruitment of marginal hunters and increased solitary hunting due to guns, to correct for a possible underestimate of human population growth rates, and to add kills made on return trajectories. In our scenarios, we use the full range of *hphy* for both technologies.

To estimate diffusivity D, we conduct a thought experiment in which we release a population of N spider monkeys in a single 1-km^2 bin at year $t = 0$, where the rest of the landscape is empty. In the next year, we observe the number of monkeys that have dispersed a distance X_i and established subpopulations. Let the mean displacement $m = \frac{1}{N}\sum_{i=1}^{N} X_i(t)$, where $X_i(t)$ is the position of the *i*-th monkey.

Diffusion is related to the mean square displacement, which is $msd = \frac{1}{N}\sum_{i=1}^{N}\left(X_i(t) - m\right)^2$. Finally, the diffusion coefficient in two dimensions, for a time step of one year, $D = \frac{msd}{4}$.

Spider monkeys exhibit high site fidelity with few sleeping trees, rarely leave their home ranges, and dispersal appears to be rare. For example, over three years of observation of two study groups at Cocha Cashu Biological Station in Manu, “mean 80% core areas,” defined as the smallest number of 1-ha quadrats that accounted for 80% of the quadrats occupied over 11 months, were on the order of only 0.5 km^2. Moreover, in three years of observations of two groups (or “communities”), only two females were deemed to have successfully dispersed, and only to neighboring groups (Symington 1988).

We therefore estimate the lower bound on diffusivity to be $D = 0.02$, by letting X_i(1 year) = 1 km for two monkeys only. Because immigration into empty territories could be greater, we set an upper bound by letting five monkeys disperse 1 km and two monkeys disperse 2 km in one year, so $D = 0.1$. These values for diffusivity can be understood more intuitively by considering the rate at which an empty bin, $N_{x,y,t} = 0$, is colonized when bordered by full bins ($N_{x+1,y,t} = N_{x-1,y,t} = N_{x,y+1,t} = N_{x,y-1,t} = 25$). By eq. (10) we see that $N_{x,y,t+1} = 2$ for $D = 0.02$ and $N_{x,y,t+1} = 10$ for $D = 0.1$.

Tuning the model. - Within our modeling framework, we can predict the offtake in any year, including years for which we have obtained offtake data. Given the parameter values above, our predicted offtake values for spider monkeys, hunted with bow and arrow, range about twice what we observed (Ohl-Schacherer et al. 2007a), so we could choose to fit our model to the observed offtake data by tuning parameters. However, we decided to err on the side of overestimating the impact of humans; should we still find little impact on spider monkeys, then we have found strong evidence for sustainability. Likewise, since we compare the effects of arrows to guns, we do not want to underestimate the effect of arrows and exaggerate the difference. Finally, tuning the model to a single year's observations can be problematic because of environmental or demographic stochasticity. In our case, in 2004-5, the hunters in Tayakome did not use prime hunting grounds across the river, for fear of encountering a temporarily encamped group of uncontacted indigenous people, likely Mashco-Piros.

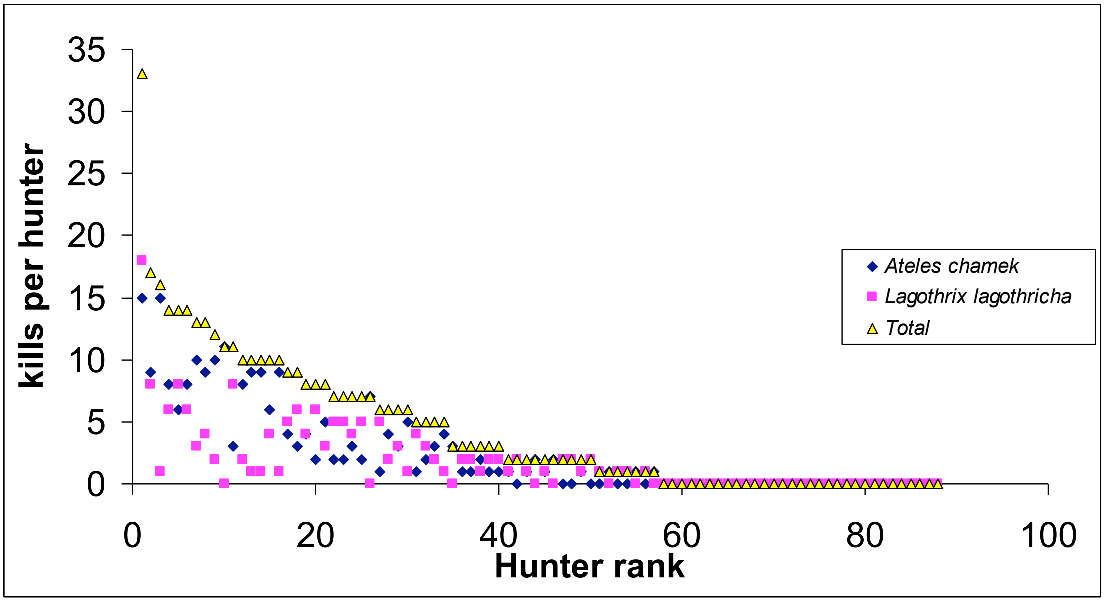


Figure 3.S1. Number of large-bodied Ateline primates (woolly and spider monkeys) killed by each hunter monitored from Oct 2004 to Oct 2005 (data from Ohl-Schacherer *et al.* 2007)

Chapter 4

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

Abstract

Subsistence hunting provides a crucial food source for rural populations in tropical forests but is often practiced unsustainably. We use the empirical observation that subsistence hunters are central-place foragers to develop three 'biodemographic' hunting models of increasing complexity and realism for assessing the sustainability of hunting of an indicator species. In all our models, we calculate the spatial pattern of depletion of an indicator species (here, a large-bodied primate) across a landscape. Specifically, we show how to identify the area surrounding a human settlement that is expected to suffer local extinction. Our approach is an improvement over well-known sustainability indices of hunting, which are error-prone and do not provide clear links to policy prescriptions. Our first approach models the long-term effect of a single settlement and (1) can be parameterized with easily obtainable field data (such as settlement maps and knowledge of the major weapon used), (2) is simple enough to be used without requiring technical skill, and (3) reveals the asymptotic relationship between local human density and the level of game depletion. Our second model allows multiple settlements with overlapping hunting zones over large spatial scales. Our third model additionally allows temporal changes in human population size and distribution and source-sink dynamics in game populations. Using transect and

hunting data from two Amazonian sites, we show that the models accurately predict the spatial distribution of primate depletion. To make these methods accessible, we provide software-based tools, including a toolbox for ArcGIS, to assist in managing and mapping the spatial extent of hunting. The proposed application of our models is to allow the quantitative assessment of settlement-stabilization approaches to managing hunting in Amazonia.

Introduction

Hunting is widely acknowledged to be unsustainable throughout the world's tropical forests (Milner-Gulland et al. 2003). Large primates—keystone seed dispersers upon which much plant diversity depends (Peres and Roosmalen 2002, Nuñez-Iturri and Howe 2007, Terborgh et al. 2008a)—are especially threatened by hunting (Peres 1990, Peres and Palacios 2007b). On the other hand, game species are important sources of protein and income for millions of forest dwellers. In the Brazilian Amazon alone, the wild-meat harvest has been estimated to exceed 89,000 tons annually (Peres 2000b). Therefore, as with fisheries, the conservation challenge with wild meat hunting is not to prevent exploitation outright but to prevent overhunting from depleting forests of their wildlife and species diversity, ultimately costing forest dwellers their food supply, and, potentially, ecotourism revenue and the political will to maintain defaunated forests in the face of alternative land-use options. This challenge is both biological and political in nature, in that we require both a robust knowledge of the amount of offtake that can be sustained by a given target species and also reliable governance mechanisms that can prevent exploitation from exceeding sustainable levels.

Within the hunting literature, sustainability has been defined and assessed most commonly via the use of 'sustainability indices' (Milner-Gulland and Akçakaya 2001a, Stephens et al. 2002), which are static algorithms that calculate a sustainable level of harvest within an arbitrarily defined catchment area. One of the most commonly used such indices, the Robinson and Redford (1991) production model, uses literature values of a target species' carrying capacity and intrinsic population growth rate to calculate a maximum annual production, a fraction of which is then taken to be the species' MSY, or Maximum Sustainable Yield, where the fraction is dependent on the lifespan of a typical individual (see Alvard et al. 1997, Slade et al. 1998, Ohl-Schacherer et al. 2007b). The MSY is then compared to observed offtakes from the catchment area to assess whether offtake is sustainable. A similar approach is the harvest model of Robinson and Bodmer (1999), which uses empirical estimates of local game species densities and calculates a sustainable offtake from the expected annual fecundity.

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

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

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

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

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

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

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

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

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

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

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

Methods

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

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

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

Analytical, single-settlement model

We start with a spatially explicit model for a single human settlement hunting for large primates, but the approach generalizes to other territorial game species. The landscape is represented by a two-dimensional array (grid) of 1 km^2 bins, where each $N_{x,y,t}$ represents the density of the focal game species in bin (x, y) at time t.

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

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

In each bin, the total population production is:

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

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

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

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

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

The spatial distribution of hunting effort. - The remaining term is the hunting effort in each bin and year, $h_{x,y,t}$, which is measured as the cumulative distance walked in each bin (*x, y*). This is the most difficult to derive. We operate on a square grid in polar coordinates with $r_{\max}(\theta)$ and $r_{\min}(\theta)$ defined as the distance to the far and near edges of a bin following the trajectory defined by the angle θ. $\theta_{\min}$ and $\theta_{\max}$ define the minimum and maximum angles that subtend bin (*x,y*) (Figure 1a). Formulas for $r_{\max}(\theta)$, $r_{\min}(\theta)$, $\theta_{\max}$, and $\theta_{\min}$ are derived with basic trigonometry (Appendix B). The contribution to hunting effort by a single trajectory $H(\theta)$ can be calculated with two terms. The probability that a hunt goes beyond the far edge of the focal bin, $\Pr\{r(\theta) > r_{\max}(\theta)\}$, contributes a distance walked of $(r_{\max}(\theta) - r_{\min}(\theta))$, and the probability that a hunt ends in a bin, $\Pr\{r_{\min}(\theta) \le r(\theta) \le r_{\max}(\theta)\}$, contributes the expected distance walked in the bin $E[r(\theta) \mid r_{\min}(\theta) \le r(\theta) \le r_{\max}(\theta)]$. In sum, the contribution to hunting effort for each trajectory is

$$\begin{aligned} H(\theta) = {} & \Pr\{r(\theta) > r_{\max}(\theta)\} \cdot (r_{\max}(\theta) - r_{\min}(\theta)) + \\ & \Pr\{r_{\min}(\theta) \le r(\theta) \le r_{\max}(\theta)\} \cdot E[r(\theta) \mid r_{\min}(\theta) \le r(\theta) \le r_{\max}(\theta)] \end{aligned} \tag{4}$$

The distribution of hunting effort measured in kilometers walked has been found empirically to approximate normality (Sirén et al. 2004, Ohl-Schacherer et al. 2007b, Smith 2008). Thus, we model the distribution of hunting distances with the bivariate normal distribution converted to polar coordinates with standard deviation σ. To clarify previous confusion about the spatial distribution of hunting, note that integrating out θ over the polar coordinate form of the bivariate normal (equivalent to multiplying by 2π), gives the related Rayleigh distribution, which unlike the normal distribution is restricted to be nonnegative (as are distances from a human settlement).

Thus the distribution of distances walked when hunting effort is isotropic is actually the Rayleigh distribution. The distribution of effort vs. distance, has been informally called “normal” (Sirén et al. 2004) because it declines with distance as e^{-r^2}, giving it half of a normal-like shape. This effort vs. distance relationship can be derived from the distribution of distances walked by noting that all hunts that have walked past a particular location contribute effort to that location. In probability terms, this is simply one minus the cumulative distribution function of the Rayleigh distribution, or $e^{\frac{-r^2}{2\sigma^2}}$, which provides the observed normal-like decline in hunting effort, and since it is a CDF it need not integrate to one. When applying this model, the parameter σ is best estimated by noting that the mean of the Rayleigh distribution (mean hunt distance from settlement center) equals $\sqrt{\frac{\pi}{2}}\sigma$.

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

$$\begin{gathered}\int_{\theta_{\min}}^{\theta_{\max}} H(\theta)d\theta = \int_{\theta_{\min}}^{\theta_{\max}} \int_{r_{\max}(\theta)}^{\infty} \frac{r}{2\pi\sigma^2}\exp(\frac{-1}{2\sigma^2}r^2)\cdot \left(r_{\max}(\theta) - r_{\min}(\theta)\right)drd\theta \quad + \\ \int_{\theta_{\min}}^{\theta_{\max}} \int_{r_{\min}(\theta)}^{r_{\max}(\theta)} \frac{r}{2\pi\sigma^2}\exp(\frac{-1}{2\sigma^2}r^2)drd\theta \cdot \int_{0}^{2\pi} \int_{r_{\min}(\theta)}^{r_{\max}(\theta)} \frac{r^2}{2\pi\sigma^2}\exp(\frac{-1}{2\sigma^2}r^2)drd\theta\end{gathered} \tag{5}$$

This integral cannot be solved in closed form; thus, we derive an approximation for a bin centered *s* distance units away as the fraction of hunts that walk at least distance *s* and fall within a wedge that is a fraction of the total circumference of a circle of radius s. The idea is that the circumference + 1 approximates the number of bins over which it is necessary to distribute the hunting effort. The addition of one both normalizes the function so that all hunts pass through the settlement (since $\frac{1}{2\pi s+1}$ = 1 when s = 0) and avoids division by zero at the settlement center. We derive our approximation to be

$$\begin{aligned}\int_{\theta_{\min}}^{\theta_{\max}} H(\theta)d\theta &\approx \frac{1}{2\pi s+1}\int_0^{2\pi}\int_s^{\infty}\frac{r}{2\pi\sigma^2}\exp\left[-\frac{r^2}{2\sigma^2}\right]drd\theta \\ &= \frac{1}{2\pi s+1}\exp\left(\frac{-1}{2\sigma^2}s^2\right)\end{aligned} \tag{6}$$

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

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

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

$$h_{x,y,t} = hphy\cdot p\cdot\exp\left(\frac{-1}{2\sigma^2}\left((x_0 - x)^2 + (y_0 - y)^2\right)\right)\frac{1}{2\pi\sqrt{(x_0 - x)^2 + (y_0 - y)^2}+1} \tag{7}$$

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

Accuracy of the approximation. - We compare the approximation to the results from numerically integrating $H(\theta)$ with the ratio $\frac{1}{2\pi s+1}\exp(\frac{-1}{2\sigma^2}s^2)$: $\int_{\theta_{\min}}^{\theta_{\max}} H(\theta)d\theta$.

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

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

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

or, more explicitly,

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

$$gN_{x,y}\left(1-\left(\frac{N_{x,y}}{K}\right)^{\Theta}\right) = E_{x,y,t}\cdot d\cdot h_{x,y,t} \tag{8}$$

$$gN_{x,y}\left(1-\left(\frac{N_{x,y}}{K}\right)^{\Theta}\right) = e\cdot N_{x,y}\cdot d\cdot hphy\cdot p\cdot \exp(\frac{-1}{2\sigma^2}s^2)\frac{1}{2\pi s+1}$$

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

$$N_{x,y} = \max\left(0,\ K^{\Theta}\left(1-\frac{e\cdot d\cdot hphy\cdot p\cdot \exp(\frac{-1}{2\sigma^2}s^2)}{g(2\pi s+1)}\right)\right)^{1/\Theta} \tag{9}$$

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

Hunting is, by definition, not locally sustainable in a region where the only steady state is zero. Alternatively, we can set a pseudoextinction threshold below the density needed to retain ecological functions (e.g. seed-dispersal services). Setting $N_{x,y} = u$ in Eqn. 9, where *u* is a pseudoextinction value, we can solve for the distance, *s*, which is the radius at which we expect the game population to be driven to pseudoextinction (or extinction, if $u=0$ is chosen). The value of *s* can be calculated graphically or numerically (see our attached Microsoft Excel spreadsheet, Appendix C) and can be used by managers to find the distance within which (pseudo-)extinction occurs.

Parameter estimates (Table 1) can be taken from the literature or by direct observation (e.g. Levi et al. 2009).

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

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

$$\text{CPUE} = \frac{\sum_{\forall x}\sum_{\forall y} e * N_{x,y} * d * \exp(\frac{-1}{2\sigma^2}(x^2+y^2))\frac{1}{2\pi\sqrt{x^2+y^2}+1}}{\sum_{\forall x}\sum_{\forall y}\exp(\frac{-1}{2\sigma^2}(x^2+y^2))\frac{1}{2\pi\sqrt{x^2+y^2}+1}} \qquad (10)$$

The denominator of the above expression for CPUE is constant, so setting the denominator equal to $\frac{1}{c}$, we get a final expression for the steady state CPUE:

$$\text{CPUE} = c * e * d\sum_{\forall x}\sum_{\forall y} N_{x,y} * \exp(\frac{-1}{2\sigma^2}(x^2+y^2))\frac{1}{2\pi\sqrt{x^2+y^2}+1} \qquad (11)$$

Note that the human population size *p* and *hphy* influence CPUE via the game population density $N_{x,y}$. Since gun hunting populations can push CPUE below that which would have been obtained if everyone had continued to be a bow hunter instead (see also Levi et al. 2009), this equality allows us to infer the human population-size threshold at which gun hunting becomes less profitable than bow hunting in the long run (with human population size incorporated through $N_{x,y}$, which is given by Equation 9). We thus have a method to calculate the effect of hunting on the viability of game species both in terms of population persistence and as a food source for humans, allowing us to explore how different management options will affect the balance between conservation and livelihoods.

Analytical, multiple-settlement model

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

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

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

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

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

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

There is no extinction envelope when multiple settlements are involved, but we can calculate a matrix of steady state population density values if we specify the location and population of each settlement. Here, we generate two spatial distributions of 25 settlements each on a 200 x 100km landscape, one dispersed and one clumped (i.e. including a large area where settlements are prohibited), and assess the resulting depletion caused by gun and bow hunters. The results can be summarized with cumulative distribution functions (CDFs), which summarize the distribution of spider-monkey depletion across the landscape (Figure 5). While the concept of an extinction envelope around a settlement does not exist here, a useful metric for comparing the sustainability of various landscape configurations is the fraction of the landscape in which the focal game species is extirpated under each configuration. The steady-state CPUE when multiple settlements are included can be considered both as the local CPUE for some subset of the total number of settlements, or as the global CPUE, which is the total catch divided by the total effort. The multiple settlement CPUE is a straight-forward extension of the single settlement CPUE. By summing the contribution to catch and effort over the desired settlements, the steady state CPUE becomes

$$\frac{e \cdot d \sum_{\forall x} \sum_{\forall y} N_{x,y} \sum_{i=1}^{settlements} p_i \cdot \exp(\frac{-1}{2\sigma^2}((x_{0,i} - x)^2 + (y_{0,i} - y)^2)) \frac{1}{2\pi\sqrt{(x_{0,i} - x)^2 + (y_{0,i} - y)^2} + 1}}{\sum_{\forall x} \sum_{\forall y} \sum_{i=1}^{settlements} p_i \cdot \exp(\frac{-1}{2\sigma^2}((x_{0,i} - x)^2 + (y_{0,i} - y)^2)) \frac{1}{2\pi\sqrt{(x_{0,i} - x)^2 + (y_{0,i} - y)^2} + 1}} \tag{14}$$

We use this formula to find the global CPUE for the spatial arrangements of settlements in Figure 5. The CPUE, CDFs, and the steady state distribution of game species can be calculated using the Matlab code in the appendix (D). The generated hunter-population and settlement-coordinate data for the clumped and dispersed settlements that we used for this work are also provided. This model can also be implemented with a provided Python script to produce depletion maps in ArcGIS (Appendix E)

Numerical, multiple-settlement model with source-sink dynamics

We now extend the model to add source-sink dynamics in the primate population. This numerical approach is not a steady-state solution, so it can be used to model populations at any point in a time series, which also makes it a useful validation tool because we can compare the predicted and observed primate populations in any year after the establishment or removal of settlements and/or after an increase or decrease in human population size. For the same reason, this method is useful for gauging transient dynamics after a management intervention or external shock, such as the introduction of new weapons, or the establishment of no-take zones.

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

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

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

$$M(N) = D \times \nabla^2 N \tag{15}$$

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

$$\nabla^2 N = \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \tag{16}$$

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

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

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

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

Validating the model: Predicting game depletion

Approach. - From published transect data we can validate the model's predictions against two variables. (*i*) The radius of local extinction ("extinction envelope"), which is determined by the radial distance beyond which individuals of the focal species can be found and (*ii*) the cumulative distribution function of the game population, which is a measure of the shape of game density recovery at increasing distance from a human settlement. Since the numerical model can be solved for any time step, it can be directly compared to empirical data when we know the demographic history of the human settlement.

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

Datasets for validation. - We first compare the model output to two vertebrate line-transect datasets (distance sampling) conducted at the same site, Yomybato, but at different times. Our earliest dataset is a gray literature report conducted by Mitchell and Luna (1991). One 8 km transect was conducted radially outward from the Matsigenka native community of Yomybato (Ohl-Schacherer et al. 2007b, Ohl et al. 2007b, Levi et al. 2009), at which time there were approximately 100 residents hunting almost exclusively with bow and arrow (Shepard et al. 2010). From 1976 to

1991, the number of hunters grew from 19 to 22, with a maximum of 24 in 1982 (G.H. Shepard *unpublished data*). Since Yomybato had a stable population, we expect the steady-state results to show only slightly more depletion than what is given from the numerical results or what is observed empirically, since there was time for the system to approach steady state.

Complementing the 1991 transects are data from a series of 4.5 km line transects conducted in 2006 and also radiating from Yomybato (Endo et al. 2010). Comparing the transect data from 1991 and 2006 provides evidence of how the spatial distribution of ateline monkeys has changed as the human population has grown over time. In order to use a spatial scale that is consistent with the 1991 data, transects of 8 km in length would have been ideal but were not conducted.

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

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

Results

Analytical, single-settlement model

We first apply our model to the simplest case of one human settlement in an otherwise pristine environment. The circular area with radius s where the steady-state spider monkey population is zero (the extinction envelope) grows asymptotically with human population size. At small human population sizes, an increase in the gun-using population increases the extinction envelope much more than does the same increase in a bow-hunting population. This nonlinearity means that even small gun-hunting communities, or the adoption of guns by a fraction of hunters in a larger community, will result in the local extirpation of the ateline population in a large area. Observation of small gun-hunting populations entering an otherwise unhunted region are rare, but this result is consistent with Peres' (1990) observations from the Riozinho River of western Brazilian Amazonia that just three gun hunters in a newly exploited hunting zone were able to kill more than 200 woolly monkeys, 100 spider monkeys, and 80 howler monkeys between early 1985 and late 1986, rapidly driving populations of the two larger-bodied atelines to local extinction. Eventually, the effect of adding more hunters on the size of the extinction envelope diminishes (Figure 2), as even a large hunter population does not increase the distance that individuals can walk in a day. A useful aspect of this result is that estimates of the size of an extinction envelope are robust to errors in estimates of hunter numbers, the fraction of hunters using shotguns, and hunter effort level (except of course for the smallest settlements).

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

Note that when the pseudoextinction threshold is zero (complete local extinction), the extinction envelope does not depend on the spider monkey carrying capacity K or the logistic theta parameter Θ, which is useful, since these are notoriously difficult to estimate. Also multiplicative changes in the kill rate, human population, or number of hunts per hunter per year all influence the extinction envelope equally. In other words, if switching from bow to gun hunting changes d by approximately an order of magnitude (Levi et al. 2009), this is mathematically the same as having ten times the human bow-hunting population or each hunter hunting ten times as often.

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

Analytical, multiple-settlement model

For both gun and bow hunters, we analyze the long term impact of different settlement arrangements in space (Figure 5). Gun hunters create larger defaunated regions than do the same number of bow hunters, leaving fewer refugia around settlements to act as a source of game. The two configurations for guns and bow hunters can be compared by the "fraction extirpated" (Figure 5), and a smaller fraction of the landscape is extirpated by bow hunters. After controlling for weapons use, there is a secondary effect of the spatial arrangement of the settlements (Figure 5). The more concentrated settlements are in space, the more limited the depletion across the landscape, as hunters from different settlements pseudointerfere with each other (Levi et al. 2009).

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

Validation results

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

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

Spider monkeys will continue to be depleted farther from settlements even by low levels of hunting effort.

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

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

Discussion

Indigenous peoples’ territories present both tremendous opportunities and challenges for tropical biodiversity conservation worldwide, perhaps nowhere more so than in the Amazon basin (see Shepard et al. 2010), where fully 21% of the landscape is under the stewardship of indigenous peoples, constituting 54% of the total forest cover under some form of state protection (Peres 1994). Moreover, over 70% of strictly protected national parks and analogous reserves include resident human populations (Brandon et al. 1998a). In Brazilian, Peruvian, and Bolivian Amazonia, indigenous reserves together total >130 million hectares of largely intact forestlands that can safeguard both full complements of biodiversity and important ecosystem services, such as carbon storage and hydrological cycles. Remote sensing analyses have shown that indigenous reserves can be equally or more effective (when the surrounding landscape mosaic is considered) than are strictly protected parks at preventing deforestation and forest fires (Nepstad et al. 2006). However, human-occupied reserves are beset by several internal threats to biodiversity, including high levels of population growth (McSweeney and Arps 2005), rapid cultural change, and overhunting associated with the recent adoption of firearms. The modeling framework that we have developed allows us to generate a map of game density, and therefore assess the sustainability of hunting, over space and time, which is an improvement over current sustainability indices. Moreover, we can do this with easily obtainable data, using maps of human settlements plus reliable literature values for key parameters (Figures 2, 6, in Levi et al. 2009). The ability to assess and project game density over space and time under different management scenarios, through demographic change, and over large spatial scales is a key result for application to the management of reserves and landscapes. For example, in Levi et al. (2009), we were able to assess the sustainability of hunting in the 1.8 Mha Manu National Park of southern Peru over the next 50 years, considering two divergent scenarios of human settlement growth and spread.

Here, our purpose has been to validate the approach taken by Levi et al. (2009) and to make its methods available to non-technical users via two analytically tractable models and via our Python script, which uses ArcGIS to automate the mapping of game depletion in space over a defined time frame under variable spatial configurations of settlements with overlapping hunting zones (Figure 7, Levi et al. 2009). We also (1) demonstrate that the hunting effort approximation used in Levi et al. (2009) closely approximates the results expected under a mechanistically derived model (Figure 1); (2) show how weapon technology is more important than human population size *per se* in determining the spatial pattern of game depletion and catch per unit effort (Figures 2-6); (3) provide a simple method to calculate the steady state distribution of large-bodied primates, catch per unit effort, and the 'extinction envelope' around single settlements (Equations 9, 11, 13, 14, Figures 2, 3, 4); and (4) use published spatial datasets to provide empirical validation for the model (Figure 6).

Neither of the analytical models can project the impact of hunting to a particular time with a growing human population since they are designed to give a steady-state solution. However, steady-state predictions are useful when considering the long term effects of an arrangement of settlements or the long-term conservation value of no-take areas. As such, the "fraction extirpated" index can be used to identify the amount of area where an indicator game species, such as the spider monkey, will persist, and by extension, so will all other species that are less vulnerable to hunting. A major advantage of the analytical approach is the simplicity of implementation on very large spatial scales. The computer memory requirements are minimal, and the model runs extremely quickly. In contrast, the numerical model must iterate over every grid cell, for every settlement and year making it computationally expensive to implement on large spatial and temporal scales. If settlement data are available by remote sensing or by government census, the long-term sustainability of hunting over very large spatial scales can now be modeled in order to assess likely trends and impacts over various scenarios without necessarily having to first invest in expensive and time-consuming fieldwork. The modeling results could later be tested and refined through more detailed fieldwork in specific study regions.

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

The assumption that we make throughout this work is that hunters are distance-limited, causing hunting effort to be concentrated in space. As a result, game populations outside hunting zones are given refuges from human predation. Because both effort and the impact of hunting are concentrated near settlements, CPUE must decline at a rate that is largely dependent on the hunting technology used (Figure 3). With bow and arrow, large primates remain in the hunting zone, and more can be killed for a given amount of effort because the rate of offtake is slow enough to allow for reproduction and migration to compensate.

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

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

Our methods can currently project the impact of hunting in space and time for game species that are both profitable and vulnerable because in the absence of a viable spatial human foraging model, we must hold hunter behavior fixed (Jerozolimski and

Peres 2003). However, this assumption cannot always hold when considering multiple game species, particularly in the context of increasing market involvement and sedentarism. On the one hand, as game is depleted near settlements, hunting might become less attractive relative to alternate activities, causing hunting effort (*hphy)* to decrease. On the other hand, if alternate sources of protein are not available, hunters might need to hunt more frequently (*hphy* increases) to meet subsistence requirements. Additionally, depending on the spatial structure and profitability of the available game species, both human diet breadth and the spatial distribution of hunting effort, σ, will change. To account for these dynamics, a major direction for future work is the development of spatial human foraging models that can account for the unique factors (central place foraging on sequentially encountered prey, spatially circumscribed depletion of game, finite supply of ammunition, opportunity costs associated with alternate economic activities) that influence human hunting behavior. However, because the steady state solutions provide long-term projections of game depletion, steady-state multispecies models are possible as long as reasonable approximations (or ranges) of long-term hunting effort (*hphy* and σ) can be intuited. Such approximations can be obtained by measuring *hphy* and σ at locations where game is already highly depleted, and at sites that have variable market involvement, to provide an empirical rather than model-based rationale for choosing parameter values.

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

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Table 4.1 Parameter values, their interpretation, and references

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

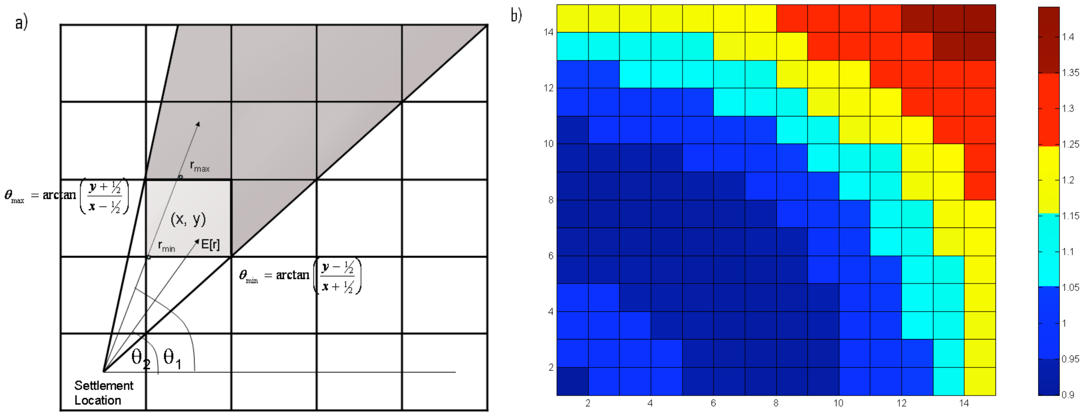


Figure 4.1 Computation of hunting effort in each grid cell. **a)** The challenge is that grid cells are square, but hunter trajectories are described using polar coordinates. Our focal bin is (1, 2). In each grid cell, hunters traveling on trajectories defined by $\theta_{\min} \le \theta \le \theta_{\max}$ can contribute to effort by walking past the bin and traveling $\left(r_{\max}(\theta) - r_{\min}(\theta)\right)$ through the bin, or by landing in the bin, in which case we assume a distance given by $E\left[r(\theta) \mid r_{\min}(\theta) \le r(\theta) \le r_{\max}(\theta)\right]$. **b)** Ratio of hunting effort approximation to actual effort obtained by numerical integration for a standard deviation of walking distance $\sigma = 5$ km.

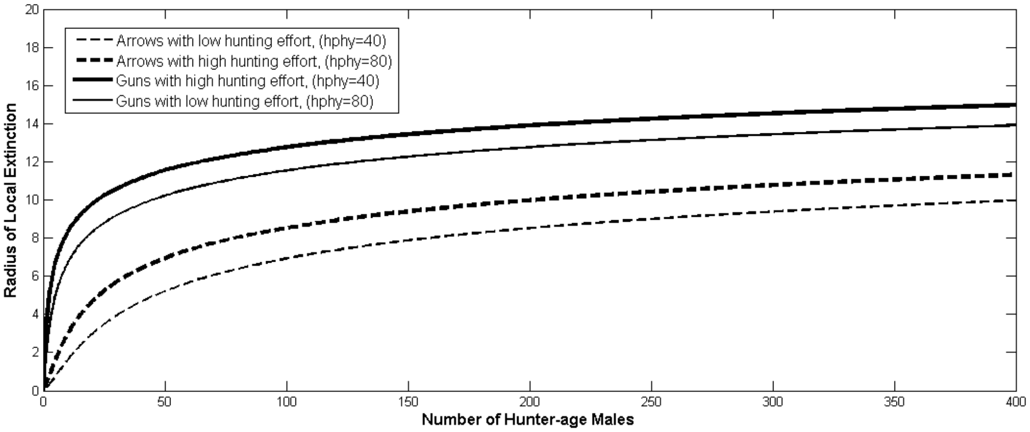


Figure 4.2 The increase in the radius of the extinction envelope increases nonlinearly with human population size and weapon choice. Gun hunting, even by very small human populations, causes larger-scale local extirpation than does arrow hunting. As human population size increases, the radius of local extinction is ultimately limited by the distance that hunters can walk in a day, which is governed by σ.

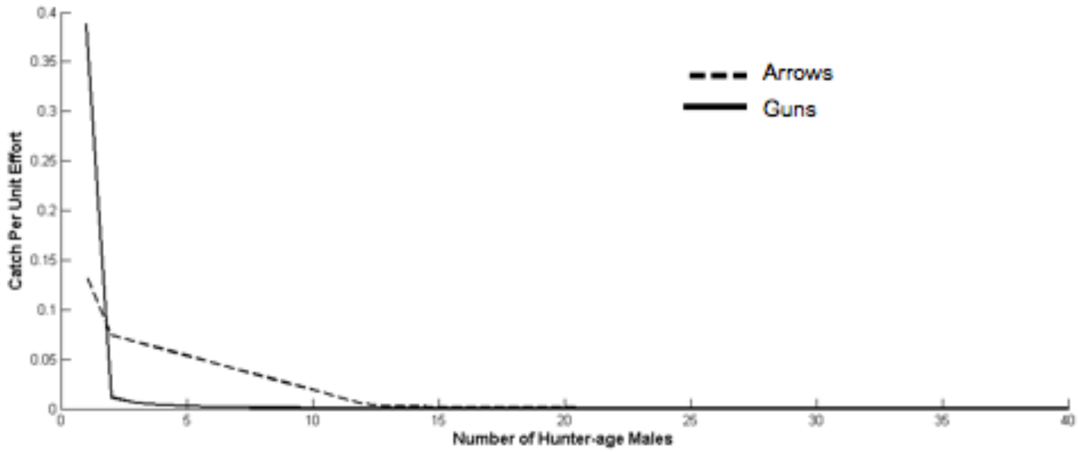


Figure 4.3 Catch per unit effort at the steady state spider monkey population size for bow hunters (dashed line) and gun hunters (solid line). Gun hunting has a higher CPUE in the long term only for unrealistically small human population sizes. For long-term access to primate meat, gun hunting performs worse than bow hunting.

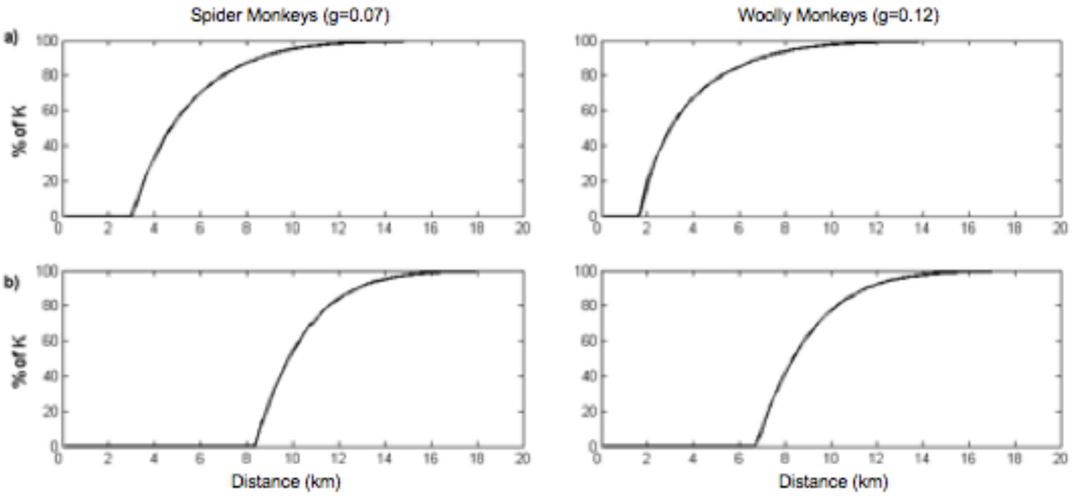


Figure 4.4 The spatial distribution of steady-state game species densities for spider and woolly monkeys. (a) Bow hunting, kill rate *d* = 0.1. (b) Gun hunting, *d* = 0.9. All four panels assume 20 hunters (the approximate number in Yomybato from 1976 to 1991) each hunting 40 times per year. The x-intercept indicates the radius of the extinction envelope ($N_{x,y} = 0$). Bow hunting creates smaller areas of local extinction than does gun hunting.

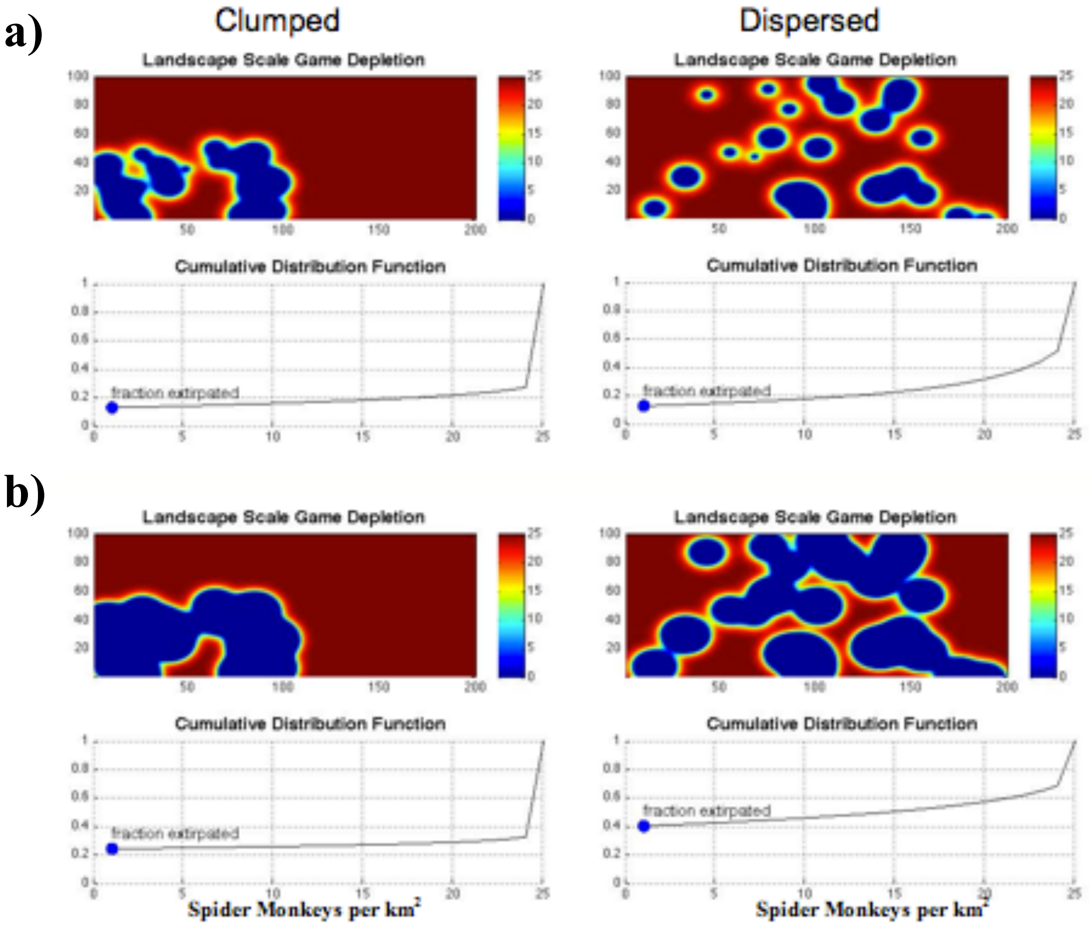


Figure 4.5 (a) The long-term, steady-state spatial distribution of spider monkey densities under hunting by arrow hunters $d = 0.1$ and (b) by gun hunters $d = 0.9$ for a clumped and a dispersed spatial arrangement of 25 settlements. The landscape-scale depletion can be visualized with a color map, where dark blue indicates local extirpation and dark red indicates no exploitation (monkeys at or near carrying capacity), and summarized with a cumulative distribution function. The blue dot signifies the fraction of the landscape that is locally extirpated (fewer than one monkey remaining per km^2) , which is an analog of the "extinction envelope" used in the single species model. There is nearly twice as much extirpation in the dispersed-settlement than the clumped-settlement gun hunting scenario, but settlement pattern makes little difference in the bow hunting scenario. Actual settlement populations and coordinates can be found in Appendix D.

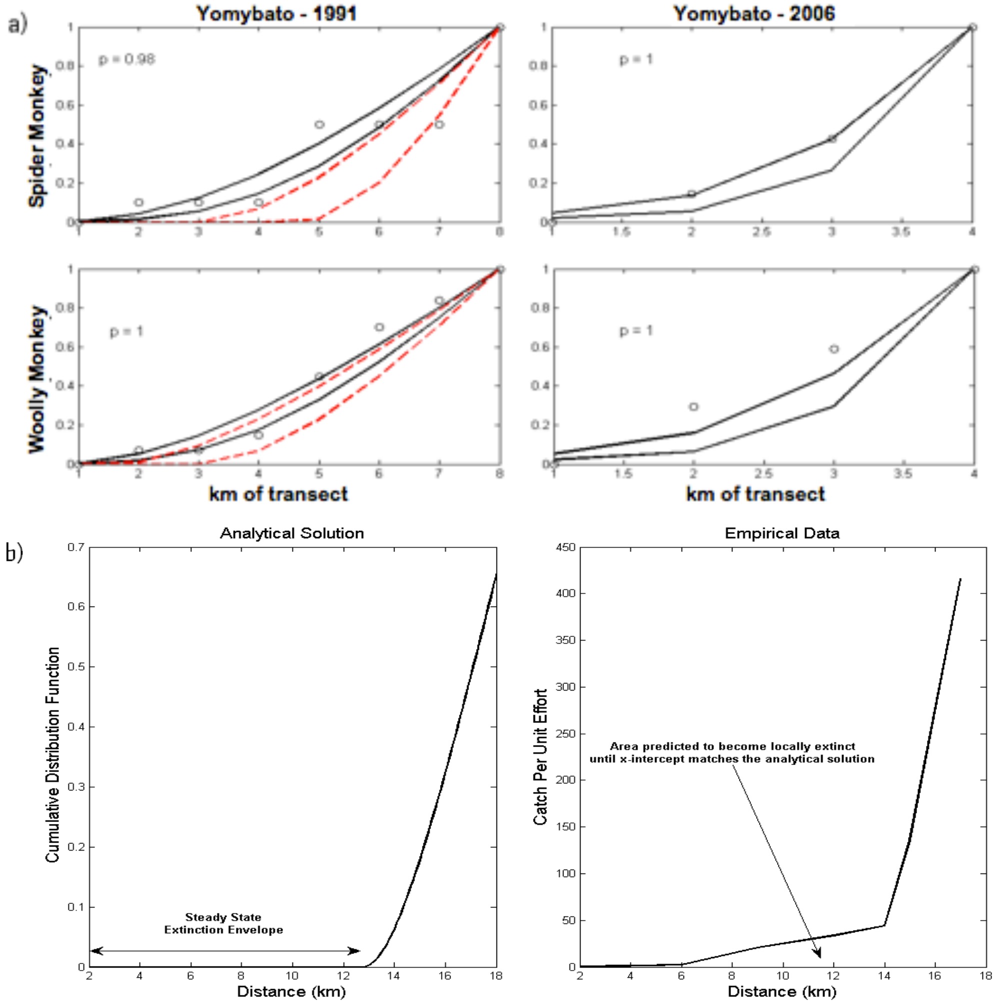


Figure 4.6 Comparing model output and data to validate the biodemographic models. **a)** Cumulative distribution functions of spider and woolly monkey (growth rate, *g*) encounters with radial distance from the Yomybato settlement in 1991 and 2006, using the numerical model with one settlement. Data points for the cumulative distribution functions are the fraction of observations from line transects occurring before the distance specified on the *x*-axis, where each fraction is the number of encounters on a transect before the distance on the x-axis divided by the total number of encounters. Thus, there are few spider-monkey encounters near settlements (flat slopes) and many encounters far from settlements (steeper slopes). Solid lines correspond to numerical model outputs and dashed lines to the analytical steady state (Eqn. 9). *hphy* = 40 and 80 hunts per hunter-year for the upper and lower lines of each pair, respectively. A p-value near unity indicates that the model and data are statistically indistinguishable. **b)** Steady-state (long-term) cumulative distribution function of woolly monkeys given by the analytical, single-settlement model of a gun hunting community with 200 hunters and *hphy* = 80 (left), compared to the data from Sarayacu (Sirén et al. 2004) (right). The model produces a reasonable fit of an extinction envelope to the observed spatial pattern of depletion in Sarayacu, as measured by catch per unit effort (CPUE). Note that we start the x-axis at 2 km, since there is local extirpation from 0 to 2 km.

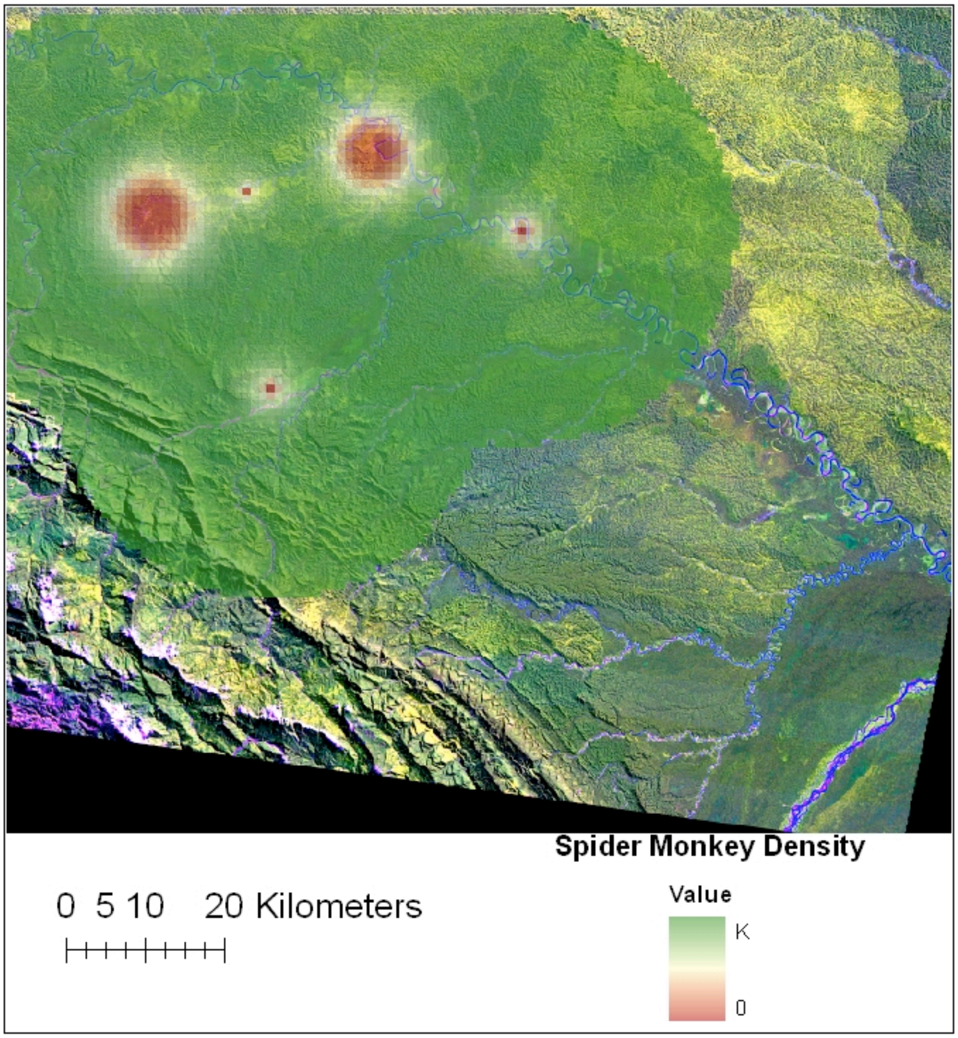


Figure 4.7 Example output of the GIS script to project the present depletion of spider monkeys for settlements in Manu National Park, Peru. Larger and older settlement have more local depletion than smaller and newer settlements.

Chapter 4: Supplementary Information

A. ***Calculating the game encounter rate*** **e_r** ***from line-transect data.***

We estimate $E_{x,y,t}$ by using the well-known "Distance" sampling protocol (Buckland et al. 1993). In distance sampling, one converts a measured encounter rate (km^{-1}) of clusters (groups) of monkeys to a monkey population density estimate using three parameters, *ESW*, *CSz*, and *CSp,* that are estimated empirically with linear transects. *ESW* is the 'effective strip width' on one side of a census trail, calculated using the distribution of observed perpendicular distances to the transect (Buckland et al. 1993), *CSz* is average cluster size, and *CSp* is an estimate of cluster areal "spread," routinely used in primate censuses to correct for density overestimates of social primates (Peres 1999). Here we reverse the process by solving for encounter rate and we define a new constant *e* that converts density to encounter rate with a simplified expression.

$$N_{x,y,t} = \frac{E_{x,y,t}}{2\left(ESW + \frac{CSp}{3}\right)} \times CSz \qquad \Leftrightarrow \qquad E_{x,y,t} = \frac{2N_{x,y,t}\left(ESW + \frac{CSp}{3}\right)}{CSz} = eN_{x,y,t}$$

B. ***Equations for*** **$r_{\max}(\theta)$, $r_{\min}(\theta)$, $\theta_{\max}$, *and* $\theta_{\min}$**

Working in the first quadrant with *x* and *y* not equal to zero, to facilitate explanation, we can calculate the following values of $\theta_{\min}$, $\theta_{\max}$, $r_{\min}(\theta)$, $r_{\max}(\theta)$ using basic trigonometry. The formulae for $r_{\min}(\theta)$, $r_{\max}(\theta)$ vary depending on which edge of the square bin is hit first and last, which depends on the trajectory defined by θ (See Figure 1)

$$\theta_{\min} = \arctan\left(\frac{y - \frac{1}{2}}{x + \frac{1}{2}}\right)$$

$$\theta_{\max} = \arctan\left(\frac{y + \frac{1}{2}}{x - \frac{1}{2}}\right)$$

$$r_{\min}(\theta) = \frac{x - \frac{1}{2}}{\cos(\theta)} \qquad \text{if } \theta > \arctan\left(\frac{y - \frac{1}{2}}{x - \frac{1}{2}}\right)$$

$$r_{\min}(\theta) = \frac{y - \frac{1}{2}}{\sin(\theta)} \qquad \text{if } \theta < \arctan\left(\frac{y - \frac{1}{2}}{x - \frac{1}{2}}\right)$$

$$r_{\max}(\theta) = \frac{y + \frac{1}{2}}{\sin(\theta)} \qquad \text{if } \theta > \arctan\left(\frac{y + \frac{1}{2}}{x + \frac{1}{2}}\right)$$

$$r_{\max}(\theta) = \frac{x + \frac{1}{2}}{\cos(\theta)} \qquad \text{if } \theta < \arctan\left(\frac{y + \frac{1}{2}}{x + \frac{1}{2}}\right)$$

Using the above values in Equation 7 we find that the integral cannot be solved so we seek an approximation.

C. Spreadsheet solver for analytical solution

We have provided an easy to use spreadsheet (See Supplement) to find (1) the extinction envelope and (2) the monkey population at a radial distance from a settlement. Both of these are functions of input parameters, and as these parameters are changed a graph of the monkey population is updated. Cells requiring inputs are highlighted in yellow.

D. Matlab solver for multiple-settlement analytical solution

We have provided fully commented Matlab code (See Supplement) to create the steady state distribution of a game species. The user can specify the size of the landscape, the number of settlements, their location and population, and hunting parameters. A colormap is output based on the users specifications.

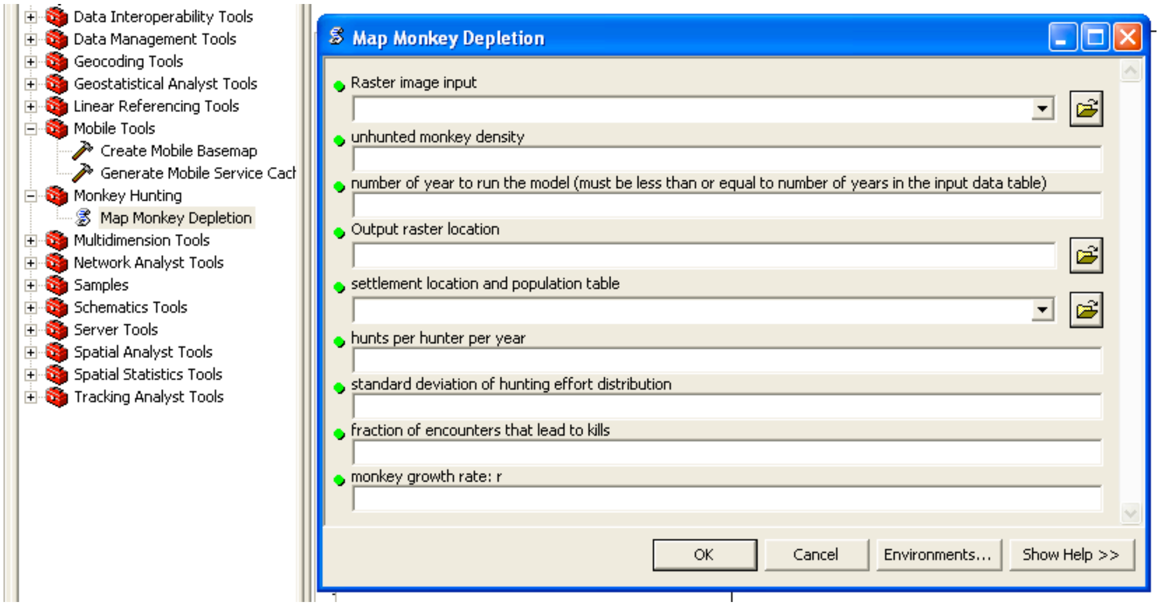
Our figures were produced with the following generated data for clumped and dispersed settlement distributions (Table 4.S1).

Table 4.S1. Generated data used to create colormaps

ID	Hunter Population	Dispersed x	Dispersed y	Clumped x	Clumped y
1	77	144	90	94	26
2	75	136	22	17	20
3	14	43	87	24	24
4	35	16	8	64	50
5	15	55	47	81	30
6	50	174	2	85	47
7	81	112	81	40	25
8	63	93	18	12	22
9	69	86	17	8	39
10	64	155	18	36	37
11	73	131	69	83	22
12	86	132	21	21	3
13	63	32	30	79	4
14	18	86	77	65	40
15	57	101	50	3	33
16	16	75	91	79	2
17	91	96	6	92	28
18	8	68	44	49	36
19	34	155	57	83	6
20	58	77	57	13	11
21	48	142	82	76	41
22	81	96	13	93	7
23	53	146	30	83	44
24	23	188	0	26	46
25	71	103	95	21	1

E. *Using the Python script in ArcGIS*

After adding the *Hunting Mapper* toolbox (See Supplement), double-click the *Map Primate Depletion* script to implement the numerical model (The analytical model can be implemented and analyzed more completely in Matlab (S4), but the script *Map Steady State Primate Depletion* is provided to facilitate map making and the implementation of the model in ArcGis). A window pops up requesting inputs. (1) A raster image of the landscape with units in Meters must be input, and a location and name for the depletion raster output must be specified. (2) Appropriate parameter values must be specified. (3) A table, most easily from a spreadsheet like Microsoft Excel, must be input with the appropriate formatting.



Data Interoperability Tools
Data Management Tools
Geocoding Tools
Geostatistical Analyst Tools
Linear Referencing Tools
Mobile Tools
  Create Mobile Basemap
  Generate Mobile Service Cact
Monkey Hunting
  Map Monkey Depletion
Multidimension Tools
Network Analyst Tools
Samples
Schematics Tools
Server Tools
Spatial Analyst Tools
Spatial Statistics Tools
Tracking Analyst Tools

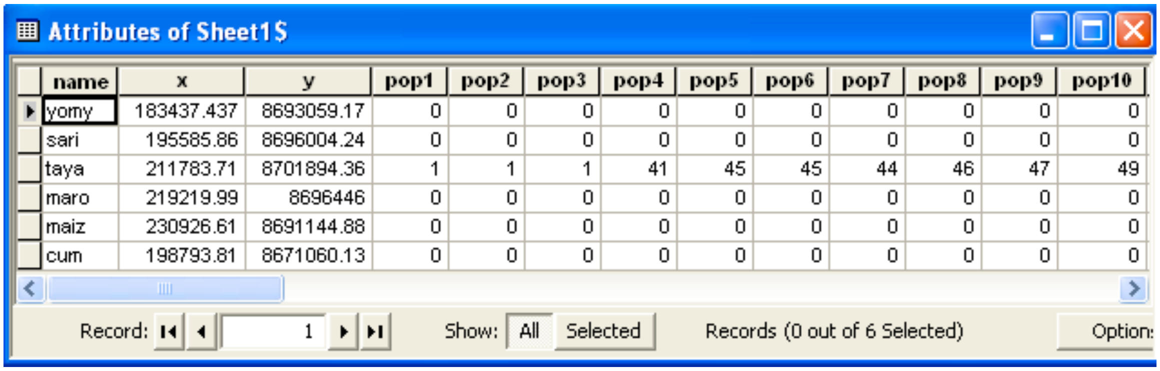
Map Monkey Depletion

- Raster image input
- unhunted monkey density
- number of year to run the model (must be less than or equal to number of years in the input data table)
- Output raster location
- settlement location and population table
- hunts per hunter per year
- standard deviation of hunting effort distribution
- fraction of encounters that lead to kills
- monkey growth rate: r

Figure 4.S1. ArcGIS window for inputting parameters

Each row in the table corresponds to a distinct settlement. At a minimum, the table needs fields labeled ‘x’ and ‘y’ with the UTM x-y values, and fields for the population size in each year to be considered. ‘pop1’ corresponds to the hunter population (males of hunter age) in year one, and in general ‘popn’ is the population in year n (Note that when implementing the analytical model, only a single population size should be input for each settlement and the header of the third column should read ‘pop’ since there is no associated year in the analytical model). The specified parameter for the number of years to run the model must be less than or equal to the number of population fields or the script will return an error (Again, with the analytical model there is no year specification because a steady-state solution is generated).

In the table above, the first ten (of fifty) years of settlement history are visible. Originally, there was only a single settlement and over time new settlements appeared. By adding settlements through time the script incorporates settlement fissioning and spread. Projected population growth and spread can also be input based on the population growth model of the users choice. The name field in the table is optional.



name	x	y	pop1	pop2	pop3	pop4	pop5	pop6	pop7	pop8	pop9	pop10
yomy	183437.437	8693059.17	0	0	0	0	0	0	0	0	0	0
sari	195585.86	8696004.24	0	0	0	0	0	0	0	0	0	0
taya	211783.71	8701894.36	1	1	1	41	45	45	44	46	47	49
maro	219219.99	8696446	0	0	0	0	0	0	0	0	0	0
maiz	230926.61	8691144.88	0	0	0	0	0	0	0	0	0	0
cum	198793.81	8671060.13	0	0	0	0	0	0	0	0	0	0

Figure 4.S2. Necessary format of the settlement location and population data

Note that the diffusion parameter (diffusivity) does not have a field to input. The diffusivity can be changed by opening the script and changing the ‘D’ parameter. The hardwired diffusivity is intended to prevent users from observing traveling waves, which occur due to discretization if the diffusivity is substantially higher than about 0.1. It is possible to allow greater diffusivity without the appearance of traveling waves, but this requires a narrower time window, making the model more computationally expensive.

Appendix F. How Sustainability Indices work, and why we need better methods

Sustainability Indices:

1) A hunting zone “catchment area” around a settlement is chosen arbitrarily.
2) The maximum production of this area is calculated using a sustainability index.
3) Field data are gathered on actual harvests, *H*, and compared to maximum production, *P*.
4) If $H > P$, hunting is unsustainable, but *P* increases with area so this conclusion is sensitive to catchment area. Additionally, $H < P$ may mean *either* that hunting is sustainable *or* that the hunted population is already depleted, causing the encounter rate between hunters and game to be low.

Being spatially explicit is important

Wildlife populations grow most rapidly when below carrying capacity. Given this, consider the following 2 examples, treating a catchment area disk centered on a human settlement:

1) The catchment area has uniform density $\frac{K}{2}$
2) The catchment area has density increasing with distance from the community center

In Example 1, the entire disk is growing at the maximum rate, but in example 2, only a small portion of the area contains a population growing near the maximum rate, and the remaining area is growing more slowly because the density is either above or below $\frac{K}{2}$. Existing sustainability indices incorrectly assume a uniformly depleted catchment area.

Advantages of the biodemographic method

1) Large and expensive field projects are not required, which allows the method to be widely used.
2) Conclusions are not binary and are not sensitive to arbitrary choices in catchment area.
3) Spatial distributions of game are predicted.
4) Multiple settlements can be incorporated, new settlements can be created, and scenarios can be projected.
5) Diffusion of game into the hunting zone can be incorporated

Conclusion

Through concerted management efforts by researchers, government agencies, and NGOs, wildlife has partially recovered from the widespread extirpation of large vertebrates in some parts of the world. As a conservation scientist and population ecologist, my research goal is to contribute to the recovery of wildlife populations and prevent future extinctions. This requires finding unique insight to (1) properly assess impact of humans on wildlife, (2) find politically acceptable management options to minimize this impact, and (3) provide road maps to success for the pressing conservation issues of the 21st century. Despite the bleak picture facing large vertebrates worldwide, there are symbols of hope for the future of wildlife conservation such as the successful recovery of bald eagles and other raptors, the large ungulates of Eastern North America, Northern elephant seals, African elephants, the recolonization of gray wolves to parts of North America, the successful captive rearing program that saved California condors from extinction, and new innovative market-driven approaches to conservation such as conservation funded by ecotourism, trophy hunting, and payments for ecological services.

During the nascent stage of conservation biology as a field of inquiry there was concern regarding its lack of objectivity. The practice of conservation biology has since evolved into a robust field focused on the application of the scientific method and ecological principles to address applied problems. The implicit assumption made throughout this field of research is that wildlife is worth saving. But why should we be concerned about the large primates of the Neotropics, or the grizzly bears and ecosystems that depend on Pacific salmon? One answer suggested by my research on Lyme disease is that altered wildlife communities can negatively impact humans. This case study argues that the removal of top predators can release low-trophic-level species that facilitate the emergence of infectious disease. The message is that perturbing wildlife populations can have unintended consequences for humans. This is a common message in conservation biology, but perhaps a wildlife ethic is not best cultivated by utilitarian arguments.

An alternative approach to wildlife conservation relies on the intrinsic value of other species. In a sense, even the utilitarian approach to conservation relies on intrinsic value at some point. For example, one argument for the conservation of large primates is that they maintain tropical tree diversity as primary seed dispersers. But this argument presupposes that tropical tree diversity has value. This value may be ‘intrinsic’, or perhaps tropical tree diversity supports local economies. However, arguments for conservation that rely on impacts to human health or economies also rely on the intrinsic value of health and livelihoods. The difference is that there is widespread agreement that human health and livelihoods are important. There has been significant progress in cultivating sufficient widespread agreement that humans should not cause the extinction of other species. This is rooted in policy in the United States with the Endangered Species Act of 1973.

Essentially, congress has decreed that as a nation we value the intrinsic value of all species and their right to exist. This is a philosophically deep message for a nation-state, but one that allows me, as a conservation scientist, freedom to research the impacts of humans on wildlife without requiring extensive justification for the importance of maintaining wildlife populations. There is growing global agreement on this issue typified by binding international agreements such as the Convention on International Trade of Endangered Species of Wild Flora and Fauna and the Convention on Biological Diversity.

In this dissertation, I have assumed agreement that wildlife is worth conserving, but I have nevertheless attempted to explicitly quantify conservation-livelihood tradeoffs. In Chapter 1, I presented a method to quantify the tradeoffs between salmon harvests and grizzly bear populations. In Chapters 3 and 4, I quantified the impact of hunting on the spatial distribution of large primate populations, but I also quantified the expected catch-per-unit-effort of this important food source to subsistence hunters. I showed that firearms only provide a short-term advantage for hunters, but in the long run bow-hunters have a higher rate of food acquisition. By limiting the efficiency of hunting, reproductive wildlife populations are locally maintained, which allows time for reproduction to compensate for harvest. Importantly, in both my research on Pacific Salmon and Neotropical primates, I found win-win scenarios for conservation and livelihoods. In the coastal salmon stocks that I assessed, both bears and fisheries are expected to benefit from allocating more salmon to river systems. Similarly, both hunters and wildlife benefit from preventing the adoption of firearms or otherwise limiting the efficiency of hunting.

In Chapter 2, my research focus switched toward understanding the impact of perturbed wildlife populations to humans. In the absence of the gray wolf, which was extirpated by the early 20th century, coyotes have expanded their range into the forests of the upper Midwest and Northeast. I quantified the timing and extent of this expansion as well as its impact on red fox populations. Using models and data, I suggested that the loss of predation services provided by red foxes significantly contributed to the continuing emergence of Lyme disease.

Literature cited

As an example of their potential abundance, in 1986 over 95,000 red fox (and an additional 46,000 gray fox) were harvested in Pennsylvania, which is more than two per square mile. Further, the harvest was consistently above 50,000 annually from 1983 to 1988. .

Albert, B. and F. M. LeTourneau. 2007. Ethnogeography and resource use among the Yanomami: Toward a model of "reticular space". Current Anthropology **48**:1-19.

Alvard, M. 1995. Shotguns and sustainable hunting in the neotropics. Oryx **29**:58-66.

Alvard, M. and H. Kaplan. 1991a. Procurement technology and prey mortality among indigenous neotropical hunters. Boulder: Westview.

Alvard, M. S. and H. Kaplan. 1991b. Procurement technology and prey mortality among indigenous neotropical hunters. Pages 79-104 *in* M. C. Stiner, editor. Human Predators and Prey Mortality. Westview Press, Boulder.

Alvard, M. S., J. G. Robinson, K. H. Redford, and H. Kaplan. 1997. The sustainability of subsistence hunting in the Neotropics. Conservation Biology **11**:977-982.

Austin, M. A., D. C. Heard, and A. N. Hamilton. 2004. Grizzly Bear (Ursus arctos) Harvest Management in British Columbia. Page 9 *in* L. B.C. Ministry of Water, and Air Protection, editor., Victoria, BC.

Bacon, R. M., K. J. Kugeler, and P. S. Mead. 2008. Surveillance for Lyme Disease --- United States, 1992--2006. CDC.

Baker, T. T., L. F. Fair, F. W. West, G. B. Buck, X. Zhang, S. Fleischman, and J. Erickson. 2009. Review of Salmon Escapement Goals in Bristol Bay, Alaska, 2009.*in* A. D. o. F. a. Game, editor. Fishery manuscript series NO. 09-05, Anchorage.

Barbour, A. G. and D. Fish. 1993. The biological and social phenomenon of Lyme disease. Science **260**:1610-1616.

Barlow, J. and C. A. Peres. 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest Philosophical Transactions of the Royal Society B **363**:1787-1794.

Barnosky, A. D. 2008. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. PNAS **105**:11543–11548.

Belgrano, A. and C. W. Fowler, editors. 2011. Ecosystem Based Management for Marine Fisheries: An Evolving Perspective. Cambridge University Press, Cambridge.

Bertrand, J., S. G. d. Salazar, L. Mazariegos, V. Salanic, J. Rice, and C. K. Sow. 1999. Promoting Birthspacing Among the Maya-Quiche of Guatemala. International Family Planning Perspectives **25**:160-167.

Bodmer, R. E., J. F. Eisenberg, and K. H. Redford. 1997. Hunting and the likelihood of extinction of Amazonian mammals. Conservation Biology **11**:460-466.

Bodmer, R. E. and E. P. Lozano. 2001. Rural development and sustainable wildlife use in Peru. Conservation Biology **15**:1163-1170.

Brandon, K., K. H. Redford, and S. E. Sanderson. 1998a. Parks in Peril: People, Politics, and Protected Areas. Island Press, Washington, DC.

Brandon, K., K. H. Redford, and S. E. Sanderson. 1998b. Parks in Peril: People, Politics, and Protected Areas. Island Press, Washington, DC.

Brisson, D., D. E. Dykhuizen, and R. S. Ostfeld. 2007. Conspicuous impacts of inconspicuous hosts on the Lyme disease epidemic. Proceedings of the Royal Society B **275**:227-235.

Browman, H. I., P. M. Cury, R. Hilborn, S. Jennings, Heike K. Lotze, P. M. Mace, S. Murawski, D. Pauly, M. Sissenwine, K. I. Stergiou, and D. Zeller. 2004. Perspectives on ecosystem-based approaches to the management of marine resources. Marine Ecology Progress Series **274**:269-303.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993a. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993b. Distance Sampling: Estimating Abundance of Biological Populations. Chapman & Hall, London.

Bulte, E. and R. D. Horan. 2002. Does human population growth increase wildlife harvesting? An economic assessment. Journal of Wildlife Management **66**:574-580.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.

Connell, J. H. 1980. Diversity and the Coevolution of Competitors, or the Ghost of Competition Past. OIkos **35**:131-138.

Cox-Rogers, S. and J. Sturhahn. 2005. Biological Escapement Goals for Rivers Inlet (Owikeno Lake) Sockeye. Fisheries and Oceans Canada, Prince Rupert, British Coulmbia.

Crooks, K. R. and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:53-566.

da Silva, M. N. F., G. H. Shepard Jr., and D. W. Yu. 2005. Conservation implications of primate hunting practices among the Matsigenka of Manu National Park. Neotropical Primates **13**:31-36.

Damania, R., E. J. Milner-Gulland, and D. J. Crookes. 2005a. A bioeconomic analysis of bushmeat hunting. Proceedings of the Royal Society B **272**:259-266.

Damania, R., E. J. Milner-Gulland, and D. J. Crookes. 2005b. A bioeconomic analysis of bushmeat hunting. Proceedings Of The Royal Society B-Biological Sciences **272**:259-266.

Daneils, T. J., D. Fish, and I. Schwartz. 1993. Reduced abundance of Ixodes scapularis (Acari: Ixodidae) and Lyme disease risk by deer exclusion. Journal of Medical Entomology **30**:1043-1049.

Darimont, C. T., H. M. Bryan, S. M. Carlson, M. D. Hocking, M. MacDuffee, P. C. Paquet, M. H. H. Price, T. E. Reimchen, J. D. Reynolds, and C. C. Wilmers. 2010. Salmon for terrestrial protected areas. Conservation Letters **3**:379-389.

Deblinger, R. D., M. W. Wilson, D. W. Rimmer, and A. Spielman. 1993. Reduced Abundance of Immature Ixodes dammini (Acari: Ixodidae) Following Incremental Removal of Deer. Journal of Medical Entomology **30**:144-150.

Denevan, W. M. 1976. The native population of the Americas in 1492. University of Wisconsin Press.

Ellis, B. 2007. Virginia deer management plan 2006-2015. Wildlife division: Virginia department of game and inland fisheries.

Endo, W., C. A. Peres, E. Salas, S. Mori, J. L. Sanchez-Vega, G. H. Shepard, V. Pacheco, and D. W. Yu. 2010. Game vertebrate densities in hunted and nonhunted forest sites in Manu National Park, Peru. Biotropica **42**:251–261.

Erlinge, S., G. Göransson, L. Hansson, G. Högstedt, Olof Liberg, I. N. Nilsson, T. Nilsson, T. v. Schantz, and M. Sylvén. 1983. Predation as a Regulating Factor on Small Rodent Populations in Southern Sweden. OIkos **40**:36-52.

Fa, J. E., C. A. Peres, and J. Meeuwig. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. Conservation Biology **16**:232-237.

Forchhammer, M. C., N. C. Stenseth, E. Post, and R. Langvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. Proceedings of the Royal Society of London B **265**:341-350.

Ford, J. K., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm, and K. C. Balcomb. 1998. Dietary specialization in two sympatric populations of killer whales (Orcinus orca) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology **76**:1456-1471.

Fowler, C. W. 2009. Systemic management: Sustainable human interactions with ecosystems and the biosphere. Oxford University Press, Oxford.

Gende, S. M. and T. P. Quinn. 2004. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. Canadian Journal of Zoology **82**:75-85.

Gende, S. M., T. P. Quinn, and M. F. Willson. 2001. Consumption choice by bears feeding on salmon. Oecologia **127**:372-382.

Gende, S. M. and M. F. Willson. 2001. Passerine densities in riparian forests of southeast Alaska: potential effects of anadromous spawning salmon. Condor **103**:624-629.

Gompper, M. E. 2002a. The ecology of northeastern coyotes: Current knowledge and priorities for future research. Wildlife Conservation Society.

Gompper, M. E. 2002b. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of North-Eastern North America by coyotes. BioScience **52**:185-190.

Groot, C. and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Hames, R. B. 1979. A Comparison of the Efficiencies of the Shotgun and the Bow in Neotropical Forest Hunting. Human Ecology **7**:219-252.

Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. Small-rodent dynamics and predation. Ecology **82**:1505-1520.

Haugaasen, T. and C. A. Peres. 2007. Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. **Biodiversity And Conservation 16**:4165-4190.

Heckenberger, M. J., J. C. Russell, C. Fausto, J. R. Toney, M. J. Schmidt, E. Pereira, B. Franchetto, and A. Kuikuro. 2008. Pre-Columbian Urbanism, Anthropogenic Landscapes, and the Future of the Amazon. Science **321**:1214-1217.

Helfield, J. M. and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology **82**:2403-2409.

Helfield, J. M. and R. J. Naiman. 2006. Keystone interactions: Salmon and bear in riparian forests of Alaska. Ecosystems **9**:167-180.

Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus, and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears Canadian Journal of Zoology **74**:2080-2088.

Hilderbrand, G. V., S. D. Farley, C. C. Schwartz, and C. T. Robbins. 2004. Importance of Salmon to Wildlife: Implications for Integrated Management. Ursus **15**:1-9.

Hilderbrand, G. V., T. A. Hanley, C. T. Robbins, and C. C. Schwartz. 1999a. Role of brown bears (Ursus arctos) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia **121**:546-550.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999b. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology **77**:132-138.

Hocking, M. D. and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. Science **331**:1609-1612.

Hocking, M. D., R. A. Ring, and T. E. Reimchen. 2009. The ecology of terrestrial invertebrates on Pacific salmon carcasses. Ecological Research **24**:1091-1100.

Hurvich, C. M. and C. L. Tsai. 1989. Regression and Time Series Model Selection in Small Samples. Biometrika **76**:297-307.

Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. Oecologia **159**:583-595.

Janson, C. and L. H. Emmons. 1991. Ecological structure of the non-flying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. Yale University Press, New Haven.

Jerozolimski, A. and C. A. Peres. 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. Biological Conservation **111**:415-425.

Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science **279**:1023-1026.

Jordan, R. A., T. L. Schulze, and M. B. Jahn. 2007. Effects of Reduced Deer Density on the Abundance of Ixodes scapularis (Acari: Ixodidae) and Lyme Disease Incidence in a Northern New Jersey Endemic Area. Journal of Medical Entomology **44**:752-757.

Joshi, N. V. and M. Gadgil. 1991. On the role of refugia in promoting the prudent use of biological resources. Theoretical Population Biology **40**:211-229.

Keesing, F., L. K. Belden, P. Daszak, A. Dobson, C. D. Harvell, R. D. Holt, P. Hudson, A. Jolles, K. E. Jones, C. E. Mitchell, S. S. Myers, T. Bogich, and R. S. Ostfeld. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature **468**:647-652.

Kermack, W. O. and A. G. McKendrick. 1927. A contribution to the mathematical theory of epidemics. Proceedings of the Royal Society of London **A115**:700-721.

Krause, G. F., F. W. Sampson, and J. M. Orr. 1969. Biased coyote harvest estimates: a paradox. The Journal of Wildlife Management **33**:444-446.

Levi, T., G. H. Shepard Jr, J. Ohl-Schacherer, C. A. Peres, and D. W. Yu. 2009. Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: Landscape-scale management implications for Amazonia. Journal of Applied Ecology **46**:804-814.

Ling, S. and E. J. Milner-Gulland. 2006. Assessment of the sustainability of bushmeat hunting based on dynamic bioeconomic models. Conservation Biology **20**:1294-1299.

Link, J. 2010. Ecosystem-Based Fisheries Management: Confronting Tradeoffs. Cambridge University Press, Cambridge.

LInk, J. S. 2005. Translating ecosystem indicators into decision criteria. ICES journal of marine science **62**:569-576.

Lu, F. and B. Winterhalder. 1997. A Forager-Resource Population Ecology Model and Implications for Indigenous Conservation. Conservation Biology **11**:1354-1364.

MacDuffee, M. 2009. The application of Ricker stock recruitment curves to salmon species in Rivers Inlet: Prepared for Rivers and Smith salmon ecosystem planning society meeting.

Major, J. T. and J. A. Sherburne. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in Western Maine. Journal of Wildlife Management **51**:606-616.

McDaniels, T. L. 1995. Using judgment in resource management: a multiple objective analysis of a fisheries management decision. Operations Management **43**:415-426.

McSweeney, K. 2005. A "Demographic Turnaround": The rapid growth of indigenous populations in lowland Latin America. Latin American Research Review **40**:3-28.

McSweeney, K. and S. Arps. 2005. Latin American Research Review. A Demographic Turnaround **40**:3-29.

Milner-Gulland, E., E. Bennett, and and the SCB 2002 Annual Meeting Wild Meat Group. 2003. Wild meat: the bigger picture. Trends in Ecology & Evolution **18**:351-357.

Milner-Gulland, E. J. and H. R. Akçakaya. 2001a. Sustainability indices for exploited populations. Trends in Ecology & Evolution **16**:686-692.

Milner-Gulland, E. J. and H. R. Akçakaya. 2001b. Sustainability indices for exploited populations. Trends In Ecology & Evolution **16**:686-692.

Mitchell, C. L. and E. R. Luna. 1991. The impact of human hunting on primate and game bird populations in the Manu Biosphere Reserve in Southeastern Peru. Wildlife Conservation International: New York Zoological Society.

Mitchell, C. L. and E. F. Raéz-Luna. 1991. The impact of human hunting on primate and game bird populations in the Manu Biosphere Reserve in Southeastern Peru. Wildlife Conservation Society, New York Zoological Society, New York.

Moore, J. W., D. E. Schindler, J. L. Carter, J. M. Fox, J. Griffiths, and G. W. Holtgrieve. 2007. Biotic control of stream ecosystem fluxes: spawning salmon drive nutrient and matter export. Ecology **88**:1278-1291.

Moore, J. W., D. E. Schindler, J. L. Carter, J. M. Fox, J. Griffiths, and G. W. Holtgrieve. 2008. Habitat saturation drives thresholds in stream subsidies. Ecology **89**:306-312.

Morris, W. F. and D. F. Doak. 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis.

Morstad, S., M. Jones, T. Sands, P. Salmomone, T. Baker, G. Buck, and F. West. 2009. 2009 Bristol Bay area annual management report. Alaska Department of Fish and Game, Anchorage, AK.

Mowat, G. and D. C. Heard. 2006. Major components of grizzly bear diet across North America. Canadian Journal of Zoology **84**:473-489.

Mowat, G., D. C. Heard, D. R. Seip, K. G. Poole, G. Stenhouse, and D. W. Paetkau. 2005. Grizzly *Ursus arctos* and black bear *U. americanus* densities in the interior mountains of North America. Wildlife Biology **11**:31-48.

Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs **39**:335-354.

Myers, R. A. and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature **423**:280-283.

Mysterud, A., N. G. Yoccoz, N. C. Stenseth, and R. Langvatn. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. Journal of Animal Ecology **69**:959-974.

Nagasawa, K. 1998. Predation by salmon sharks (Lamna ditropis) on Pacific salmon (Oncorhynchus spp.) in the North Pacific Ocean. National Pacific Anadromous Fish Commision **1**:419-433.

Naughton-Treves, L., J. L. Mena, A. Treves, N. Alvarez, and V. C. Radeloff. 2003. Wildlife Survival Beyond Park Boundaries: the Impact of Slash-and-Burn Agriculture and Hunting on Mammals in Tambopata, Peru. Conservation Biology **17**:1106-1117.

Nepstad, D., S. Schwartzman, B. Bamberger, M. Santilli, D. Ray, P. Schlesinger, P. Lefebvre, A. Alencar, E. Prinz, G. Fiske, and A. Rolla. 2006. Inhibition of Amazon deforestation and fire by parks and indigenous lands. Conservation Biology **20**:65-73.

Nuñez-Iturri, G. and H. F. Howe. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. Biotropica **39**:348-354.

Ohl-Schacherer, J., G. H. Shepard, H. Kaplan, C. A. Peres, T. Levi, and D. W. Yu. 2007a. The Sustainability of subsistence hunting by Matsigenka native communities in Manu National Park, Peru. Conservation Biology **21**:1174-1185.

Ohl-Schacherer, J., G. H. Shepard Jr., H. Kaplan, C. A. Peres, T. Levi, and D. W. Yu. 2007b. The sustainability of subsistence hunting by Matsigenka native communities in Manu National Park, Peru. Conservation Biology **21**:1174-1185.

Ohl-Schacherer, J., A. Wezel, G. H. Shepard, and D. W. Yu. 2008. Indigenous ecotourism in the Amazon: a case study of ム Casa Matsiguenka メ in Manu National Park, Peru. Environmental Conservation **35**:14-25.

Ohl, J., A. Wezel, G. H. Shepard, and D. W. Yu. 2007a. Swidden agriculture in a protected area: the Matsigenka native communities of Manu National Park, Peru. Environment, Development and Sustainability **10**:827-843.

Ohl, J., A. Wezel, G. H. Shepard Jr., and D. W. Yu. 2007b. Swidden agriculture in a human-inhabited protected area: The Matsigenka native communities of Manu National Park, Peru. Environment, Development, and Sustainability **10**:827-843.

Ostfeld, R. S. 2011. Lyme disease: The ecology of a complex system. Oxford University Press, New York.

Ostfeld, R. S., C. D. Canham, K. Oggenfuss, R. J. Winchcombe, and F. Keesing. 2006. Climate, Deer, Rodents, and Acorns as Determinants of Variation in Lyme-Disease Risk. PLOS Biology **4**:1058-1068.

Ostfeld, R. S. and R. D. Holt. 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. Frontiers in ecology and the environment **2**:13-20.

Ostfeld, R. S., E. M. Schauber, C. D. Canham, F. Keesing, C. G. Jones, and J. O. Wolff. 2001. Effects of Acorn Production and Mouse Abundance on Abundance and Borrelia burgdorferi Infection Prevalence of Nymphal Ixodes scapularis Ticks. Vector borne and zoonotic diseases **1**:55-63.

Patterson, B. R. and F. Messier. 2001. social organization and space use of coyotes in Eastern Canada relative to prey distribution and abundance. Journal of Mammalogy **82**:463-477.

Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. Nature **418**:689-695.

Peres, C. 1990. effect of hunting on Western Amazonian primate communities. Biological Conservation **54**:47-59.

Peres, C. 1999. General guidelines for standardizing line-transect surveys of tropical forest primates. Neotropical Primates **7**:11-16.

Peres, C. A. 1994. Indigenous reserves and nature conservation in Amazonian forests. Conservation Biology **8**:586-588.

Peres, C. A. 1996. Use of space, foraging group size, and spatial group structure in gray woolly monkeys (*Lagothrix lagotricha cana*) at Urucu, Brazil: a review of the Atelinae. Pages 467-488 *in* M. A. Norconk, A. L. Rosenberger, and P. A. Garber, editors. Adaptive Radiations in Neotropical Primates. Plenum Publ., New York.

Peres, C. A. 2000a. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conservation Biology **14**:240-253.

Peres, C. A. 2000b. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conservation Biology **14**:240-253.

Peres, C. A. and I. R. Lake. 2003. Extent of nontimber resource extraction in tropical forests: Accessibility to game vertebrates by hunters in the Amazon basin. Conservation Biology **17**:521-535.

Peres, C. A. and H. S. Nascimento. 2006. Impact of game hunting by the Kayapo of south-eastern Amazonia: implications for wildlife conservation in tropical forest indigenous reserves. Biodiversity And Conservation **15**:2627-2653.

Peres, C. A. and E. Palacios. 2007a. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal-mediated seed dispersal. Biotropica **39**:304-315.

Peres, C. A. and E. Palacios. 2007b. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal-mediated seed dispersal. Biotropica **39**:304-315.

Peres, C. A. and M. v. Roosmalen. 2002. Patterns of primate frugivory in Amazonia and the Guianan shield: implications to the demography of large-seeded plants in overhunted tropical forests. Pages 407-423 *in* D. Levey, W. Silva, and M. Galetti, editors. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI International, Oxford.

Peres, C. A. and J. W. Terborgh. 1995. Amazonian nature reserves: an analysis of the defensibility status of existing conservation units and design criteria for the future. Conservation Biology **9**:34-46.

Piccolo, J. J., M. D. Adkison, and F. Rue. 2009. Ecosystem-based escapement goals: a review and prospectus. Fisheries **34**:124-133.

Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology **21**:869-879.

Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E. D. Houde, J. Link, P. A. Livingston, M. Mangel, M. K. McAllister, J. Pope, and K. J. Sainsbury. 2004. Ecosystem-based fishery management. Science **305**:346-347.

Pinheiro, T., S. F. Ferrari, and M. A. Lopes. 2011. Polyspecific associations between squirrel monkeys (Saimiri sciureus) and other primates in eastern Amazonia. American Journal of Primatology **73**:1145-1151.

Quinn, T. P. 2005. The behavior and ecology of Paciic salmon and trout. University of Washington Press, Seattle.

Redford, K. H. 2000. Extracting Humans from Nature. Conservation Biology **14**:1362-1364.

Richerson, K., P. S. Levin, and M. Mangel. 2010. Accounting for indirect effects and non-commensurate values in ecosystem based fishery management (EBFM). Marine Policy **34**:114-119.

Ritchie, E. G. and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters **12**:982-998.

Robb, C. A. and R. M. Peterman. 2005. Application of Bayesian decision analysis to management of a sockeye salmon (Oncorhyncous nerka) fishery. Canadian Journal of Fisheries and Aquatic Sciences **55**:86-98.

Roberts, N. 2008. Furbearer Harvest Assessment and Management. Department of Environmental Conservation, Albany, NY.

Robinson, J. and K. Redford. 1991. Sustainable harvest of neotropical wildlife. Pages 415-429 *in* J. Robinson and K. Redford, editors. Neotropical wildlife use and conservation. University of Chicago Press, Chicago.

Roffe, T. and B. Mate. 1984. Abundance and feeding habits of pinnipeds in the Rogue River, OR. Journal of Wildlife Management **48**:1262-1274.

Sand, H., R. Bergstrom, G. Cederlund, M. Ostergren, and F. Stalfelt. 1996. Density-dependent variation in reproduction and body mass in female moose *Alces alces*. Wildlife Biology **2**:233-245.

Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Sptial relations between sympatric coyotes and red foxes in North Dakota. Journal of Wildlife Management **51**:285-293.

Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology **52**:1944–1956.

Schindler, D. E., P. R. Leavitt, C. S. Brock, S. P. Johnson, and P. D. Quay. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology **86**:3225–3231.

Schwartzman, S. and B. Zimmerman. 2005. Conservation alliances with indigenous peoples of the Amazon. Conservation Biology **19**:721-727.

Shepard, G. H. 2002. Primates in Matsigenka subsistence and worldview. Pages 101-136 *in* A. Fuentes and L. Wolfe, editors. Primates face to face. Cambridge University Press, Cambridge.

Shepard, G. H., K. Rummenhoeller, J. Ohl, and D. W. Yu. 2010. Trouble in paradise: indigenous populations, anthropological policies, and biodiversity conservation in Manu National Park, Peru. Journal of Sustainable Forestry **29**:252–301.

Shepard, G. H., K. Rummenhoeller, J. Ohl, and D. W. Yu. in press. Trouble in paradise: indigenous populations, anthropological policies, and biodiversity conservation in Manu National Park, Peru. Journal of sustainable forestry.

Sirén, A., P. Hamback, and E. Machoa. 2004. Including spatial heterogeneity and animal dispersal when evaluating hunting: a model analysis and an empirical assessment in an Amazonian community. Conservation Biology **18**:1315-1329.

Skalski, J. R., K. E. Ryding, and J. J. Millspaugh. 2005. Wildlife demography: analysis of sex, age, and count data. Acadamic Press, San DIego, CA.

Slade, N., R. Gomulkiewicz, and H. M. Alexander. 1998. Alternatives to Robinson and Redford's method of assessing overharvest from incomplete demographic data. Conservation Biology **12**:148-155.

Smith, D. A. 2008. The spatial patterns of indigenous wildlife use in western Panama: Implications for conservation management. Biological Conservation **141**:925-937.

Souza-Mazurek, R. R. D., P. Temehe, F. Xinyny, H. Waraié, G. Sanapyty, and M. Ewepe. 2000. Subsistence hunting among the Waimiri Atroari Indians in central Amazonia, Brazil. Biodiversity And Conservation **9**:579-596.

Spielman, A., M. L. Wilson, J. F. Levine, and J. Piesan. 1985. Ecology of Ixodes Dammini-Borne Human Babesiosis and Lyme Disease. Annual Review of Entomology **30**:439-460.

Stafford, K. C., A. J. Denicola, and H. J. Kilpatrick. 2003. Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) and the tick parasitoid *Ixodiphagus hookeri* (Hymenoptera: Encyrtidae) with reduction of white-tailed deer. Population and Community Ecology **40**:642-652.

Stephens, P. A., F. Frey-Roos, W. Arnold, and W. J. Sutherland. 2002. Model complexity and population predictions. The alpine marmot as a case study. Journal of Animal Ecology **71**:343-361.

Symington, M. M. 1988. Demography, ranging patterns, and activity budgets of black spider monkeys (Ateles paniscus chamek) in the Manu National Park, Peru. American Journal of Primatology **15**:45-67.

Terborgh, J. 1999a. Requiem for Nature. Island Press, Washington DC.

Terborgh, J. 1999b. Requiem for nature. Shearwater Books, Washington, D. C.

Terborgh, J. 2000. The fate of tropical forests: a matter of stewardship. Conservation Biology **14**:1358-1361.

Terborgh, J., G. Nunez-Iturri, N. C. A. Pitman, F. H. C. Valverde, P. Alvarez, V. Swamy, E. G. Pringle, and C. E. T. Paine. 2008a. Tree recruitment in an empty forest. Ecology **89**:1757-1768.

Terborgh, J., G. Nunez-Iturri, N. C. A. Pitman, F. H. C. Valverde, P. Alvarez, V. Swamy, E. G. Pringle, and C. E. T. Paine. 2008b. Tree recruitment in an empty forest. Ecology **89**:1757-1768.

Terborgh, J. and C. A. Peres. 2002. The problem of people in parks.*in* J. Terborgh, C. V. Schaik, L. Davenport, and M. Rao, editors. Making parks work: strategies for preserving tropical nature. Island Press.

Tremblay, J.-P., M. Crete, and J. Huot. 1998. summer foraging behavior of eastern coyotes in rural versus forest landscape: A possible mechanism of source sink dynamics. Ecoscience **5**:172-182.

Tsao, J. I., J. T. Wootton, J. Bunikis, M. G. Luna, D. Fish, and A. G. Barbour. 2004. An ecological approach to preventing human infection: Vaccinating wild mouse reservoirs intervenes in the Lyme disease cycle. Proceedings of the National Academy of Sciences **101**:18159-18164.

Turchin, P. 2003. Complex Population Dynamics: A theoretical/empirical synthesis. Princeton Univsersity Press, Princeton, NJ.

VanDeelen, T. R. and D. R. Etter. 2003. Effort and the functional response of deer hunters. Human Dimensions of Wildlife **8**:97-108.

Way, J. G., I. M. Ortega, and P. J. Auger. 2002. Eastern coyote home range, territoriality and sociality on urbanized Cape Cod, Massachusetts. Northeast Wildlife **57**:1-18.

Williams, R., M. Krkosek, E. Ashe, T. A. Branch, S. Clark, P. Hammond, E. Hoyt, D. Noren, D. Rosen, and A. Winship. 2011. Conflicting conservation objectives for predators and prey: estimating prey requirements of killer whales for salmon in the Pacific Northwest. PLoS ONE **6**.

Willson, M. F. and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology **9**:489-497.

Wilson, M. L., J. F. Levine, and A. Spielman. 1984. Effect of deer reduction on abundance of the deer tick (Ixodes dammini). Yale Journal of Biology and Medicine **57**:697-705.

Wilson, M. L., S. R. I. Telford, J. Piesman, and A. Spielman. 1988. Reduced abundance of immature *Ixodes dammini* ticks (Acari: Ixodidae) following removal of deer. Journal of Medical Entomology **25**:224-228.

Woodby, D., D. Carlile, S. Siddeek, F. Funk, J. H. Clark, and L. Hulbert. 2005. Commercial fisheries of Alaska. Alaska Department of Fish and Game, Anchorage.

Yu, D. W. 2009. Managing the exploitation of wildlife in tropical forests *in* N. S. Sodhi and P. R. Ehrlich, editors. Conservation Biology for All. Oxford University Press, Oxford.

Yu, D. W. 2010. Managing the exploitation of wildlife in tropical forests Pages 121-123 *in* N. S. Sodhi and P. R. Erlich, editors. Conservation Biology for All. Oxford University Press, Oxford.