Community Based Approaches to Wildlife Conservation in Neotropical Forests

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People living in and around protected areas have frequently been considered to have little interest in the conservation of biological diversity. Such local communities traditionally have exploited natural systems – turning to nature for food, fuel, medicine, material for housing construction, etc. – and the exploitation of natural systems has been considered not to contribute to their conservation. Conservationists traditionally sought to protect natural systems by excluding people from parks and reserves, and by so doing denied people access to natural resources. While generally effective at protecting natural areas, this approach is not totally satisfactory even as a conservation strategy: The land area that can be "locked-up" in protected areas is limited, and human communities living in and around these areas frequently come into conflict with protected area managers.

More recently, many conservationists have argued the opposite position – that empowering local peoples provides the most effective mechanism to conserve areas of high biological diversity. The argument goes as follows: Local peoples are the ones that live in and around the areas that the conservation community would like to protect; if they are given access to the natural resources in these areas, then they will benefit from the conservation of those resources, and thus will ally themselves with conservation efforts. Such community-based conservation efforts are becoming an increasingly popular approach to conserving natural areas (Wells and Brandon, 1992; Brandon and Wells, 1992). Community-based conservation efforts therefore direct the benefits derived from natural areas to local communities. That benefit need not be economic. Resources can also be exploited for cultural, social, and political reasons. But community-based conservation requires that benefits accrue to local peoples, and that local peoples be able to participate in the distribution and allocation of natural resources.

But there is an internal contradiction to this argument. In community-based, to a greater or lesser degree, conservation, people are allowed to use natural resources. This use will lower population densities of exploited species, decrease overall biodiversity, and simplify ecosystem functioning (Robinson, 1993). These biological losses contradict the expressed aims of most conservationists. Therefore community-based conservation requires a balance between meeting human needs while ensuring that biological losses are not excessive. Both conditions are difficult to specify. Can one ever say that "human needs have been met"? Can one state what "losses of biodiversity and ecosystem functioning" are acceptable?

The concept of sustainability presupposes that these conditions can be defined and agreed upon. By definition, sustainable use requires that at least basic human needs must be met and the biological losses must be acceptable (Robinson, 1993). One approach to defining human needs is in terms of the resource base: Human needs can be considered to have been met (to the extent possible) when any greater harvest would systematically deplete the natural resource. Depletion occurs when the resource is so reduced that it no longer constitutes a signficant resource for local communities. Biological losses can be considered to be acceptable when they are consistent with the expressed conservation goals of the area (maintaining a biological community, a level of biodiversity, or a species population, etc.).

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In this paper we consider the viability of community-based approaches to the conservation of tropical forest wildlife. Tropical forest wildlife has attracted a great deal of conservation interest. What is less appreciated is the importance of wildlife harvesting to human communities living in and around forests. Studies of hunting are still in their infancy, and policy makers interested in conservation and development have largely ignored the issue. Forest animals have not been included in calculations of "forest value" (e.g., Peters et al., 1989) or even featured in lists of benefits from the forests (e.g., World Bank 1978 in Myers 1988). We will begin by stressing the importance of hunting to many rural communities, and examine the impact of this hunting on wildlife populations. We will then outline different indices and models of sustainable harvest, and apply these to hunting data derived from five neotropical case studies. This analysis should assist in determining the potential for tropical wildlife utilization to meet the dual objectives of conservation and human needs.

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UNITED STATES

ATLANTIC OCEAN

BERMUDA
(Great Britain)

Gulf of Mexico

BAHAMAS

Tropic of Cancer

HAITI

CUBA
DOMINICAN REPUBLIC

JAMAICA
PUERTO RICO (U.S.A.)

BELIZE
GUADELOUPE (France)
MARTINIQUE (France)

HONDURAS
Caribbean
ST. LUCIA

GUATEMALA
Sea
BARBADOS

EL SALVADOR
GRENADA

NICARAGUA
TRINIDAD & TOBAGO

PANAMA

COSTA RICA
VENEZUELA
GUYANA

SURINAME

Orinoco
FRENCH GUIANA (France)
River

COLOMBIA

Equator

ECUADOR
Amazon   River

Galapagos Islands
(Ecuador)
River

BRAZIL

Tapajós
Tocantins R.

São Francisco R.

PERU
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BOLIVIA

PACIFIC OCEAN
Paraguay R.

Tropic of Capricorn
PARAGUAY

R.

Paraná

CHILE
URUGUAY

Rio de la Plata

ARGENTINA

ATLANTIC OCEAN

Falkland Islands
(Great Britain)

Tierra
del Fuego

Strait of Magellan
Cape Horn

Meat from forest animals is important in the diet of virtually all people living in tropical forests. While the value of wild meat, either in traditional economic terms or as subsistence for forest-dwelling peoples, is inadequately quantified, the available figures are compelling:

1 The annual sale value of consumed wild meat in Liberia in 1990 was estimated conservatively at British £26.5 million (Mayers, 1991)

2 Based on market price of equivalent food, Caldecott (1986) estimated the monetary value to meat of wild origin in Sarawak at Malaysian $166 million/year, and that the 1.5 million inhabitants of the state annually consumed some 18,400 metric tons of wild game

3 In a survey of global wild meat consumption, Prescott-Allen and Prescott-Allen (1982) stated that wildlife and fish contribute at least 20% of the animal protein in the diet of the human inhabitants in at least 62 countries

4 Of those rural and urban people interviewed in a recent survey in southern Ghana, 95% claimed to eat wild meat on occasion (Falconer, 1992)

5 An older estimate in Zaire, indicated that 75% of animal protein consumed in the country came from wild species (Heymans and Maurice, 1973)

6 Another survey indicated that 60% of the animal protein consumed each year in Botswana was of wild origin (von Richter, 1969).

Information on the importance of wild game to people is more complete for the neotropics. In addition, there is more information on the impact of hunting on wild populations, and also considerable work on the sustainability of subsistence hunting. Accordingly, the rest of this paper will focus on subsistence hunting in Latin America.

Redford and Robinson (1991) review subsistence uses of wildlife in Latin America. In some areas wild game provides all the animal protein available to people (e.g., Pierret and Dourojeanni, 1966, 1967). Even when people have access to processed foods and meat from domestic animals, wild meat can still be a significant part of the diet (Ayres et al., 1991). As a general rule, wild game is more important to indigenous groups than to non-indigenous colonists (Redford and Robinson, 1987). This is probably a function of a stronger hunting tradition as well as less access to domestic animals and packaged meat.

Continent-wide estimates of the subsistence take of wild species are unavailable, but more local figures give an appreciation of the importance of game to local peoples. Redford and Robinson (1991) estimate that the half million rural inhabitants in Amazonas state in Brazil annually hunt and consume at least 3 million mammals, half a million birds, and several hundred thousand reptiles. If the whole of the Brazilian Amazon is included, this estimate rises to a staggering 19 million individual animals. Other estimates come from the Peruvian Amazon

town of Iquitos, traditionally a major market town for Amazonian natural products. Gardner (1982) extrapolated from Castro et al.'s (1975-6) data from three commercial markets in the town to calculate that the annual sale of wild game was about 200 metric tons. Castro and his colleagues estimated that about 11,000 individual primates were sold in the markets on an annual basis (about 5% of the wild game by weight), and that inhabitants of the Peruvian department of Loreto, which includes Iquitos, annually consume some 370,000 primates. Bendayán (1990, in Bodmer et al., 1990) provides a more recent estimate of wild game sold in the Iquitos markets of about 30 metric tons a year. However, sale of wild meat in Peru is now illegal, and Bendayán notes that market sales represent "only a small proportion of the total amount of wild meat commercially sold in Iquitos," and most wild meat is sold directly to households and restaurants.

The importance of wild game goes beyond its nutritional value (Redford, 1993). In many indigenous languages, the word "hungry" literally means "hungry for meat," as distinct from hunger that can be satisfied by other foods (c.f. Wagley, 1977). Wild game has a high social value, and by securing game and sharing it with other members of the community, the hunter builds debts, acquires allegiances, and contributes to social cohesiveness (Stearman, 1989). A number of studies (e.g., Saffirio and Hames, 1983; Paolisso and Sackett, 1986) have suggested a link between increasing lack of wild game and a breakdown of the traditional village social structure.

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Hunting, whether subsistence or commercial, inevitably has a negative impact on prey animal densities. Animal populations do not recover instantly from hunting, and any hunted site will have lower densities of hunted species. Yet the reduction in mammalian and avian densities in hunted areas is frequently far more dramatic than would be accounted for by the temporary reduction associated with offtake. In a broad comparison of densities across the neotropics, Redford (1992) found that mammalian densities in areas subject to moderate hunting are 80.7% lower than that of non-hunted or lightly hunted areas, and in areas subject to heavy hunting, 93.7% lower than that of unhunted sites. A similar comparison of avian densities indicates that game bird densities under moderate hunting are 73.5% lower than populations that are not hunted. This broad comparison is supported by individual studies that have directly examined game densities as they vary with hunting intensity. Surveys of mammalian game indicate dramatic declines with hunting intensity (Freese et al., 1982; Johns, 1986; Peres, 1990; Glanz, 1991). Similar patterns have been reported for birds. Silva and Strahl (1991) documented the very low densities of cracids (chachalacas, guans, and curassows) where they were hunted in Venezuela. Thiollay (1989) reported densities of the macaw (*Ara chloroptera*) were 94% lower in hunted sites in French Guiana.

Not all species are equally susceptible to hunting pressure. Large-bodied species tend to be preferred targets, and are frequently extirpated in heavily hunted areas. The single-barrel 16-gauge shotgun is the hunting weapon of choice throughout the neotropics, and has generally replaced more traditional weapons. The expense of a shotgun shell encourages hunters to focus on the larger game species. In addition, colonists of European extraction tend to focus on game species that most closely resemble domestic animals: ungulates, large rodents, and gallinaceous birds (Redford and Robinson, 1987). These all tend to be large.

Neotropical forest hunters also prefer frugivorous, or fruit-eating species, which are frequently described as "fat" or "tasty." Frugivorous primates, like the spider and the woolly monkeys, are preferred over more folivorous (leaf eating) and insectivorous species, like the howler or capuchin (Freese et al., 1982). Forest ungulates are generally frugivorous and species like tapir and peccary are preferred prey throughout. Paca are generally considered to be the most tasty rodent game species.

The impact of hunting on a species depends largely on the intrinsic rate of natural increase of that species. Species with low rates are less able to withstand hunting, and are much more susceptible to local extinction. As a general rule in comparisons across species, the intrinsic rate of natural increase declines with increasing body mass (Robinson and Redford, 1986a). However, some species, like primates, have much lower intrinsic rates than would be expected from their body mass alone, while others, like peccary, have higher rates than would be expected. As a result, the former are more susceptible to hunting than the latter.

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In general, species which tend to be large relative to other related taxa, frugivorous, and those with low intrinsic rates of population growth (such as tapirs, woolly monkeys and cracids) are very susceptible to overhunting. Large primates frequently disappear from heavily hunted areas (Freese et al., 1982). Other species, such as peccary, which have high intrinsic rates, appear to better tolerate hunting. Finally, there are species which benefit from hunting, which removes their predators and competitors. These species tend to be small-bodied or are not considered tasty. Agouti populations were higher in hunted areas in Brazil (Johns, 1986). Smaller primates can also increase in less heavily hunted areas (Freese et al., 1982; Johns, 1986; Mitchell and Raez, 1991).

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To evaluate the sustainability of neotropical forest hunting, we examine five cases, four examples of indigenous or tribal peoples which illustrate a range of acculturation, and one ribereño example (traditional Amazon peasants living along water courses). In all of these cases, people are hunting to meet their subsistence needs, although in the case of the Reserva Comunal Tamshiyacu-Tuhuayo, hunters do sell meat in local markets. The case of Tamshiyacu-Tuhuayo is examined in greater detail in the case study by Bodmer and Penn (1993). In all cases, hunting patterns are described, and the sustainability of hunting is evaluated with reference to the sustainability indices and models presented in the Appendix.

The Siona-Secoya
Hunting information from the years 1973-1975 and 1979-1982 was collected by Vickers (1980, 1988, 1991) from Siona-Secoya living in and around the San Pablo settlement in the Ecuadorian Amazon. Information of the Cuyabeno Wildlife Production Reserve is based largely on the management plan for the area (Coello Hinojosa and Nations, 1987).

1 Ecological setting
The Siona-Secoya indigenous group occupies a broad region in northeastern Ecuador, southern Colombia and northern Peru. The forests are lowland forests with mean annual rainfall of between 3,500 and 4,000 mm per year with little seasonality.

2 Socioeconomic setting
The Siona-Secoya today number about 1,000 persons. In Ecuador, the largest settlement area is San Pablo, with a population of about 375 people. Settlements are semi-nucleated, semi-dispersed villages which flourish for a period of years, then dissipate, with people moving up or down river. People cultivate corn, plantains, manioc, papaya and citrus trees. The Siona-Secoya are the most numerous indigenous group in the Cuyabeno Wildlife Production Reserve, an area of 2,547 sq km, which is, in theory, managed for the sustainable use of natural resources (Coello Hinojosa, 1992).

San Pablo, a settlement on the Shushufindi river, a tributary of the Río Aguarico, was studied by Vickers between 1973 and 1982. The settlement site is just outside the reserve boundaries, but the community's hunting area is partly within the Cuyabeno reserve. Established in 1973, the community was initially composed of about 100 people. By the late 1970s, the original settlement had grown to over 250 people.

3 Hunting patterns
Bamboo-tipped spears and shotguns are the traditional weapons for hunting game, but since the 1950s, these have been largely replaced by single-shot 16-gauge shotguns. Hunters take a wide variety of mammalian and avian prey, including woolly monkeys (*Lagothrix lagothricha*) (23% of kills over Vickers's 10 year period), white-lipped peccary (*Tayassu pecari*) (16% of kills), collared peccary (*Tayassu tajacu*) (14%), Salvini's curassow (*Mitu salvini*) (7%) and piping guan

(Pipile pipile) (6%). Vickers distinguished between 'preferred' species, those that hunters always attempted to kill, and 'less-preferred' species, those that were sometimes passed up. Tapir, peccaries, large primates and birds were preferred, while deer, small primates, small birds, rodents, edentates, and reptiles were less preferred.

Throughout Vickers's study period, the community hunted primarily (81% of hunting man-days) in a 590 sq km core area. An additional 12% of hunting time was spent in an adjacent 560 sq km area, and the rest of the hunting time was spent in a more distant 1,350 sq km area (a total catchment area of 2,500 sq km). Other indigenous groups and colonists also hunted in this catchment area, although rarely in the community's core hunting area.

4 Sustainability of hunting
In Vickers's study, most hunting yields tended to decline during the first three years of the study, but did not do so continuously over the 10 years. The exceptions were woolly monkeys, curassows, and trumpeters *(Psophia crepitans)*, for which continuously declining yields suggested that their hunting was not sustainable. Some of the yields for less-preferred species increased over the period, possibly indicating a general decreased availability of preferred species and a switch to less-preferred. Application of Robinson and Redford's (1991) model to kill numbers indicates that harvest of woolly monkeys is not sustainable even within the entire 2,500 sq km catchment area, but the harvests of collared and white-lipped peccary might be sustainable, even within the 590 sq km core area. However, since Vickers's study, the human population in the San Pablo community has continued to grow (from 250 to 375 persons) and how this has affected harvests is unknown.

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5 Management of wildlife resources
A management plan for the Cuyabeno Wildlife Production Reserve was submitted to the Dirección Forestal de Ecuador in 1987, funded in part by World Wildlife Fund - U.S. The plan recognizes that any management must take into account the needs of the indigenous groups, but it includes no direct indigenous involvement in the management of the reserve and the surrounding area. The implementation of the management structure is still at a preliminary stage so it is difficult to say who will manage the wildlife resources and whether they will be managed effectively for the benefit of or by the local communities.

The Chimane
Hunting was only surveyed for a three-week period in May 1987 at the end of the wet season (Redford and Stearman, 1989; Stearman, 1992). The results of this work largely agree with a more comprehensive but as yet unpublished study (Chicchón, 1992). Information on the Beni Biosphere Reserve was mostly derived from Chicchón (1991) and Campos Dudley (1992).

1 Ecological setting

The Chimane are an indigenous group in lowland Bolivia inhabiting a transitional zone between the lowland tropical forests extending outwards from the base of the Andes mountains and the westernmost edge of the Beni savannas. Annual rainfall averages around 2,000 mm, and there is a pronounced dry season between May and September.

2 Socioeconomic setting

The Chimane practice horticulture (planting upland rice, plantains, manioc, corn, squash and a variety of fruits) combined with fishing and hunting. Although they have had contact with Europeans since the seventeenth century, and so have had a long history of acculturation, they have largely retained a traditional culture and traditional methods of resource extraction. They have a history of semi-nomadism ranging widely over a region centered in the modern Bolivian department of Beni that they have hunted and fished for generations. Many Chimane now work as day laborers on the large open-range cattle ranches, which were established in the grasslands of the Beni (for additional information see Stearman, 1992; Chicchón, 1991, 1992).

Approximately 500 Chimane inhabit a zone at the northern edge of the Beni Biosphere Reserve, and this discussion focusses on the sustainability of this group's hunting. These Chimane have only inhabited this area for about five years, and they enter the reserve to hunt. This hunting is primarily for their direct subsistence, because the reserve is isolated, and commercial hunting for skins and meat appears to be relatively unimportant. The Chimane are responsible for most of the hunting within the reserve.

The Beni Biological Station was created in 1982, and comprises some 1,350 sq km. The area was declared a biosphere reserve in 1986 and entered UNESCO's Man and the Biosphere Program. The reserve is part of a larger area known broadly as the Chimane Forest which originally comprised production forest, a cattle ranching savanna area, and forested watershed protection areas. In 1990, the Bolivian government ceded significant portions of the Chimane Forest, including all of the biosphere reserve, to the Chimane and three other indigenous groups (for more information see Chicchón, 1991; Campos Dudley, 1992).

3 Hunting patterns

Over 85% of the Chimane households hunt at least once a week, and an additional 13% hunt once every 1-2 weeks. All households own and use bows and arrows, and 60% also own firearms. Hunters take a wide range of mammalian and avian prey, including white-lipped peccary (44% of kills in Redford and Stearman's sample), collared peccary (7%), and a number of monkey species (32%). Peccary, both collared and white-lipped, are preferred prey, although fish, monkeys, tapirs, and deer were preferred by some people. Nevertheless, fish was the most frequently eaten food.

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4 Sustainability of hunting

Redford and Stearman's hunting survey was limited to a three-week period and focused on Chimane living away from towns, nevertheless the data are instructive. White-lipped peccary, the preferred prey, are being taken by the Chimane at four times the harvest of the average Amazonian hunter (from Redford and Robinson, 1987) – over 4.1 white-lipped peccary/person/year. In the Chimane community of about 500 persons, this is equivalent to over 2,000 white-lipped peccary/year. Using Robinson and Redford's (1991) population growth model to calculate the catchment area to produce this many animals generates a figure of about 2,500 sq km. This figure is about twice the size of the Beni Biosphere Reserve. This intensity of hunting is not sustainable.

5 Management of wildlife resources

It is clear that the Chimane need to be integrated into the planning and management of the Beni Biosphere Reserve and its associated areas. At the time of their survey, only 7% of respondents in Redford and Stearman's interviews had even heard of the reserve in which they were hunting, although this has changed now. The Chimane in and around the reserve have no centralized form of political organization, which makes interaction with government and reserve planners difficult. Nevertheless, in 1990, supported by indigenous rights activists, the Chimane participated in the march which resulted in the establishment of the Chimane territory. This decision theoretically gives the Chimane considerable autonomy over management of their wildlife resources.

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The Yuquí

The hunting patterns described here are largely based on a 56-day study by Allyn Stearman in September-December 1983, and a comparable time in February-May 1988 (Stearman, 1990, 1992).

1 Ecological setting

The Yuquí are forest-dwellers, living in lowland forest whose annual rainfall averages between 4,000 and 5,000 mm. The land is flat, containing marshy areas flooded throughout the year, and seasonally flooded areas dominated by Socratea palm. It is about 60 km from the eastern edge of the Andes in central Bolivia. The region is marked by old river meanders and ox-bow lakes. There is a short two-month dry season.

2 Socioeconomic setting

The Yuquí are not as acculturated as the Chimane. Traditionally they practiced no horticulture, and most of their caloric intake and animal protein derived from game and fish. Up until very recently, fish provided the Yuquí with more than 50% of their animal protein intake. The Yuquí were first contacted in 1968 by the New Tribes Mission, and one group of 43 people settled at a mission station on the banks of the Chimoré river. By 1982, this group had grown to 73 people. In 1986, a second band of 23 Yuquí joined the settlement. Recently a third and last group has been added.

3 Hunting patterns

Traditionally, the Yuquí hunted with bows, but by 1983, hunters had shifted to 16-gauge shotguns and .22 rifles. By 1988, these hunters had shifted largely to shotguns, but still occasionally used bows. The newly contacted group still hunted with bows. Hunters take a wide variety of prey. In 1983 tortoises (*Geochelone*) accounted for 11% of all kills, guans (*Penelope*) for 9%, armadillos (*Dasypus novemcinctus*) for 9%, curassows (*Mitu*) for 8%, capuchin monkeys (*Cebus apella*) for 8%, white-lipped peccary for 6%, capybara (*Hydrochaeris hydrochaeris*) for 6%, and collared peccary for 5%.

The Yuquí primarily hunt within 5 km of the mission station – the core game catchment area is about 78.5 sq km. In Stearman's 1988 study, 72% of all game, by weight, were harvested in this area. A larger, less intensively hunted area extends out some 10 km, defining a total catchment area of 314 sq km.

4 Sustainability of hunting

The Yuquí have been using a tiny catchment area, but the 1983 figures indicate that at the time game harvest was also low. Application of Robinson and Redford's (1991) population growth model to the 1983 harvests, so as to calculate necessary catchment area for selected important species, indicates the following: The capuchin monkey harvest requires a catchment area of at least 433 sq km, the tapir an area of at least 216 sq km, the white-lipped peccary an area of 71 sq km, and the collared peccary harvest an area of at least 22 sq km. These figures indicate that capuchin monkey and tapirs were being overharvested in 1983, while harvest of the two peccaries might have been sustainable. Yet in 1988, three species (the most important by weight in 1983) – capybara, white-lipped peccary, and tapir - had disappeared from the list of hunted species. The species that were most frequently killed in 1988 were coatis (*Nasua nasua*) (12% of kills), a species according to the Yuquí that "taste bad and make you sick," tortoises (11%), guans (7%), and four species of monkeys (together accounting for 23% of kills). The Yuquí had not sighted or killed a white-lipped peccary since 1985. Collared peccary were still being taken but the relative frequency of kills had dropped. Less-preferred species contributed significantly more to the Yuquí diet.

The drop in yield apparently resulted from colonist hunting and fishing in the area. Since 1986, there has been extensive colonist incursion in the territory of the Yuquí, primarily for the purpose of coca production. Colonists tend to remain on their farms only during the planting and harvesting of the coca, and return to their highland settlements at other times of the year. Colonist activities apparently have had a major impact on the fish and game resources available to the Yuquí: colonist hunting focused on peccaries, tapir, paca and deer, and often used dogs; colonist fishing often uses dynamite and gill nets stretched across the river – techniques which strip a river of its fish populations; and colonist forest-clearing inteferes with the migrations of the white-lipped peccary.

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By 1988, the Yuquí had lost some of their most important sources of animal protein, and in addition were unsustainably hunting many of the remaining species. The 1988 harvest of capuchin monkeys could only be generated sustainably in an area of at least 800 sq km, and of howler monkeys (*Alouatta seniculus*) in about 350 sq km. Harvests of coatis and cracids (see Silva and Strahl, 1991) were unlikely to be sustainable.

5 *Management of wildlife resources*
To insure that game hunting is sustainable, the Yuquí require access to a much larger catchment area. Up until 1990, their legal holdings only encompassed 78 sq km, in a rough square around the main settlement. However the area was included in a regional development project funded by the Interamerican Development Bank (IDB), and the Yuquí now have legal access to a territory of 1,100 sq km. The express goal of this expansion was to assure the Yuquí of continued access to game resources.

The Xavante
Harvest information is based on a year-long study of the Xavante hunting in the village of Pimentel Barbosa between February 1991 and January 1992 (Leeuwenberg, 1991, 1992a, 1992b).

1 *Ecological setting*
The Xavante occupy a transitional zone between the drier cerrado and the wetter Amazonia in the state of Mato Grosso in Brazil.

2 *Socioeconomic setting*
Traditionally the Xavante were semi-migratory, practicing extensive hunting, small-scale agriculture and a little fishing. In recent years they have developed more agriculture in response to incentives provided by FUNAI, the Brazilian institute for Indian affairs. There is some cattle raising.

The Xavante Indigenous Reserve of Pimentel Barbosa occupies some 2,200 sq km, with most of the 270 people living in the village of Pimental Barbosa, roughly in the center of the reserve. The hunting area for the community is restricted however to a smaller area extending out some 25 km from the village (comprising about 650 sq km). A significant portion of the reserve is rarely visited by hunters from the village.

3 *Hunting patterns*
Over the course of a year, Leeuwenberg documented the harvest of 499 mammals belonging to 18 different species. As in many other areas, ungulate species are the most important by number and weight. Ranked by number, collared peccary accounted for 27% of kills, white-lipped peccary for 23% of kills, giant anteater (*Myrmecophaga tridactyla*) for 18%, armadillos (*Euphractes sexcinctus*) for 9%, and pampas deer (*Ozotocerus bezoarticus)* for 7%. The principal hunting season was between June and September, during the dry season.

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The Xavante traditionally hunted using fire to drive game, and presumably to manage vegetative production for game species. Fires were generally lit at the end of the dry season, on the advice of Xavante elders who monitored time of year, condition of vegetation, and celestial conditions. Different habitats were burnt at different frequencies – every one or two years for open grasslands, to every four or five years for shrub woodland.

4 Sustainability of hunting

Within the 650 sq km catchment area, Leeuwenberg was able to delineate the area covered by different habitats, and thus the habitat available to different game species. His application of Robinson and Redford's (1991) model indicated that at least three of the ten most important species (pampas deer, grey brocket deer (*Mazama gouazibira*), and tapir) were being overhunted. In the case of the two deer species, this conclusion was supported by an age distribution of harvested animals which showed few adults over two years of age. In addition, the high harvest of giant anteaters relative to average density indicated that this species was also being overharvested. Harvest of the two peccary species was possibly sustainable, although the age distribution of white-lips gave some cause for concern.

5 Management of wildlife resources

The community group, Associação Xavante de Pimentel Barbosa, is considering management responses to the overharvesting problems. It has been proposed that:

a A temporary moratorium of a year be placed on hunting the four species of concern (pampas deer, grey brocket deer, tapir, and giant anteater) within the 650 sq km main catchment area

b Hunting and fruit harvesting be extended to other areas of the reserve (this policy would also allow the Xavante of Pimentel Barbosa to patrol the boundaries of the reserve and exclude non-resident hunters, fishermen, and miners)

c Traditional family hunting, a practice whereby family groups undertake long hunting expeditions into distant areas, should be reinstituted (this would also serve to instruct the younger generation in hunting traditions)

d Traditional fire management of habitats be re-instituted, with burning restricted to periods when fruits were not being collected.

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The Reserva Comunal Tamshiyacu-Tuhuayo

The biology of the game populations was extensively studied between 1984 and 1988 (Bodmer, 1989). Hunting patterns were surveyed between June 1985 and July 1986 (Bodmer et al., 1988a, 1988b) and between October 1990 and October 1991 (Bodmer et al., Unpubl. ms.) The economic value of game was calculated from market surveys (Bodmer, 1992; Bodmer et al., 1990a, Unpubl. ms.). The reserve itself is described in Bodmer et al. (1990b).

1 Ecological setting

The Tamshiyacu-Tahuayo reserve is predominately (over 75%) *terra firme* forest, and is located about 25 km south of Iquitos in northern Peru. The remainder is seasonally flooded varzea forest. Human disturbance of the forests is minor, derived mostly from low-intensity selective logging and shifting agriculture.

2 Socioeconomic setting

The ribereño communities along the Tamshiyacu and Tahuayo rivers acted together with the scientific community and the Ministerio de Agricultura in Iquitos to form the Reserve Comunal Tamshiyacu-Tahuayo. The reserve was established in February 1990, and received final legislative approval in June 1991. The 3,225 sq km reserve is divided roughly equally into a fully protected core area and an area of subsistence use. People can collect forest products from the latter for their subsistence use. The 31 permanent settlements along the Tamshiyacu and Tahuayo occur outside of the reserve, and have a total human population of about 4,250 inhabitants.

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Bodmer and his colleagues examined hunting patterns in a 500 sq km area exploited by inhabitants of one village at the edge of the reserve. The village comprised 310 people in approximately 44 family groups. The major economic activities were shifting agriculture, hunting, fishing, and lumbering. The ribereños rely on wild fish and game for much of their protein needs.

In addition to hunters from the villages adjacent to the reserve, three other groups hunted in this area: small-scale timber operations based in Iquitos whose workers were supplied with ammunition instead of processed foods; subsistence hunters from other nearby villages; and illegal commercial hunters.

3 Hunting patterns

Hunters relied exclusively on single-shot 16-gauge shotguns. During the 1990-1991 year-long study, 1,278 mammals (excluding small rodents) were harvested from the 500 sq km area. Of these, 36% were ungulates, 26% were primates, 25% were large rodents, 8% were carnivores, and 6% were edentates. Ungulates, being generally large-bodied, comprised 79% of the harvest biomass, and most of this meat was transported downriver to the commercial markets of Iquitos. Peccaries, white-lipped and collared, each comprised 36% of the ungulates killed, while red brocket deer comprised 13%, tapir 8%, and grey brocket deer 6%. The ribereños themselves consumed the primates and rodents. Of the large rodents, pacas (*Agouti paca*) comprised 95% of the sample, while capybara (*Hydrochaeris hydrochaeris*) comprised the rest.

Before the reserve was established, hunting by logging crews and by illegal commercial hunters was greater than that of ribereño hunters. Logging crews had the greatest impact, taking about 51% of all ungulates. Commercial hunters harvested an additional 11%. The remainder was taken by subsistence hunters, but of this, 58% was taken by hunters not living in the reserve villages. Now however, the lumber concessions in the area have been annulled, primarily because of their impact on the wildlife.

4 *Sustainability of hunting*
Bodmer and his colleagues used a number of approaches to evaluate the sustainability of hunting:

a Based on density surveys and actual harvests, they estimated that the annual harvest took 7% of the primate population, and 8% of the ungulates. These figures are not high by temperate game standards.

b They compared densities of game species at Tahuayo with those in non-hunted areas, and noted that primate densities were much lower than at non-hunted sites.

c They compared survivorship curves for each species with those in non-hunted areas, and suggested that the artiodactyls did not appear to be overhunted.

d They calculated total production (#/sq km) for the five ungulate species by multiplying species density (#/sq km) by total reproductive productivity (average # young/individual/year), and then compared this figure to actual harvest pressure (#/sq km). The comparison revealed that 15% of the collared peccary production was taken by hunters, 38% of the white-lipped peccary production, 22% of the red brocket deer, 20% of the grey brocket deer, and 160% of the tapir production. They concluded that tapir and large-bodied primates were not being hunted at sustainable levels, that carnivores and edentates were probably also being overhunted, but that the other ungulates and large rodents were being hunted at sustainable levels.

5 *Management of wildlife resources*
The ribereños have taken the initiative in developing and implementing management regulations to prevent overexploitation of the reserve's fish and game resources. Many of the ox-bow lakes scattered along the rivers have been overfished, and ribereño communities have prohibited the use of nets and harpoons in these lakes during the low water season – permitting only hook-and-line methods. The communities have forbidden entry of commercial fisheries from Iquitos and have attempted to stop the use of illegal fish-poison. Fish populations appear to be rebuilding.

Bodmer and his associates have calculated the economic benefits of hunting within the 500 sq km study area. Based on commercial value, the area was sustainably producing about US$20,868 a year in artiodactyl ungulates and large rodents. It was non-sustainably producing about $5,465 in tapir, large primates, edentates, and

carnivores. To establish a sustainable hunt therefore, would require that hunting of these species be prohibited at the present time. To maintain the economic condition of the villages therefore would require an annual subsidy of $5,465 (or $11/sq km). Such a subsidy probably should not be reimbursed directly with cash, but indirectly through social activities such as increased health, education, and transportation services – services that villagers presently pay for and wish to have improved. The researchers also suggested that a male-only hunt of artiodactyl ungulates would increase overall production.

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All the cases examined are examples of community-based resource utilization, however, the question remains whether they are examples of community-based conservation. The community-based approach to wildlife utilization only meets conservation criteria if the use of wildlife species is sustainable. At its simplest, this means that wildlife species are harvested at levels that allow them to continuously renew themselves. This is more easily stated than accomplished, and in individual situations one needs to consider the sociopolitical, economic, and ecological consequences of different harvest regimes. These considerations are included in Robinson's (1993) general definition of sustainable use: "Sustainable use only occurs when the rights of different user groups are specified, when human needs are met, and when the losses in biodiversity and environmental degradation are acceptable." Let us briefly consider each of these requirements as they apply to community-based conservation.

1 In community-based conservation, local communities obtain use rights over natural resources. This is a political and social decision. In most countries, local communities do not have an *a priori* right to exploit the wildlife resources in the areas in which they live; such a right is reserved to the state. An argument can be made that local communities should have rights based on moral, ethical, historic, legal, or pragmatic reasons, but harvest rights can just as easily be, and frequently are, assigned to other interested user groups (e.g., local commercial operations, state or national wildlife agencies, trophy hunting enterprises, etc.).

2 In community-based conservation, the needs that must be met are those of the local communities. If those needs are met, then the wildlife resources, while they will be impacted, will not be overhunted. If those needs are not met, then, barring some intervention by a segment of the community, wildlife will be depleted, and people will be forced to turn to other economic activities.

3 In community-based conservation, the loss of biodiversity associated with the harvest of wildlife must be acceptable to interested parties, be they the local communities themselves, government agencies, or conservation organizations. The declines in the population densities of the harvested species, the local extinction of certain species, the ancillary ramifications throughout the biological community, the biological simplification of the ecosystem – all must be acceptable to conservation planners. In addition, when human beings hunt in an area, they will invariably extract other natural products and will systematically alter the landscape. All of these biological changes must be acceptable, but the question remains: acceptable to whom? In strict community-based conservation the community may be the ultimate decision-maker, but within a community and even between genders acceptability may differ. In a co-management regime both government agencies and the community must determine the limits of acceptability. In addition, conservation organizations and donors may have their own criteria.

We have discussed five cases that provide some information on the sustainability of wildlife harvesting. In all of the cases there is evidence that some game species are not being harvested sustainably. In at least three of the cases (Siona-Secoya, Xavante, Tahuayo), some game species appear to be harvested sustainably, and there are management initiatives that will regulate the harvest of overhunted species. In one case (Yuquí), every indication is that even the low harvest is not sustainable, and a very significant expansion of their hunting area will be necessary to allow sustainability. Recent developments suggest that this might now be possible. One generalization suggested by these cases is that catchment areas of about 2,500 sq km seem to be necessary to provide the subsistence hunting needs for human communities of a few hundred people in neotropical forests. If catchment areas are much smaller than this, or human populations much higher, it is likely that many species, such as primates, tapir, and eventually peccary will be extirpated from hunting areas. Even if they are not, their densities will be too low to meet the needs of local peoples. The conclusion that one must draw is that with an insufficient resource base, community-based conservation efforts oriented towards game animals is not possible – no matter how clearly the goals are defined, or how effective the management structures. **19**

Who or what group will manage these systems of harvest is a question on which there is little agreement. Community-based approaches presuppose a delicate balance between the ecological situation, the socioeconomic needs of local communities, and the political power of these communities relative to other interested user groups. One possibility is to allocate all power to the local communities themselves, and this approach is most attractive to those who believe that left to themselves, local communities will live harmoniously with the natural environment. Yet few local communities are not involved in market economies, and even if this were not the case, it is doubtful whether the "ecologically noble savage" (Redford, 1990) – at least as envisioned by some conservationists – ever existed. People everywhere act in their self-interest, and economic considerations contribute importantly to the equation. In addition, local communities by themselves also rarely have the human resources required to manage natural resources and also deal with regional and national markets (Browder, 1992). Another possibility is to assign the responsibility to regional and national government agencies. Yet throughout much of the world, these agencies have traditionally not been sensitive either to the socioeconomic needs of local communities or to the mandates of resource conservation. Governments tend to have policies which foster national economic development at the expense of resource conservation, and of cultural and social integrity; and even where this is not the case, they rarely have the resources to monitor a resource utilization in remote areas. Still another possibility is to give the responsibility of managing areas to national non-governmental organizations (NGOs). While the actions of these groups is frequently more determined by idealistic goals and less by economic self-interest, they rarely have the expertise necessary for the task, and their goals tend to be too narrowly focussed. It is likely that for the foreseeable future, a loose alliance of local communities, NGOs, and

government agencies will be charged with managing community-based efforts The five cases reviewed here each show a different mix of players, and it is likely there will not be a single management structure that is generally recognized as being the most effective.

The challenge of managing community-based conservation efforts will increase as population growth and rising material expectations place greater pressures on the forest. Rural local communities will increasingly participate in market economies (e.g., Stearman and Redford, 1992), and this will encourage ever greater wildlife harvests. Other development demands will encroach on the land necessary to support a sustainable harvest. The Siona-Secoya settlement of San Pablo has grown from about 100 people in 1973 to a community of 375 persons today, and this is likely to increase overall hunting pressure in the catchment area. And other human interest groups will increasingly compete for access to the wildlife resources of the forest. In Tahuayo, logging crews, commercial hunters, and subsistence hunters from communities outside of the reserve compete with local communities for the wildlife.

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Local communities will be able to contribute to the conservation of natural systems only if their needs are met. But to date, tropical forests are not proven to be systems that can support high human populations while at the same time retaining a significant proportion of their biodiversity. As human populations climb, as material expectations of people increase, and as other human groups benefit from the exploitation of the tropical forest, we can expect a progressive erosion in forest biodiversity. What is the acceptable loss in biodiversity? And at what point do local communities cease to contribute to conservation and become net exploiters? Empowering local communities is also difficult. Will local people be able to control their own destinies if projects are successful? Finally there remains the important question of project management. Who or what group will define the overall goals of these efforts, and can projects be managed towards those goals? The future of community-based conservation efforts depends on the answers to these questions.

Acknowledgements

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Sustainability of hunting activities

We consider hunting to be sustainable if people are able to supply their needs without depleting their prey resources, and hunting does not drive any species to local extinction. A minimum requirement that meets these two conditions is if the harvest of a species does not exceed its potential population yield – in other words the population as a whole is maintained at a level that produces a sustainable yield.

A sustainable yield is produced when a harvested population remains stable (neither decreasing or increasing) through time. A population will increase, through births (b) and immigrations (i), and decrease through deaths (d) and emigrations (e). Production (P) is the addition to the population through births and immigration. If a population is harvested, a portion of that production goes into Yield (Y). In other words, yield is the potential that could be harvested at a specified game density. If the actual harvest exceeds the potential yield, then the population will decrease. If a harvested population is stable then all production goes into either yield or natural loss (d + e). These relationships are illustrated in Fig. 1.

One goal of classic wildlife management is to ensure that the Harvest (H), the actual take from the population, is sustainable – this requires that the harvest not exceed the potential yield. There are many population levels at which any species can be sustainably harvested. Very small populations, for instance, will have a very small yield, but as long as harvest does not exceed that yield, it will be sustainable. Another goal is to ensure that the proportion of production that goes into yield is maximized. There is a population level at which this occurs – termed the maximum sustainable yield (MSY) – and managing populations to this level is the goal of many resource managers. The maximum sustainable harvest is accomplished at the maximum sustainable yield.

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Applying these theoretical concepts to real situations is much more complicated. Ideally one needs to know the population density for the wildlife species, the carrying capacity of the species in the habitat of interest, the age-sex structure of the population, the production at a range of different population densities and different age-sex structures, and the actual harvest. These data are available, in a very approximate fashion, for a few species, such as the white-tailed deer at a few locations in North America, but even in this case, there is little confidence that data are robust (Caughley, 1985).

For tropical wildlife, the data necessary for these calculations are virtually non-existent. The evaluation of whether a harvest is sustainable therefore is highly speculative. We discuss below five indices that have been used by field researchers to evaluate sustainability. These indices do not do so directly but instead measure parameters that might relate to sustainability. In addition to these indices we discuss two models which attempt to measure sustainability directly. Both depend on some knowledge of the biology of harvested species, and must make a number of biological assumptions derived from studies of temperate species.

Sustainability Indices
These five indices have been used by different authors as measures of
sustainability. Differences in values between sites are assumed to reflect different
hunting pressure or history. All of these indices however only measure one
component of sustainability, and thus inference on sustainability is weak.

1 Population density comparisons
The simplest index of sustainability relies on comparisons of wildlife densities in
hunted areas with densities in unhunted or control areas. The assumption is that, if
hunted populations are low, then people are overharvesting the resource and
hunting is not sustainable. Such an assumption however presupposes that one
knows something about how densities vary among sites in the absence of hunting,
and also how yield varies with population density. Let us consider each of these
suppositions in turn.

A lower density at a hunted site, compared to a unhunted one, does not by itself
indicate that hunting is not sustainable. While differences might result from
overhunting, they might merely reflect geographic variation in densities. For
neotropical mammals, there are enough surveys in the absence of hunting to
provide a general appreciation of geographic variation in density for some
mammalian taxa (Emmons, 1984), and some understanding of average densities
(Robinson and Redford, 1986b; 1989). For neotropical birds, fewer studies have
examined densities (but see Thiollay, 1989; Terborgh et al., 1990; Silva and Strahl,
1991; Iñigo-Elias, 1991), and while general patterns have not been described, it is
likely that the determinants of avian densities will be similar to those described for
mammals (Terborgh, pers. comm.). Nevertheless, a lower density at a hunted site
allows little inference on hunting sustainability.

A low population density, relative to the supposed carrying capacity (K) of the
habitat for that species, also does not, by itself, indicate that hunting is not
sustainable. First, because hunting will always lower a population density of the
prey. Second, because one also needs to know how yield varies with population
density. What is the range of densities that would generate yields that will meet
the needs of the hunters? Classic wildlife management theory predicts that
maximum sustainable yield (MSY) is achieved at 0.5K – at half the density of an
undisturbed, unhunted population. There is some empirical support in the case of
white-tailed deer for this largely theoretical prediction (McCullough, 1979), but
there is no such support for most other species, and no information at all for
tropical forest species. There is some theoretical indication that populations of
many species maximize yield when they are much closer to their carrying
capacity – densities in the range of 0.65K to 0.90K have been suggested (see
Robinson and Redford, 1991). What this would mean is that if a population density
is much below the carrying capacity, it is likely that yield would be low, and any
significant harvest would not be sustainable. Nevertheless, any inference on
sustainability based on a low population density is weak.

Despite these uncertainties, a number of studies have used relative densities as a general index of sustainability. For instance, Bodmer and his colleagues (Bodmer et al., 1988a, 1990a) have argued that the primate harvest in the Tamshiyacu-Tahuayo reserve in northern Peru was not sustainable because densities were much lower than the Manu National Park in southern Peru. All that really can be said from this comparison however – assuming the two sites are roughly comparable – is that the potential yield in Tamshiyacu-Tahuayo is much lower than in Manu, and that the lower densities in the former are the result of hunting. In and of themselves, density comparisons actually tell us little about the sustainability of the harvest.

2 Population density declines

A slightly better index of sustainability relies on density changes at a single site through time. A steadily declining wildlife population under hunting indicates that harvest is not sustainable. Unfortunately, such data are rarely available. Most studies examining population densities are of short duration, and thus longitudinal data are not available. One exception is Silva and Strahl's (1991) study in which densities of cracids were recorded over a two and a half year period. Even over this short time period, most species showed a decline in density over this period, **29** a decline the authors ascribe to overhunting.

3 Hunting yields comparisons

Hunting yields have also been used as an index of sustainability. Hunting yields have been measured in a variety of ways. The simplest measure involves tabulating the total number of animals taken during a specified period, but this does not take into account the number of hunters nor their hunting effort. A better measure is hunting yield per unit effort, where unit effort is measured by the distance, frequency, duration of hunts, or number of hunters (e.g., Hames and Vickers, 1982; Saffirio and Scaglion, 1982; Stearman, 1990). One inclusive measure that has been proposed is kill rates, which measure the number of kills per man-hour of hunting (Vickers, 1991). Note that Hunting yields (HY) are not the same as the game population yields (Y) discussed above. Hunting yields are actual harvests (H), usually measured in terms of unit hunting effort.

Researchers have compared hunting yields among sites and suggested that lower than expected yields indicate that hunting was or is unsustainable. The assumption is that game population densities among sites would be similar in the absence of hunting, and that hunting effort at different sites is similar. For instance, Smith (1976) examined colonist hunting at three locations along the Transamazon highway in Brazil, and concluded that low hunting yields around established settlements were the result of previous overhunting. Beckerman (1978) ascribes the low yield of tapir obtained by the Bari to heavy colonist hunting in the past. However, like comparisons of population densities, comparisons of hunting yields can suggest that game densities are depleted, and that hunting is or was unsustainable, but the argument is indirect and non-conclusive.

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4 Hunting yield changes

Changes in hunting yield over time indicate more strongly the sustainability of the harvest. Continuous declines generally indicate that hunting is not sustainable and population densities of harvested species are falling. A decline must be maintained however, as a population recently opened to hunting will always decline until actual harvest balances potential yield, and the increased wariness of animals will accentuate the decline in hunting yields.

The most extensive data set on neotropical wildlife yields has been provided by the study by Vickers (1980, 1991) of a native Siona-Secoya community in northeastern Ecuador. Vickers tabulated hunting yields in 1973, 1974 and 1975, and again in 1979, 1980, and 1981-1982. During the first 3-year period, which immediately followed the establishment of the settlement, hunting yield (measured by weight of meat taken per man-hour of hunting and by kill rates) declined continously, and Vickers (1980) concluded that game was being depleted. This conclusion may have been premature, because, for most species, hunting yields did not decline further in succeeding years. Accordingly, in the later paper (1991), Vickers revised the earlier conclusion and suggested that the harvest of many species was sustainable.

One complication with interpreting hunting yield patterns is that they must take into account changes in the species composition of harvested game. Hunters in the neotropics tend to prefer large-bodied animals, which have a lot of meat, and "tasty" animals (see above). When populations of these species are overhunted, then densities decline, and hunters shift to less-preferred prey, which generally tend to be smaller (Hames and Vickers, 1982; Stearman, 1990; Vickers, 1991). Small-bodied prey generally occur at higher densities than large-bodied (Robinson and Redford, 1986b), and therefore, under these circumstances, overall hunting yield, when measured by kill rates, can actually increase following overhunting of preferred game species. Vickers (1991), for instance, reported increases in kill rates of less-preferred species such as agoutis, squirrels, armadillos, and caiman over the 10-year period, and decreases in kill rates of woolly monkeys and cracids. Yet hunting yield (measured as kg of meat per man-hour of hunting) did not decline over the study period.

Another complication is the need to take into account changes in human community. For instance, Ayres and Ayres (1979) examined hunting yields in the town of Dardanelos, a small town in the Brazilian state of Mato Grosso in 1978. Two years later, hunting yields were again surveyed (Ayres et al., 1991), after a road had reached the town and allowed much easier movement of people and goods. Game yield (measured by meat weight) had declined to 30% of its earlier total. The diversity of game species declined dramatically, and certain groups like primates, had disappeared entirely. Yet Ayres and his colleagues did not ascribe these declines to declining populations of wildlife species. Instead, they pointed to social changes in the community: the increased commercialization of game with specialized hunters focussing on the most saleable species; the increased access to domestic meat; the influx of newcomers with little knowledge of tropical forest

hunting and the outflux of previous residents to gold-producing areas; and the need of many people to work their land to secure land title.

In summary, whether hunting yields decline or not, the interpretation is problematic: Wildlife densities might be declining or stable, the immigration of wild animals into hunting areas might be masking changes in game populations, or hunting yields might merely be a result of changes in game compositions and/or the human community.

5 Age-structure comparisons

The distribution of ages within a population respond to harvesting, and thus can provide an index of the sustainability of that harvest. Harvested populations generally are subject to greater mortality in the older (and larger) age classes. This decreased survivorship is reflected in juveniles making up a higher proportion of the population and in a 'flatter' age-pyramid.

The proportions of juveniles and adults in three rodent species which are extensively hunted throughout Latin America are illustrated in Fig. 2. The data from San José de Payamino in the Ecuadorian Amazon (Irvine, 1987), the Colombian llanos (Collett, 1981) come from actual harvests. The agouti (*Dasyprocta sp.*) and the paca (*Agouti paca*) samples from Barro Colorado Island (Smythe et al., 1982) come from demographic censuses of wild populations. The sites are arranged by intensity of hunting, and illustrate how the proportion of adults falls in hunted populations. A similar pattern is evident in Fig. 3 which compares age-structures in collared peccary (*Tayassu tajacu*) populations. With the exception of the San José de Payamino sample, which was based on harvests, all the other sites are based on field censuses, and again are ordered in increasing hunting intensity. A high proportion of juvenile animals in a population therefore can be used as a measure of hunting intensity, and has been used to comment on sustainability (e.g. Irvine, 1987).

More complete age-structure descriptions for neotropical forest game are rarely available, with a few notable exceptions. Collett (1981) used tooth eruption patterns and annual rings in the cementum of upper molars in *Agouti paca* to generate 13 age classes, and then relate age-specific survivorship to hunting intensity. Bodmer and his colleagues (Bodmer, 1991; Bodmer and Fang, Unpubl. ms.) have used a similar technique to generate population age-structures for ungulates at Taperinha, an eastern Brazilian Amazon site near Santarém, and at Tahuayo-Blanco in the Peruvian Amazon. Both studies were able to relate differences in age-specific survivorship at different sites to putative hunting intensity.

Variation in the age-structure of populations therefore can quantify the impact of hunting on wild game populations, and thus allow some statement on relative sustainability, but in the absence of other measures, age-structure differences do not indicate whether hunting is sustainable or not.

Sustainability models

Two theoretical models have been developed to evaluate the sustainability of

hunting in neotropical forests. Both models require information on the characteristics of game populations.

1 Population analysis model

Bodmer and his colleagues at Tahuayo have developed a simple and elegant model of harvest sustainability that estimates population production (P). The model requires estimates of (i) reproductive productivity (young produced/female/year) and (ii) population density. Comparison of production with a known harvest in a specified catchment area then can provide a direct measure of sustainability.

Few sites are studied well-enough to allow estimates of these parameters for the game species, but the exception is Tahuayo in the Peruvian Amazon. Bodmer and his colleagues (Bodmer, 1991; Bodmer and Fang, Unpubl. ms.) were able to describe the age structure of populations of ungulates. The investigators then calculated an index of reproductive activity for female animals by noting whether animals were carrying fetuses, were lactating or had no reproductive activity. These data allowed them to calculate an index of total reproductive productivity (average number of young/individual-year). Field censuses generated population densities of game species, and multiplied by reproductive productivity allowed an estimate of production (P) measured by individuals/sq km. Estimates of total harvest and known catchments areas (hunting areas) then allowed an estimate of hunting pressure (individuals harvested/sq km). Comparison of these two last figures allow a direct measure of sustainability.

An example from Tahuayo will illustrate the model. Examination of the reproductive condition of female collared peccary brought in by hunters revealed that 43.6% were reproductively active, having about 1.5 gestations per year with an average litter size of 1.7. This generated 1.11 young/female/year. Assuming a 1:1 population sex ratio, the average number of young/individual/year will be 0.55. Surveys revealed an overall density of 3.3 collared peccary/sq km, yielding a total production (P) of 1.83 individuals/sq km. Measured harvest was 0.27 individuals/sq km. Hunters were therefore taking about 15% of total production, which, based on comparable temperate mammal data, is probably sustainable.

The model makes no assumptions about the relationship between game population density and yield and does notestimate MSY. The model does assume that pre-harvest mortality is not significant, and this might be significant in some species. And the model itself does not indicate what proportion of production could be harvested.

2 Population growth model

Robinson and Redford (1991) have developed a more general model for neotropical forest mammals. This population growth model evaluates whether an actual harvest is possibly sustainable under conditions of maximum game production.

From the published literature, we calculated the population density at carrying capacity (K) for a number of game species, and also the intrinsic rate of population increase (r max) of those species, defined at the highest rate of population increase

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by a population not limited by food, space, resource competition, or predation. The model assumes that

1 R max is achieved at 0.6K,

2 R max is achievable, and

3 That harvested populations can be managed so that they remain at or near 0.6K.

These assumptions are not conservative – the model generates the maximum potential production (individuals/sq km) for each species.

The model then makes a further assumption:

4 That the proportion of production (P) that can go into yield is 60% for very short-lived species, 40% in short-lived species, and 20% in long-lived species. This allows calculation of the maximum potential yield of these species. Real populations would be unlikely to generate yields as high, and it is impossible for them to generate higher yields.

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A general example will illustrate the model. The expected density of spider monkeys (*Ateles sp.*) in unhunted sites, based on a large number of surveys across the neotropics, is 16.6 individuals/sq km. The model assumes that hunted populations will have a density of 10.0 individuals/sq km (or 0.6K). Based on reproductive parameters under optimal conditions, the expected finite rate of population increase is 1.08. The total annual sustainable production of spider monkeys is then 0.8 animals/sq km ((10.0 x 1.08) - 10.0). Of these, only 20% are potentially available for harvest because this species is long-lived, generating a potential sustainable harvest of 0.16 animals/sq km/year. Any harvest greater than this is almost certainly not sustainable.

The harvest available to a local community varies with the catchment area over which hunters are taking game. To illustrate the maximum potential harvests based on this model for a number of important game species, we plot in Figs. 4, 5, and 6 potential harvests for primates, rodents, and ungulates across a range of catchment areas. Actual harvests above each line for each species will not be sustainable.

The strength of the model is that it allows one to evaluate whether an actual harvest is not sustainable. However, it does not allow one to state that an actual harvest is sustainable. Low harvests might be a consequence of depleted game densities. A further weakness of the model is that it makes a number of assumptions. Bodmer (pers. comm.) has pointed out for instance, that the model equates K with the maximum observed density at non-hunted sites, while it is reasonable to suppose that many species are held below K by natural predation. In addition, the model assumes specified relationships between population density, yield, and natural mortality, which while reasonable, have not been demonstrated for neotropical forest mammals.

Figure 1

*Interrelations among
production (births
plus immigrations),
yield, and natural loss
(deaths plus
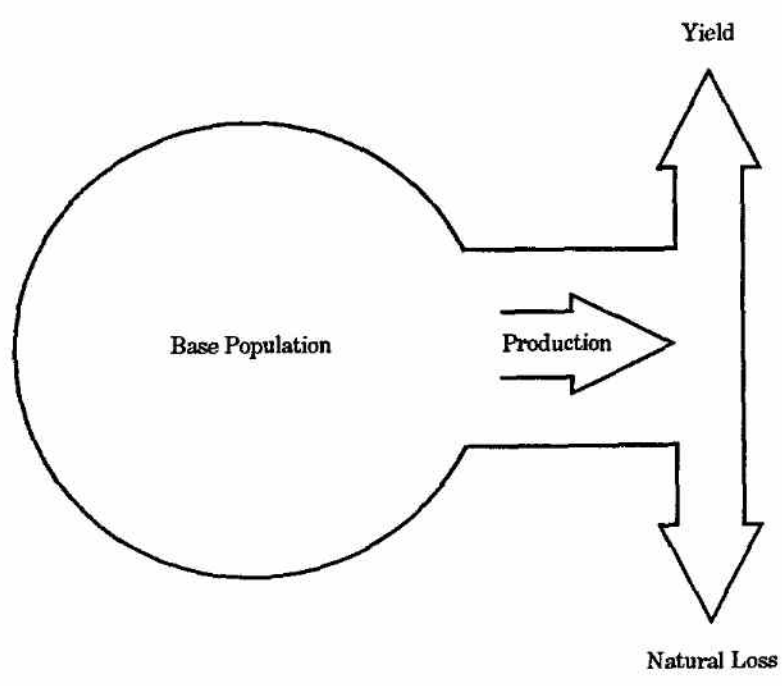emigrations) in a
population being
harvested.*

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Yield

Base Population

Production

Natural Loss

Figure 2 & 3

Figure 2
Variation in age structure of rodent populations with hunting intensity. Within each species, study sites are arranged in decreasing hunting pressure. The data from San José de Payamino in the Ecuadorian Amazon come from Irvine (1987). Tuparro I is an unhunted site in the Colombian llanos, El Porvenir is moderately hunted, and Tuparro II is a heavily hunted site (Collett, 1981). The Barro Colorado Island (BCI) data come from Smythe et al. (1982).
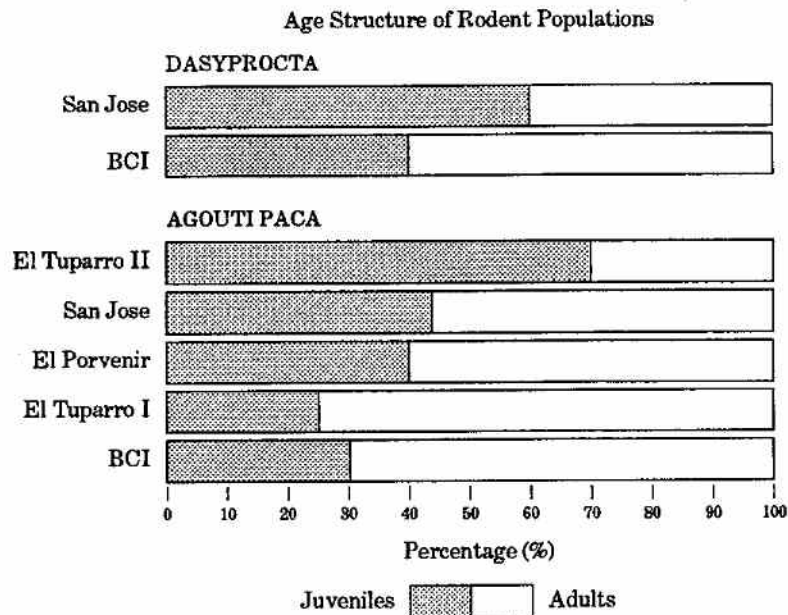
Age Structure of Rodent Populations

DASYPROCTA

San Jose
BCI

AGOUTI PACA

El Tuparro II
San Jose
El Porvenir
El Tuparro I
BCI

0 10 20 30 40 50 60 70 80 90 100
Percentage (%)

Juveniles   Adults

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Figure 3
Variation in age structure of peccary populations with hunting intensity. Sites are arranged in decreasing hunting pressure. Populations at San José de Payamino are hunted, while those at Masaguaral, in the Venezuelan llanos (Robinson, unpubl. data), and Manu (Kiltie, 1980) are infrequently hunted.
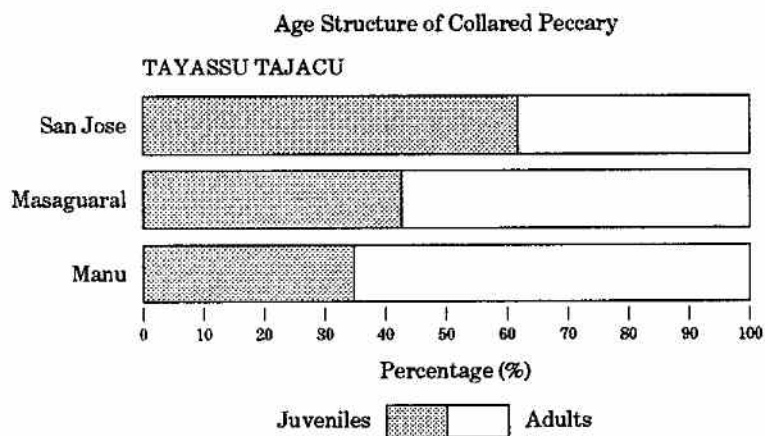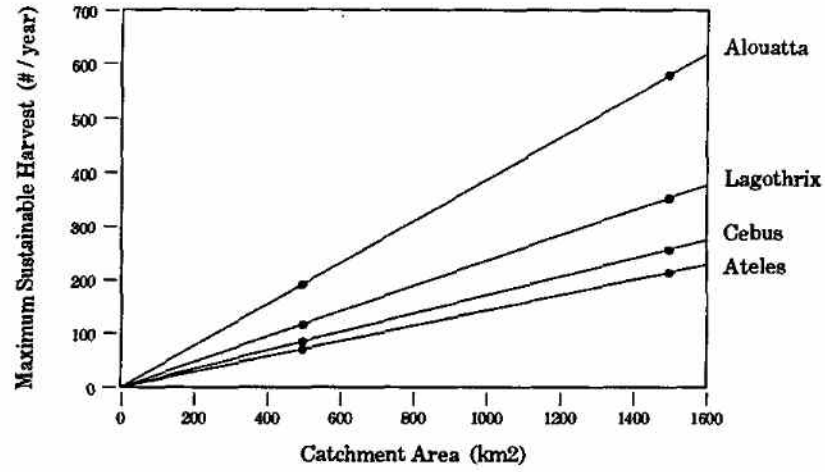
Age Structure of Collared Peccary

TAYASSU TAJACU

San Jose
Masaguaral
Manu

0 10 20 30 40 50 60 70 80 90 100
Percentage (%)

Juveniles   Adults

Figure 4
Variation in maximum
potential harvest of
primates with hunting
catchment area. For each
species, a harvest rate
above the line cannot be
sustainable.

36 *Figure 5*
Variation in maximum
potential harvest of
rodents with hunting
catchment area. For each
species, a harvest rate
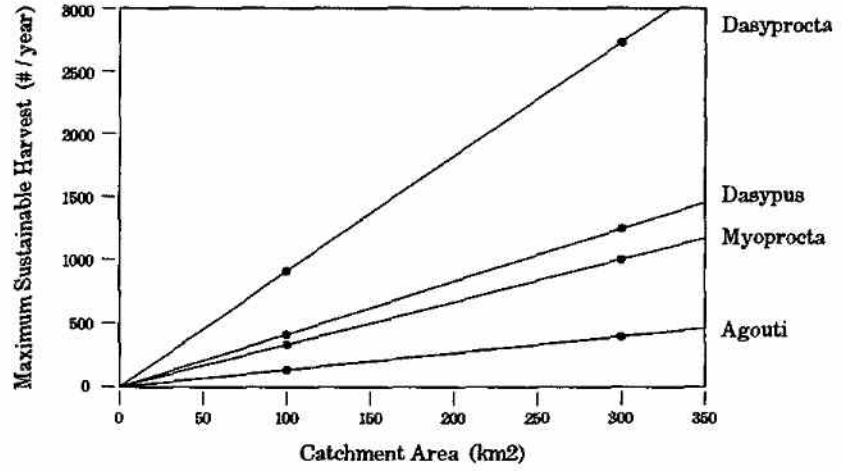*above the line cannot be*
sustainable.

Figure 6
Variation in maximum
potential harvest of
ungulates with hunting
catchment area. For each
species, a harvest rate
above the line cannot be
sustainable.