Including Spatial Heterogeneity and Animal Dispersal When Evaluating Hunting: a Model Analysis and an Empirical Assessment in an Amazonian Community

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Abstract: Hunting in tropical forests is typically most intense near human settlements, and this creates gradients of decreasing animal densities toward those settlements. Within the context of this spatial pattern, we evaluated the status of game in the hunting grounds of an indigenous community in eastern Ecuador. We constructed a spatially explicit model of hunter-prey interactions that mimicked the hunting in the village and included realistic animal-dispersal rules. We compared predictions from the model with distributions of animal harvest rates and catch per unit effort of 12 game species. Six species were overharvested in part or all of the area, and two other species were probably being overharvested, although high dispersal rates complicated the interpretation. We then compared our method with methods that have been used previously. We argue that because our method provides information about the spatial extent of overharvesting, it could be particularly useful in informing decision makers about where to establish no-take areas and could therefore aid in improving the sustainability of hunting in tropical forests.

Key Words: Amazonia, hunting effort, no-take areas, spatially explicit harvest model, sustainable harvesting

Inclusión de Heterogeneidad Espacial y Dispersión de Animales al Evaluar Cacería: un Análisis de Modelo y una Estimación Empirica en una Comunidad Amazónica

Resumen: Típicamente, la cacería en bosques tropicales es más intensa cerca de asentamientos humanos, y esto crea gradientes de densidades animales decrecientes hacia esos asentamientos. En el contexto de este patrón espacial evaluamos el estatus de animales en los terrenos de cacería de una comunidad indígena en el este de Ecuador. Construimos un modelo espacialmente explícito de interacciones cazador-presa que imitaba la cacería en el poblado e incluía reglas reales de dispersión de animales. Comparamos las predicciones del modelo con las distribuciones de tasas de cosecha y de captura por unidad de esfuerzo de 12 especies cinegéticas. Seis especies eran sobre explotadas en parte o toda el área, y probablemente dos especies más eran sobre explotadas, aunque altas tasas de dispersión complicaron la interpretación. Luego comparamos nuestro método con métodos utilizados previamente. Debido a que nuestro método proporciona información sobre la extensión espacial de la sobre explotación, sostenemos que puede ser particularmente útil para informar a tomadores de decisiones sobre donde establecer áreas sin captura y por tanto ayudar al mejoramiento de la sustentabilidad de la cacería en bosques tropicales.

Palabras Clave: Amazonía, áreas sin captura, cosecha sustentable, esfuerzo de caza, modelo de cosecha espacialmente explícito
Introduction

Wild game is an important source of food and income for the inhabitants of rural Amazonia and other tropical rainforests (Redford 1992). Game species also perform important functions as herbivores, seed predators, and seed dispersers, and the absence of these animals could lead to significant ecological chain effects (e.g., Redford 1992; Fragoso & Huffman 2000; Roldán & Simoniatti 2001). For both reasons, it is problematic that game populations in tropical rainforests are being overharvested (Redford 1992; Robinson & Bennett 2000).

Adjusting harvest levels based on the productivity of each game species requires understanding how different harvest levels affect game populations. In that respect, two important models have been constructed. First, Robinson and Redford (1991) calculated maximum sustainable yield (MSY) for Amazonian game mammals, based on species-specific estimates of carrying capacity and intrinsic rate of natural increase (see also Slade et al. 1998). The MSYs are then compared with observed harvest rates to evaluate whether these rates are sustainable. The model has been used for evaluating the sustainability of hunting in tropical forests of South America (Alvaredo et al. 1997; Hill & Pawde 2000; Mena et al. 2000) and Africa (Fa et al. 1995; Fitzgibbon et al. 1995; Muchaal & Ngandjui 1999). Second, Bodmer (1994; see also Robinson & Bodmer 1999; Bodmer et al. 2000; Townsend 1996) elaborated a model based on population-specific birth rates and densities to calculate production values for comparison with harvest rates. A practical problem with this method is that it requires the use of labor-intensive line transects to calculate population density.

Milner-Gulland and Akçakaya (2001) evaluated how current methods for evaluating sustainability of hunting in tropical forests performed under conditions of uncertainty, bias in parameter estimation, and habitat loss and concluded that current methods are prone to overestimate the sustainable level of harvest. These authors also point out that current methods do not incorporate spatial heterogeneity. Hunting effort in tropical forests is typically highest near human settlements. Therefore, densities of major game species tend to decrease with distance from settlements (Robinson & Bennett 2000; Peres & Lake 2003). Moreover, Townsend (1996), Begazo and Bodmer (1998), and Novaro et al. (2000) suggest that many species function as source-sink systems, where remote areas with low hunting pressure produce a surplus of animals that disperse to areas closer to settlements, where they are hunted. Thus, to understand the dynamics of the interactions between hunters and game populations, it is necessary to take into account two separate spatial phenomena: (1) uneven distribution of hunting effort, which tends to create gradients in animal densities and (2) animal dispersal, which tends to smooth out these gradients.

The approach we used is different from that of previous models. Instead of asking how much can be sustainably harvested, we asked where production can be increased. We believe that this question is relevant to the management of Amazonian wildlife because, for instance, no-take areas have been proposed by scientists as promising management tools in situations with a high level of uncertainty (e.g., Quinn et al. 1993; Mosquera et al. 2000; Milner-Gulland & Akçakaya 2001; Lockwood et al. 2002). Specifically, we show that hunting effort, harvest rate, and catch per unit of effort (CPUE) varied over the hunting territory of an Amazonian community. We then used this spatial gradient of hunting effort as a quasi-experimental setting and, for each species, made a preliminary assessment of the spatial extent of overharvest, where overharvest means that animal density is reduced to a point where its full productive potential is not realized. Finally, we developed a spatially explicit model to evaluate how animal dispersal affects observed spatial patterns of harvest rates and CPUE.

Study Area, Species, and Hunting Methods

Our study area was in the Quichua community of Sarayacu (1°44’S, 77°29’W), situated in roadless land along the Bobonaza River in eastern Ecuador. The community consisted of five clustered hamlets (Fig. 1) of 137 households and 960 inhabitants. The area was dominated by old-growth tropical rainforest, except next to the settlement (Table 1). The elevation was 330–640 m above sea level, and local people recognized two dominant forest types, plain forest and hill forest, which were fairly evenly distributed over the area. For most terrestrial animals, the area was fairly homogenous in terms of habitat quality, an important assumption underlying the methods we used for interpreting our field data.

Hunting and fishing were the most important sources of animal protein for local people. Shotguns were the dominant hunting weapons, although occasionally spears, blowguns, machetes, or stones were used. Most hunting was done by walking, sometimes with a dog, through the forest in the daytime. At night, hunters with torchlights followed waterways. Hunters also waited for animals at fallen fruit or at bait they had set, for instance when hunting large rodents and armadillos and occasionally when hunting deer and tapir. To hunt birds that sing at night, hunters first located the tree where the bird was singing and then waited there until dawn to shoot it. We recorded hunting kills of over 60 species, but we limited our analysis to the 12 most preferred game species (Table 2).

Methods

Field Study

Volunteer community members reported on hunting activities. Primarily, we used the household as our sampling unit because this provided a sample of both frequent and
occasional hunters. Random sampling was not an option because some people initially regarded the project with suspicion and could have misinterpreted a random selection of their households as an attempt of coercion. Avoiding such potential sources of conflict was particularly important because the fieldwork coincided with a period of extreme social tension related to planned oil-prospecting activities in the area. Therefore, because sampling was based on voluntary participation, we could have a skewed sample. To control for this possibility, we asked key informants from each hamlet to group the households into four categories according to their level of hunting activity: (1) do not hunt, (2) hunt little, (3) hunt much nearby, or (4) hunt much far away. This grouping showed that households of all categories, except that of do not hunt, were fairly equally represented among participants. Excluding the households that do not hunt, 122 households remained. Out of these, 85 households (70%) participated in the study. We are therefore confident that the participating households constitute a representative sample of the community.

At the start of the study, participating households received a form for reporting their hunting activities. One person, usually the most active hunter in the household, recorded his own hunting activities and those of other household members. After 8 months of data collection, we recruited field assistants in each hamlet to collect data. Most assistants had previously been in charge of reporting hunting activities from their own household and were selected because they had shown particular skills and interest in the study. The assistants were 16–35 years old and had primary or secondary schooling. They were also employed in other research activities, and various training events were arranged to increase their skill. On a rotational basis, A.S. and J.M. accompanied the assistants to supervise their work. Occasionally, assistants switched

Table 1. Hunting effort and land cover in the Sarayacu community for each zone (according to interpretation of a Landsat ETM+ satellite image from 2001).

| Zone | Hunting effort (km/km²/year) | Area (km²) | Old forest (%) | Young forest (%) | Gardens (%) |
|------|-----------------------------|------------|----------------|-----------------|------------|
| 1    | 8                           | 222        | 99.9           | 0.1             | 0.0        |
| 2    | 20                          | 161        | 99.8           | 0.2             | 0.0        |
| 3    | 34                          | 143        | 99.0           | 0.9             | 0.1        |
| 4    | 54                          | 148        | 99.0           | 0.9             | 0.0        |
| 5    | 75                          | 156        | 98.0           | 1.8             | 0.1        |
| 6    | 114                         | 136        | 96.9           | 3.0             | 0.2        |
| 7    | 285                         | 63         | 74.6           | 23.5            | 1.9        |
| Total| 61                          | 1028       | 97.7           | 2.2             | 0.2        |

a Zones pictured in Fig. 1.

b Old forest includes primary forest and fallows older than 20 years, whereas young forest refers to fallows younger than 20 years.
Table 2. Biological characteristics of study species and annual harvest and hunting methods in the Sarayacu community.

| Species                      | Annual harvest % of weight (kg) | Maximum total weight (%) | Home range (km²) |
|------------------------------|--------------------------------|--------------------------|------------------|
| **Agouti paca** (rodent)    | 16.1                           | 7.9                      | 1.95             |
| **Tayassu tajacu** (ungulate)| 9.1                            | 20.4                     | 3.45             |
| **Tapirus terrestris** (ungulate) | 8.7                          | 120.8                    | 16.3             |
| **Dasyprocta fuliginosa** (rodent) | 6.2                          | 120                      | 2.1              |
| **Mazama americana** (ungulate) | 4.9                            | 120                      | 1.4              |
| **Mazama gouazoubira** (ungulate) | 4.9                            | 120                      | 1.4              |
| **Tayassu pecari** (ungulate) | 4.4                            | 32.0                     | 2.3              |
| **Lagothrix lagotricha** (primat) | 3.3                          | 5.8                      | 7.69             |
| **Nothocrax urumutum** (bird) | 3.3                            | 1.7                      | ND               |
| **Alouatta seniculus** (primate) | 1.3                            | 7.0                      | 1.46             |
| **Mitu salvini** (bird)      | 0.3                            | 3.1                      | 1.51             |
| **Ateles belzebuth** (primate) | 0.2                            | 6.8                      | 1.08             |

a Abbreviation: ND, no data.

Based on references 16 and 17, (see footnote d) and our own data.

Annual divided by maximum sustainable yield (MSY) according to reference 5 (see footnote d).

Hunts realized while walking carrying a shotgun, regardless of the primary purpose of the trip.

Originally defined as canoe trips with the specific purpose of hunting. Because of some confusion among field assistants and among recording hunters, this also includes some hunts

Waiting and dawn under the tree of a singing bird.

Hunts of animals encountered while not carrying a shotgun. In some cases animals were killed with a harpoon or arrow.

A.F.C. Gaulin & C.K. Gaulin, quoted in reference 6. A. Nishimura 1990, quoted in reference 6. N. Robinson & D. Redford 1990; 3, T.R. Defler, quoted in reference 6. 4, J.R. Delano, quoted in reference 6. 5, S.H. Defler & D. Redford 1990; 6, T.R. Defler, quoted in reference 6. 1, S.H. Defler, quoted in reference 6. 2, T.R. Defler, quoted in reference 6. 3, T.R. Defler, quoted in reference 6. 4, J.R. Delano, quoted in reference 6. 5, S.H. Defler & D. Redford 1990; 6, T.R. Defler, quoted in reference 6. 7, C.A. Peres 1994, quoted in reference 6. 8, D.P. Stevenson 1994, quoted in reference 6. 9, Defler & Defler 1994; 10, C.A. Peres 1994, quoted in reference 6. 11, T.R. Defler, quoted in reference 6. 12, J.L. Fragoso 1998; 13, B. Bezago & G. Bodmer 1998; 14, J. Herrera & M. Taber 2001; 15, J. Herrera & M. Taber 2001; 16, M. Medici et al. 2001; 17, M. Medici et al. 2001; 18, T.R. Defler, quoted in reference 6. 19, B. Bezago & G. Bodmer 2000; 20, M. Palacios & M. Rodriguez 2001; 21, J. Suarez 2002.

j Based on observations of a tagged, free-ranging, semiwild tapir in our study area.
duties, collecting data forms in hamlets other than their own.

One side of the form featured a map of the community territory and its surroundings divided into 145 areas, each with a unique number, that were similar in size and had limits represented by well-defined terrain features. Out of these 145 areas, we excluded 48 from the analysis because interviews with key informants showed that these were principally used by hunters from neighboring communities. On the map, hunters drew the trajectories traveled while hunting and marked with a cross places where they used sit-and-wait hunting methods. Later, we measured trajectories with a ruler in order to use the trajectory length as a measure of hunting effort in each area. The other side of the form contained drawings of 58 game animals, with the local name and columns for indicating the area number, hunting method (according to categories indicated in Table 2), and habitat. The drawings made it possible for illiterate people to indicate the number of animals hunted by putting crosses next to the animal. When collecting the forms, about every 2 weeks, we performed detailed interviews to double-check and complement the recorded information.

Because of an annual hunting festival and adjustments in the sampling regime half-way through the study, we had three data sets: nonfestival, festival, and large animals. The nonfestival data set was collected from May 1999 to July 2000 and includes all regular hunting activities by the participating households. During this period, participating households in hamlets changed about every 3 months, usually in connection to hamlet workshops, where we presented results and treated issues related to the project. The sample was geographically stratified because the number of participating households from each hamlet was roughly proportional to the total number of households in the hamlet. Similarly, during school vacations, when households move to secondary homes to enjoy better hunting and fishing, households were grouped into eight geographical zones. The number of households in the sample increased with time from 14 to 24. To avoid bias due to variation in sample size between seasons, we applied month-specific weighting factors when converting the harvest data to an estimate of annual harvest in each area.

Prior to the hunting festival, groups of hunters belonging to three festival houses spend about a week going to the remotest corners of the community territory to hunt huge amounts of game. So we collected data at the individual rather than household level during festival time. Out of 48 festival hunters, 40 reported their hunting activities, providing a weighting factor of 1.2 for estimating annual harvest rates for festival hunting. At the same time we collected the festival data, recording of hunting activities not directly related to the festival continued as usual. To estimate total annual harvest, we added annual harvest rates from the two data sets, festival and nonfestival.

After 1 year of data collection, we had sufficient data on hunting effort and harvest of most small species but insufficient data for larger species. Therefore, from April 2000 to April 2001, we collected data on large animals by using a simplified form featuring all 12 species except A. paca, D. fuliginosa, and N. urumutum and asking for data only on harvest and not on hunting effort. We assumed our results on hunting effort from the first year could be extrapolated to the following year. The sample size for this data set was 35–40 households but varied between hamlets, such that we applied hamlet-specific weighting factors when calculating annual harvest rates.

For species not included in the large-animal data set, all calculations were based only on the nonfestival and festival data sets, which included data from 7532 household-participation days (the sum of the number of days each household participated) and 12,716 km walked by hunters. For the species included in the large-animal data set, the annual harvest was calculated as a weighted (according to the number of household participation days) average of one estimate based on the nonfestival and festival data sets and another estimate based on the large-animal data set. Together, this included data from 20,800 household-participation days and approximately 35,000 km walked by hunters.

Because the majority of recorded hunting kills were made when hunters were walking (Table 2), we used the kilometers walked per square kilometer per year as a measure of hunting effort in each area. Other researchers have used time rather than distance as a measure of hunting effort in tropical forests (e.g., Vickers 1988; De Souza-Mazurek et al. 2000), but this was not possible because of the high spatial resolution of our data collection. To aggregate the areas into hunting effort zones, we first smoothed the hunting effort with geographic information system software. We converted the map into a grid of cells of 250 × 250 m, in which each cell was assigned the average hunting effort of all cells within the surrounding 8 × 8 km square. We calculated the smoothed value for each area as the average value for all cells within the area. Finally, areas were grouped into seven zones according to hunting effort: zone 1 had the lowest hunting effort and zone 7 the highest (Fig. 1). Hunting effort for each zone was calculated by summing the original (unsmoothed) values for all the areas within a zone and dividing by the total area of the zone.

Harvest rates were calculated as annual harvest in a zone divided by its area in square kilometers. Catch per unit effort (CPUE) was calculated as the number of killed individuals in a zone divided by hunting effort. We used CPUE as a proxy for population density, as is commonly done in studies of fish (e.g., Salthaug & Godø 2001; Marchal et al. 2002) and occasionally in studies of game mammals (Novak et al. 1991; Lancia et al. 1996). Using CPUE as a proxy for density rests on the assumption that an animal encounter always leads to a hunting attempt, which
is fairly reasonable for the 12 species we examined. For *A. pacas*, *D. fuliginosa*, *N. urumutum*, and *M. salvini*, which were frequently hunted using sit-and-wait methods, only hunting kills achieved when walking were included in the calculations of CPUE. For other species, particularly *Mazama* spp., *T. terrestris*, and *M. salvini*, even when these species had been hunted with sit-and-wait methods, the actual encounter (finding tracks or hearing song) occurred while walking. Therefore, all hunting kills of these species, regardless of method, were included in the calculations of CPUE.

For each species, we examined harvest rate as a function of hunting effort and CPUE as a function of effort. To interpret these data, we performed linear regressions on harvest rate versus hunting effort and on ln(CPUE) versus ln(hunting effort). The log transformation in the latter regression was used because of the obvious nonlinearity in the data. A decreasing harvest rate with increasing hunting effort indicates overharvest because the local population is reduced below the density that yields maximum production. Also, decreasing CPUE with increasing hunting effort indicates that hunting reduces population densities, and, when this decrease is substantial, it may indicate overharvesting.

**Model of Spatial Interactions between Hunter and Prey**

To determine whether observed patterns could be affected by animal dispersal, we developed a spatially explicit model of hunter-prey interactions that mimicked the hunting practices in the village. With this model, we evaluated the role of animal dispersal and total hunting intensities on the spatial distribution of CPUE and harvest rates.

We used a standard, discrete-time population model (Yodzis 1989) to which we added spatial structure (for a similar continuous-time model, see Quinn et al. 1993). Spatial structure was introduced by separating the area into 100 patches that were linearly connected (results are independent of the number of patches and the specific location of patches relative to each other). Within each patch, population dynamics depended on the local reproduction, the number of animals killed, and the number of animals migrating to and from the patch. Mathematically, the different processes were entered sequentially into the model, and the dynamics of individuals (*N*) in patch *i* from time *t* to *t* + 1 were then described as

\[ N_{i,t+1} = (1 - E_i)(1 - H_i)R_i(N_{i,t})N_{i,t} + \sum_j E_j N_j, \]

where *E* is the emigration probability from patch *i*, *H* is the proportion killed in patch *i*, *R* is the density-dependent reproductive rate, and the last term is the sum of immigration from other patches.

To make the model specific to the problem, we made the following additional assumptions: (1) prey birth rates were density-dependent as a logistic growth function; (2) hunting effort was normally distributed, with the highest effort at the village in the center (Fig. 2); and (3) most dispersal was local, with a smaller number of long-range dispersers, as is known for both mammals and birds (Waser 1987; Turchin 1998). We assumed that the redistribution of individuals followed a Gaussian distribution similar to dispersal functions used in fisheries management models (Quinn et al. 1993; Lockwood et al. 2002).

We introduced these assumptions into Eq. 1 in the following way. First, local birth rates were assumed to depend on local density according to a standard logistic growth function,

\[ R(N) = r \left( 1 - \frac{N}{K} \right)^\beta, \]

where *r* is the maximum number of offspring per individual, *K* is the maximum number of individuals per patch, and *β* is a parameter describing the shape of the density dependence. Second, local hunting effort (*b*) was modeled as a Gaussian distribution,

\[ b = ab_{max}e^{-\frac{1}{2}(z/a)^2}, \]

where *b* is the hunting intensity at the area center, *s* is the standard deviation of the distribution in hunting intensity, *z* is the distance from the village, and *a* is a parameter describing the probability of discovering and killing an animal in the patch. Assuming a standard type I functional response (Yodzis 1989), local hunting effort
was transformed to the proportion of surviving animals ($S_i$) as

$$S_i = 1 - H_i = e^{-b}.$$  \hspace{1cm} (4)

Third, we assumed that the redistribution of animals followed a Gaussian distribution,

$$E_x = \frac{1}{2\sqrt{\pi d}} e^{-[x^2/4d]},$$  \hspace{1cm} (5)

where $E$ is the probability of dispersing $x$ distance units from the previous position and $d$ is a space-independent dispersal rate. Dispersal here means the redistribution of individuals over time (sensu Turchin 1998) and does not necessarily correspond to speed of movement or similar physical measures. When calculating the redistribution, we assumed that there was no net migration across area borders.

We started each simulation with animal densities at carrying capacity and ran it 100 time units, at which point the total number and the distribution had stabilized. Through simulations, we explored a range of hunting intensities ($P_{max} = 0.1-65000$), animal dispersal rates ($d = 0-1250$), and maximum birth rates ($r = 0.01-0.6$), while keeping the remaining parameters fixed ($K = 100$, $\beta = 2.4$, $s = 7$).

**Results**

**Field Study**

Hunting effort was 37 times higher in the central area (zone 7) than in the most remote area (zone 1), and the distribution of hunting effort in space approximately followed a Gaussian distribution (Fig. 2). According to the results of the regression analysis, we divided the species into four groups, representing different degrees of overharvesting.

Group 1 ($L. lagotricha$) was the most overharvested (Fig. 3a & 3b). There was a negative correlation between harvest and hunting effort and a negative correlation between CPUE and hunting effort.

Group 2 species ($T. tajacu$, $T. terrestris$, $M. salvini$, $N. urumutum$, and $M. gouazoubira$) (Fig. 3c–l) showed signs of overharvesting but to a lesser degree than group 1 species. Similar to group 1, there was a negative correlation between CPUE and hunting effort, but there was no correlation between harvest rate and hunting effort. Instead, harvest rate peaked at an intermediate hunting effort. The sharp decrease in CPUE values therefore occurred at higher hunting efforts for the group 2 species than for the group 1 species, indicating that populations in the zones of low hunting intensity may be less reduced by hunting.

Group 3 species ($M. americana$, $T. pecari$, and $A. seniculus$) showed ambiguous results. Similar to group 1 and 2, CPUE and hunting effort were negatively correlated for $M. americana$ (Fig. 3m), but there was also a positive correlation between harvest rate and effort (Fig. 3n). $T. pecari$ and $A. seniculus$ showed no correlation for either regression (Fig. 3o–r). The lack of correlation between CPUE and hunting effort may mean that species are not being overharvested, whereas the lack of correlation between harvest rate and hunting effort may indicate overharvesting. Hunters often killed several individuals of these species at the same time, however, so the results are sensitive to single hunting events.

Group IV species ($A. paca$, $D. fuliginosa$, and $A. belzebul$; Fig. 3s–y) showed no indications of overharvesting. Harvest rate and hunting effort were positively correlated, and there was no correlation between CPUE and hunting effort.

For those species showing signs of overharvesting (groups 1 and 2), we visually examined where each species was overharvested based on the criterion that CPUE should be considerably less than 60% of the maximum CPUE (see Robinson & Redford 1991). According to this criterion, all group 2 species are overharvested in zones 6 and 7 and in some cases also in zones 4 and 5 ($T. tajacu$ and $T. terrestris$), whereas $L. lagotricha$ is overharvested in zones 2–7. Because the maximum CPUE may underestimate carrying capacity, this criterion provides only minimum estimates of the spatial extent of overharvest.

**Spatial Interaction Model**

In the model analysis, we related the total harvest for the area to the maximum total harvest at a given dispersal and reproduction rate because the maximum total harvest occurs at different levels of hunting effort for different dispersal and reproduction rates. For all scenarios, the maximum harvest occurred at an intermediate effort, and we examined three hunting scenarios in relation to the peak harvest (Fig. 4): good management (90% of maximum harvest; Fig. 5a–d); moderate overharvesting (80% of maximum harvest; Fig. 5e–h); and severe overharvesting (20% of maximum harvest; Fig. 5j–m). We selected a harvest level of less than the maximum harvest to represent good management because (1) this way total hunting effort is reduced, which is desirable for hunters per se and (2) the maximum harvest is rather unstable because a small increase in hunting effort would lead to a considerable reduction in harvest (Fig. 4).

The analysis showed that the harvest and CPUE within each patch depended predictably on the animal dispersal and reproduction rates. When a species with a low dispersal rate was overharvested, harvest rate was highest at very low hunting effort, and there was a sharp decrease in CPUE from the minimum hunting effort to slightly higher efforts (Fig. 5j–k, dotted lines). This occurred because individuals were exterminated in the heavily hunted areas around the village, and most animals were therefore
Figure 3. Harvest rate (graphs on the left) and catch per unit effort (CPUE, graphs on the right) as a function of local hunting effort for 12 game species hunted in the Sarayacu community. Each graph shows mean values for each of seven hunting zones, where a higher value on the x-axis indicates a higher hunting effort. The right y-axis in the graphs on the left show values of harvest/maximum sustainable yield as calculated according to the method of Robinson and Redford (1991). Species were divided into four groups, depending on the shape in the relation between variables. Group 1 species showed a negative relation for both harvest rate and CPUE with respect to hunting effort. Group 2 species showed a negative relation only between CPUE and hunting effort. Group 3 species showed ambiguous results. Group 4 species showed only a positive relation between harvest rate and hunting effort.
killed far from the village (Fig. 5l–m, dotted lines). For a well-managed population, on the contrary, the harvest diagram is almost linearly increasing and CPUE only slightly decreased (Fig. 5a–b, dotted lines).

On the other hand, when a species with a high dispersal rate was overharvested, the pattern of harvest and CPUE in relation to the local hunting effort (Fig. 5j–k, solid lines) was almost indistinguishable from that for a well-managed
Figure 4. Distribution of total harvest in relation to hunting effort from computer simulations. The simulations used total hunting efforts corresponding to 90%, 80%, and 20% of maximum harvest for each dispersal and reproductive rate, representing good management, moderate overharvesting, and severe overharvesting. The x-axis shows the hunting effort across the entire area. The top of the curve should not be confused with maximum sustained yield.

population (Fig. 5a–b, solid lines). In these cases, there was always an almost linear relation between local hunting effort and local harvest rate, and therefore almost no relation between hunting effort and CPUE. This occurred because animals redistributed themselves much faster than depletion occurred in the heavily hunted area. At intermediate dispersal rates (Fig. 5, hatched lines), the differences between a well-managed and an overexploited population were discernible, although less apparent than at low dispersal rates.

The effect of varying the animal reproductive rate had consequences similar to those of varying the dispersal rate (Fig. 6). A high reproductive rate had the same effect as a low dispersal rate on the relation between local hunting intensity and harvest, and a very low reproductive rate had roughly the same effect as a high dispersal rate. These results should be understood in light of the fact that we related total harvest to maximum harvest for a given dispersal and reproductive rate.

Figure 5. Model output of local harvest rates and catch per unit effort in relation to local hunting effort and of the distribution of harvested individuals and the animal population density for good management (90% of maximum harvest), moderate overharvesting (80% of maximum), and severe overharvesting (20% of maximum) at three dispersal rates.
Model Results Compared with Field-Data Results

The model analysis showed how dispersal reduced differences in population densities, moved the peak of local harvest rates toward higher hunting efforts, and therefore affected the correlation between effort and harvest rate from positive for animals with a high dispersal rate to negative for animals with a low dispersal rate. This caused CPUE at high dispersal rates to become constant across different levels of hunting effort, similar to the pattern that for species with low dispersal rate indicates no overharvesting. Also, it showed that low reproductive rates can have effects similar to those for high dispersal rates. To use the spatial pattern of harvest and CPUE to assess game depletion, one must take into account the rates of both reproduction and dispersal of a species.

Most of our study species have home ranges small enough that movements within them would not contribute to dispersal of a magnitude corresponding to that of a species with a high dispersal rate in the computer simulation (Table 2). This suggests that the dispersal mainly consisted of young individuals that leave their maternal home range. Consequently, high dispersal rates occur only for animals with high reproductive rates, and it is therefore unlikely that species would have both a low reproductive rate and a high dispersal rate. Most of our study species have fairly low reproductive rates (Table 2), meaning that only a small proportion of the population would be dispersing at any given time. It is therefore unlikely that high hunting intensity in the center of the area would depress population densities across the entire area, as it would for a severely overharvested, highly mobile species in the computer simulation (Fig. 5j–m, solid lines). This supports our initial conclusions, with a few exceptions.

The most important exception is T. pecari, which is seen only occasionally in Sarayacu nowadays. Although the spatial pattern of harvest and CPUE suggest that this species is not overharvested, its high dispersal rate may have obscured the effects of intensive hunting. Also, T. terrestris has a home range large enough to span two or three hunting-intensity zones, and the use of spatial pattern of harvest rate and CPUE as indicators probably underestimated the extent of overharvesting. Finally, the classification of A. belzebuth into group 4, representing species showing no signs of overharvesting, is a puzzle, given that a similar species, L. lagotricha, is severely overharvested. We believe that A. belzebuth, being a highly
social species, actually increased its dispersal rate when its population density got so low that dispersing individuals had a hard time finding groups to join. The observed increase in harvest rate with increase in hunting effort therefore was probably a result of a high dispersal rate. Thus, contrary to the initial conclusion, this species actually may be critically overharvested.

Discussion

We have shown how the status of hunted animal species in Amazonia can be assessed based on knowledge about animal dispersal rates and the spatial distribution of harvest rates and CPUE. The effects of animal dispersal have previously been documented in predator-prey systems (e.g., Holt 1984; Oksanen 1990) but have received less attention in the hunting literature. The inclusion of spatial structure and dispersal therefore provides a complement to earlier methods of evaluating the sustainability of hunting. For instance, Robinson and Redford’s (1991) method may be more powerful if contrasting heavily hunted and less hunted areas on a relatively small spatial scale, as in our study. Our analysis showed that their method failed to identify any species in our study area as overharvested (Table 2), but at the finer spatial scale (the seven zones of hunting effort) it did identify overharvested zones for some species (Fig. 3a, 3c, & 3x).

Similarly, our method may also be combined successfully with that of Bodmer (Robinson & Bodmer 1999). By performing a line-transect inventory and CPUE measurements in the same area, it would be possible to establish a rough conversion factor from CPUE to population density. The CPUE values could then be converted into population density estimates for comparison with estimated carrying capacities or for calculating production. Furthermore, our method and Bodmer’s method complement each other because line-transect inventories are more feasible in areas with high animal densities than in heavily hunted areas with low densities (Bodmer et al. 2000). On the other hand, calculating CPUE is most feasible where hunting effort is fairly high but becomes problematic in areas with low hunting effort because of a small sample size.

One problem with our method is that our indicators likely underestimated the spatial extent of overharvesting. The first indicator, a decreasing harvest rate with an increasing hunting effort, may do so because animal dispersal moves the peak of harvest rates toward higher hunting efforts, changing the correlation between local
The second problem is that the usefulness of CPUE as a proxy for population density depends on the selection of a proper unit of effort (Salthaug & Godø 2001; Marchal et al. 2002). The CPUE estimates in our study could be improved by refining the classification of hunting methods. It would, for instance, be desirable to collect information on the use of dogs because hunters used dogs in zones close to the village but less so in remote areas. This may be one reason the CPUE estimates were high for *L. lagotricha* in zone 1 and why the maximum CPUE for *T. terrestris* and *T. tajacu* was not found in zone 1 but in zones of slightly higher hunting effort. Similarly, it would be desirable to collect information on such hunting methods, such as digging out animals from burrows, or on the variability in walking speed between the wide trails near the village and the almost invisible trails in remoter areas.

Finally, our method assumes a steady state and therefore has reduced validity when change is rapid. Until the rate of change can be verified by repeated observation, our method must be complemented with an assessment of past changes in hunting effort. Our assessment, based on ethnographic sources, interviews, censuses, and retrospective mapping (see Sadomba 1996), is that hunting effort in our study area is increasing but at a fairly moderate rate (Sirén 2004).

The main practical use of our method may be for identifying suitable locations for no-take areas. Such areas may be the most viable option for wildlife managers in tropical forests. Parallel to this research, we facilitated a process in the community of discussing the problems and possible solutions of wildlife depletion. Community members suggested that the establishment of no-take areas may be a strategy with a potential for success. The management of such areas can be based on traditional arrangements...
of hunting rights and existing social structures, whereas banning hunting of certain endangered species may be less socially feasible. In the design of no-take areas, we suggest that a first step would be the identification of a limited number of target species, to reduce the complications of multispecies management. We further argue that these species should show clear indications of being overharvested but remain important sources of game meat. Moreover, no-take areas should probably be established where animal densities are reduced but still high enough to have the potential to recover within a reasonable time span. Unless a fairly quick recovery can be observed, motivation on the part of hunters to maintain and comply with hunting restrictions is likely to deteriorate. To adopt these criteria for the present situation, we suggest that three potential target species within the following zones have the most certain potential for fairly rapid improvement: L. lagotricha in zones 2 and 3, T. terrestris in zone 4, and T. tajacu in zones 3 to 6.

In the final decision about where to allocate no-take areas, it will also be necessary to account for the cost of enforcement and the short-term cost to hunters in the form of lost hunting opportunities. Our method provides a fairly low-cost alternative for assessing the status of tropical forest game species at a high spatial resolution, and therefore to inform decisions that could improve the sustainability of hunting in tropical forests.

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Literature Cited

Alvarado, 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.

Barrientos-Segundo, J., and L. Maffei. 2000. Radio telemetría en la urina Mazama gouazoubira en el campamento Cerro Cortado, Izozog, Santa Cruz, Bolivia. Pages 369–372 in E. Cabrera, C. Mercolli, and R. Resquin, editors. Manejo de Fauna Silvestre en Amazonía y Latinoamerica, Asunción, Paraguay.

Beck-King, H., and R. Beck-King. 1999. Home range, population density, and food resources of Agouti pacá (Rodentia: Agoutidae) in Costa Rica. study using alternative methods. Biotropica 31:675–685.

Begazo, A. J., and R. E. Bodmer. 1998. Use and conservation of Cracidae (Aves: Galliformes) in the Peruvian Amazon. Oryx 32:301–309.

Bodmer, R. E. 1994. Managing wildlife with local communities in the Peruvian Amazon: the case of the Reserva Communal Tamshiyacu-Tahuayo. Pages 113–134 in D. Western and R. M. Wright, editors. Natural connections: perspectives in community-based conservation. Island Press, Washington, D.C.

Bodmer, R. E., R. Aquino, and J. G. Gil Navarro. 2000. Sustentabilidad de la caza de mamíferos en la cuenca del Rio Samiria, Amazonia Peruana. Pages 447–469 in E. Cabrera, C. Mercolli, and R. Resquin, editors. Manejo de Fauna Silvestre en Amazonía y Latinoamerica. Fundación Moises Bertoni, Asunción, Paraguay.

Campbell, A. F., and R. W. Sussman. 1994. The value of radio tracking in the study of Neotropical rain forest monkeys. American Journal of Primatology 32:291–501.

Defler, T. R. 1996. Aspects of the ranging pattern in a group of wild woolly monkeys (Lagothris lagotricha). American Journal of Primatology 38:289–302.

De Souza-Mezurek, R. R., T. Pedrinho, X. Feliciano, W. Hilário, S. Gerônico, and E. Marcelo 2000. Subsistence hunting among the Waimiri Atroari Indians in central Amazonia, Brazil. Biodiversity and Conservation 9:579–596.

Fa, J. E., J. Juste, J. Perez Del Val, and J. Castroviejo. 1995. Impact of market hunting on mammal species in Equatorial Guinea. Conservation Biology 9:1107–1115.

Fitzgibbon, C. D., H. Mogaka, and J. H. Fanshawe. 1995. Subsistence hunting in Arabuko sokoke Forest, Kenya, and its effects on mammal populations. Conservation Biology 9:1116–1126.

Fragoso, J. M. V. 1998. Home range and movements patterns of white-lipped peccary (Tayassu pecari) herds in the northern Brazilian Amazon. Biotropica 30(4):46–49.

Fragoso, J. M. V., and J. M. Huffman. 2000. Seed-dispersal and seedling recruitment patterns by the last Neotropical megafaunal element in Amazonia, the tapir. Journal of Tropical Ecology 16:369–385.

Herrera, J. C., and A. B. Taber. 2001. Lowland tapir (Tapirus terrestris) ranging behavior, habitat use and diet in Santa Cruz, Bolivia. Pages 30–31 in Abstract book of the first international tapir symposium. Species Survival Commission, World Conservation Union, San Jose, Costa Rica.

Hill, K., and J. Pawde. 2000. Sustainability of Aché hunting in the Mbaracayu Reserve, Paraguay. Pages 79–105 in E. L. Bennet and J. G. Robinson, editors. Hunting for sustainability in tropical forests. Columbia University Press, New York.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. The American Naturalist 124:377–408.

Judas, J., and O. Henry. 1999. Seasonal variation of home range of collared peccary in tropical rainforests of French Guyana. Journal of Wildlife Management 63:546–552.

Lang, R. A., J. W. Bishir, M. C. Cronin, and C. S. Rosenberry. 1996. Use of catch-effort to estimate population size. Wildlife Society Bulletin 24:731–737.

Lockwood, D. R., A. Hastings, and L. W. Botsford 2002. The effects of dispersal patterns on marine reserves: does the tail wag the dog? Theoretical Population Biology 61:297–309.

Marchal, P. C. Ulrich, K. Korsbrekke, M. Pastoors, and B. Rackham 2002. A comparison of three indices of fishing power on some demersal fisheries of the North Sea. International Commission on Endangered Species (ICES) Journal of Marine Science 59:604–623.

Medici, E. P., P. R. Mangini, and C. B. Valladares-Padua 2001. Conservation biology of lowland tapirs (Tapirus terrestris) and their potential as landscape detectives at the Pontal do Paranapanema Region, São Paulo State, Brazil. Pages 13–14 in Abstract book of the first international tapir symposium. Species Survival Commission, World Conservation Union, San Jose, Costa Rica.

Mena, P. J. R. Stallings, J. Regalado, and R. Cueva. 2000. The sustainability of current hunting practices by the Huaorani. Pages 57–78 in E. L. Bennett and J. G. Robinson, editors. Hunting for sustainability in tropical forests. Columbia University Press, New York.

Milner-Gulland, M. J., and H. R. Açakayla 2001. Sustainability indices for exploited populations. Trends in Ecology & Evolution 16:686–692.
Mosquera, I., I. M. Côte, S. Jennings, and J. D. Reynolds. 2000. Conservation benefits of marine reserves for fish populations. Animal Conservation 4:321–332.

Muchaal, P. K., and G. Ngandjui. 1999. Impact of village hunting on wildlife populations in the western Dja reserve, Cameroon. Conservation Biology 13:385–396.

Novak, J. M., K. T. Scribner, W. D. Dupont, and M. H. Smith. 1991. Catch-effort estimation of white-tailed deer population size. Journal of Wildlife Management 55:31–38.

Novaro, A. J., K. H. Redford, and R. E. Bodmer. 2000. Effect of hunting in source-sink systems in the Neotropics. Conservation Biology 14:713–721.

Oksanen, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. Evolutionary Ecology 4:220–234.

Palacios, E., and A. Rodriguez. 2001. Ranging pattern and use of space in group of red howler monkeys (Alouatta seniculus) in a southeastern Colombian rainforest. American Journal of Primatology 55:233–251.

Peres, C. A. 1996. Population status of white-lipped Tayassu pecari and collared peccaries T. tajacu in hunted and unhunted Amazonian forests. Biological Conservation 77:115–123.

Peres, C. A. 2000. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. Pages 31–56 in E. L. Bennet and J. G. Robinson, editors. Hunting for sustainability in tropical forests. Columbia University Press, New York.

Peres, C. A., and I. R. Lake. 2001. Extent of non-timber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon Basin. Conservation Biology 17:521–535.

Quinn, J. E. S. R. Wing, and L. W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, Strongylocentrotus franciscanus. American Zoologist 33:537–550.

Robinson, J. K. 1992. The empty forest. BioScience 42:412–422.

Robinson, J. G., and E. L. Bennett. 2000. Carrying capacity limits to sustainable hunting in tropical forests. Pages 13–30 in J. G. Robinson and E. L. Bennett, editors. Hunting for sustainability in tropical forests. Columbia University Press, New York.

Robinson, J. G., and R. E. Bodmer. 1999. Towards wildlife management in tropical forests. Journal of Wildlife Management 63:1–13.

Robinson, J. G., and K. H. Redford. 1991. Sustainable harvest of Neotropical mammals. Pages 415–427 in J. G. Robinson and K. H. Redford, editors. Neotropical wildlife use and conservation. The University of Chicago Press, Chicago.

Roldán, A. I., and J. A. Simonetti. 2001. Plant-mammal interactions in tropical Bolivian forests with different hunting pressures. Conservation Biology 15:617–623.

Sadomba, W. Z. 1996. Retrospective community mapping: a tool for community education. PLA Notes 25.

Salthe, A., and O. R. Godø 2001. Standardisation of commercial CPUE. Fisheries Research 49:271–281.

Santamaria, M., and A. M. Franco. 2000. Frugivory of salvins curassow in a rainforest of the Colombian Amazon. Wilson Bulletin 112:473–481.

Sireń, A. 2004. Changing interactions between humans and nature in Sarayaku, Ecuadorian Amazon. Acta Universitatis Agriculturae Suecia. Agraria vol. 447. Uppsala, Sweden.

Slade, N. A., 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.

Strier, K. B. 1992. Atelinae adaptations: behavioral strategies and ecological constraints. American Journal of Physical Anthropology 88:515–524.

Suarez, S. A. 2002. Behavioral ecology of the white-bellied spider monkey (Ateles belzebuth belzebuth) in Eastern Ecuador. American Journal of Primatology 57:41–42.

Townsend, W. R. 1996. Nyao Itó: caza y pesca de los Sirionó. Instituto de Ecología, Universidad Mayor de San Andrés, Fundación para el Desarrollo de la Ecología, La Paz, Bolivia.

Turchin, P. 1998. Quantitative analysis of movement. Sinauer Associates, Sunderland, Massachusetts.

Vickers, W. T. 1988. Game depletion hypothesis of Amazonian adaption: data from a native community. Science 239:1521–1522.

Waser, P. M. 1987. A model predicting dispersal distance distributions. Pages 251–256 in B. D. Chepko-Sade and Z. T. Halpin, editors. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago.

Yodzis, P. 1989. Introduction to theoretical ecology. Harper & Row, London.