The Sustainability of Subsistence Hunting in the Neotropics

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Abstract: Hunting is an important component of native subsistence strategies in Amazonia. It is also a serious threat to biodiversity in some areas. We present data on the faunal harvests of two native Neotropical subsistence hunting peoples, Machiguenga bow-hunters and Piro shotgun hunters of Peru. The rate of annual harvest per square kilometer of catchment is estimated and compared to rates of sustainable harvest calculated by Robinson and Redford (1991). We used indicators of prey abundance to test for the depletion of species that hunters killed in numbers greater than what the model predicts to be sustainable. As predicted, we found the strongest evidence for local depletion of the large primates at the Piro site. The woolly monkey (Lagothrix lagothricha) harvest at the Machiguenga village and the deer (Mazama americana) and collared peccary (Tayassu tajacu) harvests at both sites were not predicted to be unsustainable and we found no evidence for depletion. Machiguenga bow hunters killed spider monkeys (Ateles paniscus) in quantities that were slightly above what the model predicted to be sustainable, yet we found no evidence for depletion. Differential species vulnerability, catchment size, and consumer population size could be important factors in determining sustainability.

La Sustentabilidad de la Caza de Subsistencia en el Neotrópico

Resumen: La caza es un componente importante de las estrategias nativas de subsistencia en el Amazonía. Es también una amenaza seria para la biodiversidad en ciertas áreas. Presentamos datos de cosechas de fauna de dos grupos de cazadores de subsistencia, los cazadores con arco de Machiguenga y los cazadores con arma de fuego de Piro en Perú. La tasa de cosecha anual por kilómetro cuadrado es estimada y comparada con tasas de cosecha sostenible calculadas por Robinson y Redford (1991). Utilizamos indicadores de abundancia de presas para analizar la disminución de especies que los cazadores matan en números mayores a los que el modelo predice como sostenibles. Encontramos una fuerte evidencia de disminución local de primates grandes en el sitio Piro. El mono aullador (Lagothrix lagothricha) cosechado en la villa Machiguenga, el venado (Mazama americana) y el pecarí de collar (Tayassu tajacu) cosechados en ambos sitios no fueron predecidos como insostenibles y no encontramos evidencias de disminución. Los cazadores con arco de Machiguenga mataron monos araña (Ateles paniscus) en cantidades que estuvieron ligeramente por encima de lo que el modelo predice como sostenible, aún así, no encontramos evidencias de disminución. La vulnerabilidad diferencial de las especies, el tamaño de las capturas y el tamaño poblacional de los consumidores pueden ser factores importantes en la determinación de la sustentabilidad.
**Introduction**

Subsistence hunting is crucial to the livelihoods of natives who live in the rain forests of Amazonia (Redford & Robinson 1987). Although data suggest that some traditional native societies need not have a negative impact on their prey populations (Vickers 1988, 1991), it is clear that more centralized and growing human populations, more efficient hunting technology, and a burgeoning market for bush meat are driving many Neotropical prey species to the point of local extinction (Bodmer et al. 1994; Mittermeier & Cheney 1987; Peres 1990; Smith 1976). Although habitat destruction has the greatest negative impact on rain forest wildlife, in areas where the forest is still standing hunting remains the greatest threat to tropical biodiversity (Redford 1992). To balance the needs of subsistence hunters with the potential threat they represent, the question of what constitutes a sustainable harvest for the important Neotropical game species must be answered.

To do this we collected hunting data from two native subsistence Neotropical communities during 1988–1989 and again in 1990–1991. The Machiguenga village of Yomiwato is located on the Quebrada Fierro tributary of the Manú River, in Manú National Park in southeastern Peru. The Piro community of Diamante is 90 km to the southwest of Yomiwato, just outside Manú Park. It is situated on a terrace above the vast floodplain of the braided Madre de Diós river. Yomiwato’s site abuts the low foothills of the Andes. Both sites are in moist tropical rain forest (Holdridge 1967). The Diamante Piro have hunted their site for at least 30 years, moving from a location about 6 km away in the late 1960s (Alvard 1993a). Half of the current residents moved to Yomiwato in 1973, where previously one extended family resided. The other half moved to the site in 1985 (Hurtado et al. 1987).

The Machiguenga hunt solely with bow and arrow, whereas the Piro procure 85% of their harvest (by weight) with shotguns (Alvard 1993a). We identified consumers as individuals over 3.5 years of age. Yomiwato has a total population of 99 and a consumer population of 85. For Diamante we estimated a total of 191.5 consumers.

The prey species important in the diet of the Piro and Machiguenga include ungulates: the Brazilian tapir (Tapirus terrestris), collared peccary (Tayassu tajacu), and brocket deer (Mazama americana). Capybara (Hydrochaeris hydrochaeris), a large rodent, is also killed. Black spider (Ateles paniscus), red howler (Alouatta seniculus), and capuchin monkeys (Cebus apella) are present at both sites. Woolly monkeys (Lagothrix lagothricha) are only found around Yomiwato. Both groups hunt a number of other birds and small mammals but these prey contribute less than 10% of the game diet at either site (Alvard 1993a).

**Methods**

We compared the actual faunal oftakes of the two groups to estimates of sustainable harvests calculated by Robinson and Redford’s (1991) model. We did this to predict which species were being overhunted at each site. If the model’s estimates are accurate, evidence of local depletion should be found for the species killed in numbers determined to be nonsustainable.

Robinson and Redford (1991) argue that the size of a sustainable harvest from a prey population of a given size depends on (1) the number of animals produced through reproduction and (2) the proportion of those animals that die naturally and thus hunters cannot harvest.

Robinson and Redford (1986a) derived carrying capacity estimates from a linear regression model of log-density versus log-body weight for Neotropical mammals divided into dietary categories. Estimates of maximum rate of population growth (\(r_{max}\)) were derived from Cole’s equation (1954) which incorporates age at first reproduction, last reproduction, and the annual birth rate (Robinson & Redford 1986b). These estimates can be used to calculate the potential harvest—the maximum number of animals or equivalent kilograms of biomass per square kilometer that hunters can take per year and not deplete the standing population. See Robinson and Redford (1991) for additional details of the model. We present the potential harvests for the important prey species in the study in Table 1.

To determine the actual annual harvest at both sites, Piro and Machiguenga households were visited either every day or every third day. During these visits, we conducted interviews to determine the number and characteristics of all mammalian game killed since the last visit. This was done for the entire population of 85 consumers in Yomiwato and for a subsample of 116 consumers in Diamante. We determined the number of consumer days sampled by counting the number of days each consumer was present in the community during the study period and then summing across the entire consumer sample. The number of consumer-days observed at Diamante and Yomiwato was 37,003 and 7,133 days respectively. We used species-specific age and sex body weight estimates to calculate the total biomass harvested for each species. This figure was divided by the total number of consumer days to determine the grams per consumer per day harvested for each species.

We estimated the hunting catchment by noting that the majority of Piro and Machiguenga hunts were single day events by foot along trails that radiate from the villages. This limits the effective range of day trips to distances that hunters can travel round-trip in about 12 hours. Hunters from both groups occasionally hunted during multi-day foraging trips away from the central area. At Diamante, overnight camps tended to be within 2–4 km from the village; the duration of these trips was...
The annual harvest of *A. paniscus* at the two communities were similar (Diamante: 1.6 kg/km²; Yomiwato: 1.7 kg/km²) and slightly higher than the maximum sustainable rate (1.22 kg/km²). The *C. apella* harvest at Diamante (1.1 kg/km² per year) also exceeded the maximum limits calculated from the model. The *L. lagotricha* harvest at Yomiwato (2.1 kg/km² per year) and the *A. seniculus* harvest at Diamante (1.7 kg/km² per year) both approached, though did not exceed, the quantity that should cause depletion according to Robinson and Redford.

There was no evidence that the harvests of the other ungulate species are not sustainable. *Tayassu tajacu*, which can sustain a large harvest of 42 kg/km² a year, were harvested at lower annual rates in both communities (20.2 kg/km² and 5.5 kg/km² at Diamante and Yomiwato respectively). *Mazama americana* at Diamante were harvested at less than 30% of the maximum sustainable of 17.49 kg/km². No deer were killed at Yomiwato.

If these assessments of harvest sustainability are accurate, measures of prey abundance in the catchment areas should agree; that is, prey that the model predicts to be overhunted should show evidence of being locally depleted. Estimates of actual prey density do not exist for the two sites, but satisfactory data do exist on the number of encounters with prey per hour during observed hunts. Encounter rate was assumed to be a function of prey abundance, and because hunting pressure was greatest near the village (Alvard 1994), local depletion should be indicated by lower rates of encounter at distances closer to the village.

Logistic regression was used to examine for an effect of distance from the village of Diamante (0–10 km) on encounter rates, as well as for differences in encounter rates between the two villages (Tables 2 and 3). The analysis indicates that *T. tajacu* did not appear to be depleted in the area around the two villages. There was no relationship between encounter rate and distance from the village of Diamante (chi-square = 0.73, *p* = 0.391). No data on encounter distance exist for Yomiwato, but
Table 2. Results of logistic regression analyses testing for the effect of distance from the village of Diamante on the probability of prey encounter during hunts.*

<table>
<thead>
<tr>
<th>Prey type</th>
<th>Encounters per hour</th>
<th>Number of encounters</th>
<th>Intercept</th>
<th>Parameter estimate</th>
<th>Chi-square</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capuchin monkey</td>
<td>0.041</td>
<td>16</td>
<td>−5.06</td>
<td>0.42</td>
<td>10.22</td>
<td>0.001</td>
</tr>
<tr>
<td>Spider monkey</td>
<td>0.018</td>
<td>7</td>
<td>−5.48</td>
<td>0.54</td>
<td>3.04</td>
<td>0.081</td>
</tr>
<tr>
<td>Howler monkey</td>
<td>0.018</td>
<td>7</td>
<td>−3.09</td>
<td>−0.03</td>
<td>0.02</td>
<td>0.881</td>
</tr>
<tr>
<td>Red brocket deer</td>
<td>0.020</td>
<td>8</td>
<td>−4.18</td>
<td>0.08</td>
<td>0.20</td>
<td>0.655</td>
</tr>
<tr>
<td>Collared peccary</td>
<td>0.071</td>
<td>28</td>
<td>−2.89</td>
<td>0.08</td>
<td>0.73</td>
<td>0.391</td>
</tr>
</tbody>
</table>

*The sample is 56 observed hunts (394 hours) for which distance was known or estimated.

overall peccary encounter rates were not significantly different at the two sites (Diamante: 0.065/hour, Yomiwato: 0.079/hour, chi-square = 0.24, p = 0.623). There was no significant effect of distance on deer or howler monkey encounters and no significant difference between villages. The small number of tapir encounters precluded analysis. These animals are rare even in un-hunted areas (Janson & Emmons 1990).

The evidence shows that the large primates as a group were locally depleted at the Diamante site. Encounter rates with A. paniscus and C. apella were significantly lower near, compared with away from the village (chi-square = 3.04, p = 0.081; chi-square = 10.22, p = 0.001 respectively). In addition, overall encounter rates with large primates were significantly lower at Diamante compared to Yomiwato. For the four largest primate species, L. lagotricha, A. seniculus, A. paniscus, and C. apella, the combined encounter rate at Diamante was 0.089/hour, versus 0.227/hour at Yomiwato (chi-square = 13.896, p = 0.0002). In addition, harvests of the large primates were significantly less at Diamante than we expected if their densities had been similar to primate densities at the nearby unhunted site of Cocha Cashu, assuming harvest rates were proportional to prey availability in the habitat (Alvard 1993a).

The lack of evidence for collared peccary and deer depletion around either village provides support for the conclusion that the Diamante and Yomiwato harvests for these species are sustainable. The issue is not so clear for the other species. The harvest rates for spider monkey were nearly equal at both villages and slightly above what the model says is sustainable, yet this species appeared to be depleted only at Diamante. Piro hunters kill howler monkeys at half the maximum sustainable rate, yet these animals probably suffer from over-hunting around Diamante as do the other primates. Howler monkeys had the same overall low encounter rate as spider monkeys at Diamante, but there was no apparent increase in the probability of encounter with distance. The apparent lack of evidence for howler monkey depletion may be due to uniform depletion across the hunting range or low population densities for this species in this habitat.

If large primates are currently depleted around Diamante, the observed harvest rate may not be the same as the hunting pressure that led to the depletion. Differences in village size may explain the finding that overall per capita primate harvests at Diamante are lower than at Yomiwato, yet the primate populations are more depleted around the Piro village. Yomiwato hunters had a large per capita harvest of spider monkeys, but the village population was small (85 consumers). Diamante hunters had a smaller per capita harvest, but their village was more than twice the size of Yomiwato (191.5 consumers). This created a nearly equal total annual harvest for spider monkeys.

To examine this issue we calculated the total annual harvest (kg/year) using the per capita harvest of the magnitude observed at Yomiwato, but with a consumer population the size of Diamante. What this exercise assumes is that the per capita harvest at Yomiwato approximates what the per capita harvest at Diamante might have been in the past when the Diamante environment was as dense in animals as the area around Yomiwato. It also assumes that consumer demand in-

Table 3. Results of logistic regression analyses comparing encounter rates for observed hunts at Yomiwato to those at Diamante.α

<table>
<thead>
<tr>
<th>Prey type</th>
<th>Diamante</th>
<th>Yomiwato</th>
<th>Intercept</th>
<th>Parameter estimate</th>
<th>Chi-square</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capuchin monkey</td>
<td>0.056</td>
<td>0.020</td>
<td>106.41</td>
<td>−1.09</td>
<td>2.95</td>
<td>0.086</td>
</tr>
<tr>
<td>Spider monkey</td>
<td>0.014</td>
<td>0.079</td>
<td>−180.22</td>
<td>1.76</td>
<td>10.68</td>
<td>0.001</td>
</tr>
<tr>
<td>Woolly monkey</td>
<td>—</td>
<td>0.109</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Howler monkey</td>
<td>0.018</td>
<td>0.020</td>
<td>−12.34</td>
<td>0.09</td>
<td>0.01</td>
<td>0.914</td>
</tr>
<tr>
<td>Primates combinedb</td>
<td>0.089</td>
<td>0.227</td>
<td>−112.33</td>
<td>1.10</td>
<td>13.90</td>
<td>0.0002</td>
</tr>
<tr>
<td>Red brocket deer</td>
<td>0.025</td>
<td>0.009</td>
<td>92.95</td>
<td>−0.96</td>
<td>1.12</td>
<td>0.288</td>
</tr>
<tr>
<td>Collared peccary</td>
<td>0.065</td>
<td>0.079</td>
<td>−22.77</td>
<td>0.20</td>
<td>0.24</td>
<td>0.623</td>
</tr>
</tbody>
</table>

αThe sample is 549 hours and 101 hours of observed hunts at Diamante and Yomiwato respectively.

bSpider, capuchin, howler and woolly monkeys.
creases proportionally with population and that the catchment area stays roughly the same.

First, we calculated the forest area required to produce enough prey to sustainably support the total consumer demand. Next, we compared this figure to the catchment hunting area of 314 km². We considered species good candidates for over-exploitation and depletion if total consumer demand requires more than 314 km² of territory to be sustainable. Figure 1 examines the relationship between human consumer population size and the catchment necessary for a sustainable annual harvest given the per capita harvests for spider and woolly monkeys and the collared peccary.

The territory required to sustain the per capita harvest of spider monkeys (7.4 g per consumer per day) at Diamante for the consumer population at that site is 396 km²—a size that is only slightly greater than the area that receives most of the hunting pressure. This result reiterates the previous one, that the current spider monkey harvest at Diamante is just above the maximum sustainable. If the hunters at Diamante were harvesting at the same per capita rate as at Yomiwato, which might be expected if spider monkey populations were not depleted at Diamante, they would require more than 1017 km² of catchment for a sustainable harvest. A catchment that size is nearly 3.25 times more forest than the Piro hunt now. This result is consistent with the spider monkey depletion found around Diamante.

The current woolly monkey per capita harvest at Yomiwato (23 g per consumer per day for a consumer population of 85), requires a territory of about 278 km² to be sustainable—12% less than 314 km². This is consistent with the lack of evidence for over-exploitation of woolly monkeys at Yomiwato. The modest harvest rate of 8 g of howler monkey per consumer per day at Diamante requires only an area of 207 km² to be sustainable for the consumer population at that site. If Piro hunters harvested howler monkeys at the rate that Yomiwato hunters kill woolly monkeys (23 g per consumer per day), they would require 595 km² of catchment for sustainability. These results agree with the depletion of howler monkeys found around Diamante.

In contrast, hunters at both sites take collared peccaries at per capita rates that require much less territory to be sustainable than do primates. For the harvest of 97 g per consumer per day observed at Diamante, a catchment of 314 km² could support a population of 400 consumers. At the per capita rate observed at Yomiwato, 60 g per consumer per day, nearly 650 consumers could be supported.

Although the large primates are being harvested at or over the sustainable rate, they account for a much smaller proportion of the meat diet at Diamante, or even Yomiwato, than do other species. Primates account for 8% and 18% of the total meat harvested by weight at Diamante and Yomiwato respectively. Tapir, in contrast, account for 27.5% at Diamante and 47% at Yomiwato of the total biomass harvested. The local extinction of tapir is a more serious subsistence problem than the local extinction of primates. Collared peccaries, alone, on the other hand, apparently could sustainably satisfy the entire current bushmeat demand for each community according to the Robinson and Redford calculations. Hunters could increase the deer and probably the capybara harvests and still be within the sustainable range. We require more information on the population dynamics of these species, however, before we suggest that they can replace the more threatened species in subsistence hunters’ diets.

Discussion

Robinson and Redford’s model was partially successful at predicting over-hunting at the two sites. The model predicted the depletion of the large primates found around Diamante. The lack of evidence for overhunting of peccaries and woolly monkeys was also consistent with the model. The model predicted depletion of spider monkeys at Yomiwato, but we found no evidence of overhunting, suggesting refinements of the model or better measurement of prey abundance are needed.

Although the results are promising, the model and the
data we presented are limited in a number of ways. The estimates of potential harvest calculated by Robinson and Redford assume maximum population production under optimal conditions. Harvests that are larger than the theoretically maximum potential yield can not be sustained. For this reason the model is suitable for evaluating whether a harvest is not sustainable. But, because conditions are never optimal, actual population production will be lower than maximum, and for this reason the model alone can not determine if a given harvest is sustainable (Robinson & Redford 1994). Because densities of a prey species can differ in different local habitats, what constitutes a sustainable harvest will vary as well. For such conclusions additional evidence such as the comparative prey density data we presented here are required.

In addition, the model estimates potential harvests for a defined catchment area. Implicit in the calculation of prey production is the assumption that prey do not enter the catchment area from elsewhere. Nonetheless, prey immigration from unhunted areas act to replenish, to some degree, each hunting zone. This may explain, for example, why the particularly vulnerable species have not gone completely extinct within the core Piro catchment area after 30 years of hunting. Studies of long-term regional depletion should address refugial sources of prey production as well as the regional density of the human population (Pulliam 1988; Alvard 1993a).

The data presented here represent only 2 years of what is a long-term, dynamic process. Current prey depletion is the result of hunting in the past: each catchment area discussed has experienced at least 20–30 years of recent exploitation, perhaps more. Harvesting rates also certainly vary according to changes in prey availability and consumer population size (Vickers 1988; Winterhalder et al. 1988; Robinson & Redford 1994). The harvest rate data used to create Fig. 1, for example, are not intended to represent static constants and we expect them to vary in complex ways over time. Current low harvest rates are not necessarily indicative of a sustainable harvest but can be a reflection of depletion that has already occurred in the past, as is probably the case for Diamante. Refinements of sustainability models need to consider such temporal dimensions. These factors are crucial to consider as conservationists develop schemes to balance the subsistence needs of Amazonian residents with goals of conservation.

Acknowledgments

We thank T. Phillips, K. Kopischke, and M. Gornikiewicz who assisted with data collection. We also thank two anonymous reviewers for their insightful comments. This research was funded by the Charles Lindbergh Foundation, the L.S.B. Leakey Foundation, the Tinker Inter-American Research Foundation, the University of New Mexico, and the National Science Foundation (Grant BNS-8717886 to H. K.).

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