PART IV

Hunting Impacts—Biological Basis and Rationale for Sustainability

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Evaluating the Sustainability of Hunting in the Neotropics

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Rural people throughout the Neotropics hunt for subsistence food and to sell meat and hides in urban markets, actitivities that pose one of the greatest threats for tropical vertebrates and that create one of the most important conservation issues for developing countries (Robinson and Redford 1991; Robinson and Bennett 2000b). Many species are impacted more by hunting than by deforestation (Bodmer 1995b). Ensuring that wildlife hunting is sustainable is important both for the long-term benefits people receive from wildlife and for the conservation of species and ecosystems (Swanson and Barbier 1992; Freese 1997b). However, setting up more sustainable hunting is a complex process that must integrate the socioeconomics of rural people, the biology of species, institutional capacities, and national and global economic pressures. One of the fundamental aspects of sustainable wildlife use is the biological capacity of species to be used sustainably: if species are overhunted then there is no scope for sustainable use.

Wildlife management in the Neotropics takes a variety of forms, including community-based strategies, landowner strategies, and sport hunting programs. In tropical forests most wildlife hunting is done either by local indigenous or nonindigenous people or by small-scale timber operations (Robinson and Bennett 2000b). Managing this wildlife use requires information on the sustainability of hunting.

In most cases the first step in evaluating sustainability of hunting is to determine if current hunting appears sustainable or is obviously not sustainable. Most of the simple population models that have been used to evaluate the sustainability of hunting in the Neotropics have evaluated current hunting (Ojasti 1991; Fitzgerald, Chani, and Donadío 1991; Vickers 1991; Bodmer 1994; Alvard 1998; Hill 2000; Jorgenson 2000; Leeuwenberg and Robinson 2000; Mena et al. 2000; Peres 2000; Townsend 2000, among others). These studies have used a variety of models to evaluate sustainable use, including effort models, production models, age models, harvest models, and source-sink models (Robinson and Bodmer 1999). It is important to note that these models are not appropriate for predicting the outcome of increases in harvests or in developing harvest strategies in areas that are currently not hunted. Although model development has proceeded rapidly in the last decade, we are not yet at the stage where we can set harvesting levels based on the biology of species in specific areas.

This article will focus on models that have been used to evaluate sustainability of hunting in the Neotropics. These models are practical field-based approaches that can be used in rural and wilderness settings to assess hunting at a specific time and location. Wildlife management in the Neotropics will only be successful if field-based people, whether they be biologists or local hunters, have relatively straightforward techniques that they can use to evaluate the sustainability of hunting. The strength of these models lies in the field data that is employed. Unlike more theoretical population models, the models described in this article have been developed in a way that allows people to input population parameters and hunting pressure collected from specific field sites.

Simple population models can indicate whether species are overhunted. There are some important guidelines for using these models and interpreting their outcomes (Robinson and Bodmer 1999). First, the confidence in assessing the sustainability of harvest is greatly enhanced by using a combination of models that use independent variables (Robinson and Bodmer 1999; Fragoso, Silvius, and Prada 2000). If the results of the different models point to the same conclusion, then the confidence of the conclusions is greatly augmented. If three different models all suggest that a certain species is overhunted or, conversely, that it appears to be hunted sustainably, then one has greater confidence in the conclusion.

Second, given the assumptions of models and the error margins of data, specific results should be considered as approximate values and the actual numerical results of models should not be used for management recommendations. Specific results should not be used to fine tune actual harvests. For example, if a model shows that a certain species has 20% of production harvested and the model uses 40% as the limit of sustainability, the model should not be used to make recommendations to increase the harvest to 40%. Rather it should be used to suggest that current levels of hunting appear to be sustainable.

Third, it is important to understand clearly the strengths and weaknesses of each model. Each model has assumptions, and these assumptions must be clearly grasped. In many cases we do not know how valid some of these assumptions are or whether they apply equally to different game species. As more information on tropical wildlife populations become available, these assumptions can be revised and perhaps become variables in the models rather than background unknowns.

Finally, the strength of the models lies in their ability to evaluate current hunting. The models presented in this article should not be used to model population projections, to increase harvests, or to initiate harvests in areas where hunting does not currently occur.

DESIGNING THE STUDY

To evaluate sustainability of wildlife hunting, it is necessary to have a clear understanding of the physical, biological, and temporal boundaries of the assessment (Robinson and Bodmer 1999). Physical space may include a nature or extractive reserve, a project area, or a state or region. In some cases the hunting of a single species might be evaluated, while in other groups of species might be evaluated. In terms of time the evaluation can be carried out over the short-term (three to five years) or over the long term (thirty to fifty years).

One must also define exactly what is meant by sustainable use. Some definitions are very general. For example, hunting is sustainable if a species population is healthy and stable under harvest. Other definitions might be specific to certain quantitative models. For instance, a harvest model might define a short-lived species to be sustainably hunted if less than 40% of its production is harvested.

One must be clear about the null hypothesis. In general it is much easier to demonstrate that hunting is not sustainable than to demonstrate that it is. If the null is accepted (or there is no evidence of overhunting), then hunting is apparently sustainable. If the null hypothesis is rejected, then the population is clearly overhunted. To actually prove that hunting is sustainable, one would need to measure all of the biological and socioeconomic variables that might influence sustainability. Such a feat is obviously not possible, and once you have shown sustainability, some variables will change, and the system would again be unsustainable.

Finally, one must determine which models can be used to accept or reject the null hypothesis. There are a variety of models to evaluate the sustainability of hunting, some of which will be discussed in this article. Each model has its strengths, weaknesses, and assumptions, and the different models require different types of data. In turn, the models determine what needs to be measured, what data needs to be collected, and the study design that needs to be set up.

The two approaches most commonly used to evaluate the sustainability of hunting of Neotropical wildlife are the comparative design and monitoring (Robinson and Redford 1994). The comparative design usually compares variables between nonhunted, slightly hunted, and heavily hunted sites. This design is useful if sustainability of hunting needs to be determined in a relatively short period of time.

The comparative design assumes that the sites being compared vary only in hunting pressure. This assumption is often not met, and studies need to be carefully designed to come as close as possible to meeting it or, failing this, to account for deviations in habitat quality between sites. Hunting pressure should be the variable that differs most between sites, with all other variables being as constant as possible. Thus sites being compared should have the same habitat. Adjacent sites with similar habitat have usually been used for comparisons. However, it is difficult to convincingly show the consistency of tropical habitats between sites, and the habitat variables measured in a study might not be the ones that are most important for the animals. Additionally, hunting pressure must be measured in order to discriminate between nonhunted, slightly hunted, and heavily hunted sites.

Monitoring implies a long-term commitment to a hunted site. The sustainability of hunting is evaluated by observing changes over time. Monitoring is a very important technique and is often used to evaluate hunting impact, especially for studies looking at animal exports under CITES regulations. As in the case of the comparative design, there are important assumptions about monitoring that must be understood in setting up and later analyzing the results of the study.

Once again, hunting pressure is the variable being measured, and all other variables should be as constant as possible. Hunting pressure must be monitored over time to document changes. Habitat at the site should be constant over time. Changes in the quality of the habitat can alter the food or nesting sites of species and override the impact of hunting. However, habitats do not remain constant over time, especially with respect to food availability. It is therefore important to monitor habitat quality and to account for it in the final analysis of hunting data. However, few studies monitor environmental changes in parallel with hunting changes, and those that do have not attempted to incorporate these variables into the models used to assess sustainability of hunting. Habitat constancy thus remains an important untested assumption in all models.

THE MODELS

Models that have been used to evaluate the sustainable use of tropical wildlife and that we will discuss in this article include:

1. abundance, densities, or standing biomass comparisons;
2. stock-recruitment models;
3. effort models;
4. age structures;
5. harvest models;
6. unified harvest models;
7. production models;
8. source-sink models.

Data derived from research conducted in the Tamshiyacu-Tahuayo Community Reserve and the Pacaya-Samiria National Reserve will be used to illustrate the usefulness of the models. The Tamshiyacu-Tahuayo Community Reserve is an upland forest site in the northeastern Peruvian Amazon and is situated in the forests that divide the valley of the Amazon from the valley of the Yavari. The Pacaya-Samiria National Reserve is a flooded forest protected area in the confluence between the Marañon and Ucayali rivers (fig. 19.1). Data are available from nonhunted and

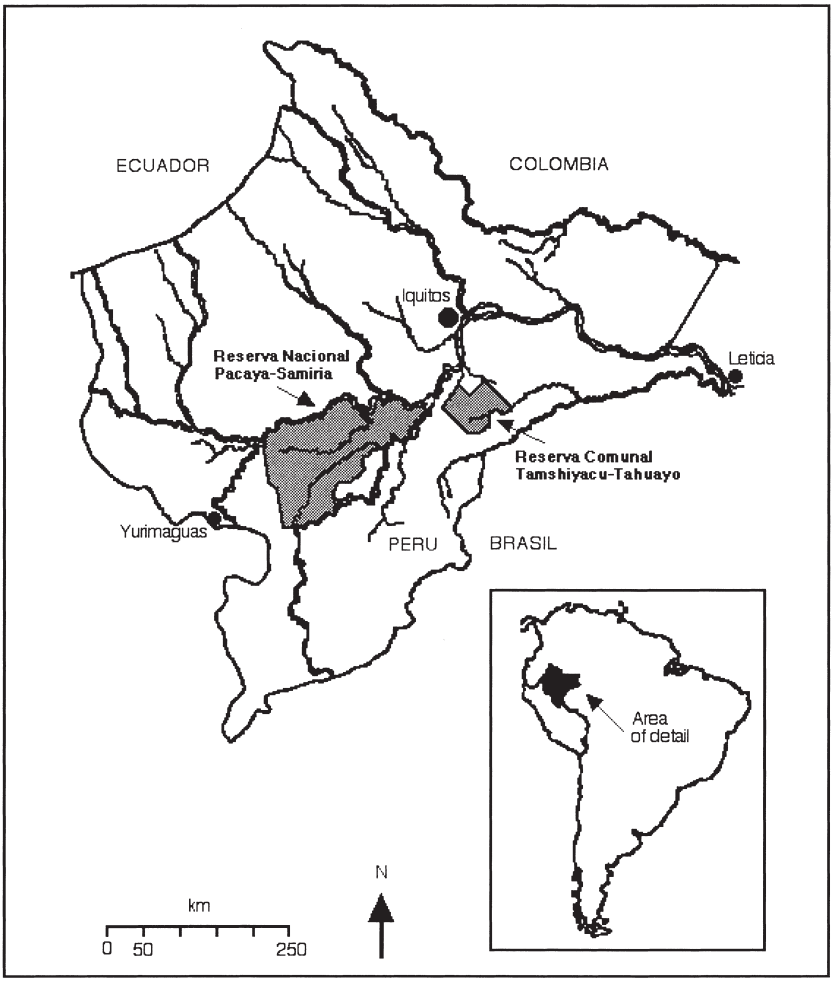

FIGURE 19.1 Map of Loreto, Peru, showing the Pacaya-Samiria National Reserve and the Tamshiyacu-Tahuayo Community Reserve.

hunted sites in both protected areas. The sites have been described in Bodmer (2000).

ABUNDANCE, DENSITIES, OR BIOMASS COMPARISONS

Changes in abundance, density, or biomass of species can be monitored in a site over time and such measurements are often used to determine whether a species is sustainably harvested. Impact of hunting can be indexed by the degree of decline. Harvests are usually classed as nonsustainable if an animal population continually decreases over time.

Changes in abundance, density, or biomass of species can also be compared between nonhunted, slightly hunted, and heavily hunted sites, and these comparisons have been used to evaluate the impact of hunting (Robinson and Redford 1994; Bodmer, Eisenberg, and Redford 1997; Peres 2000). Indices of abundance, such as tracks or other signs, have been used as proxies for direct measures of abundance (Fragoso, Silvius, and Prada 2000; Naranjo 2002). This approach assumes that a differences in density, biomass, or abundance of animal populations between different sites is a consequence of hunting. Using this model in a comparative design is not very useful in determining whether a species is sustainably harvested (Robinson and Redford 1994). The major concern is that differences in the density, biomass, or abundance of a species do not necessarily signify overhunting because harvests will generally result in decreases in population density. Whether harvests are sustainable depends on how the rate of recruitment varies with population density (Caughley and Sinclair 1994; Caughley 1997).

Comparing changes in density, biomass or abundance of species between sites is useful for determining the susceptibility of different species to overhunting. For example, comparisons were made in the Tamshiyacu-Tahuayo Community Reserve between the persistently hunted Blanco site and the slightly hunted Yavari-Miri site. The two sites had similar habitats, they were only 40 km apart, and they had continuous forests with no major rivers dividing the area. Differences in abundances of mammals were correlated to different life history characteristics including intrinsic rate of increase, longevity, and generation time (Bodmer, Eisenberg, and Redford 1997).

The comparison clearly showed that mammals with higher intrinsic rates of increase, shorter longevity, and shorter generation times had smaller or negative differences in their abundance between the slightly hunted and persistently hunted sites. In contrast, mammals with smaller intrinsic rates of increase, longer life spans, and longer generation times had greater differences in abundance between the slightly hunted and persistently hunted sites. This analysis indicates that mammals with higher intrinsic rates of increase, shorter life spans, and shorter generation times are less susceptible to overhunting than mammals with smaller intrinsic rates of increase, longer life spans, and longer generation times.

STOCK-RECRUITMENT MODEL

A variant of the density comparisons is the stock-recruitment model, which is based on density-dependent population models that use maximum sustained yield estimates (MSY) and carrying capacity (K). Most species of tropical wildlife that are hunted are K-selected species and should therefore have density-dependent recruitment (Caughley 1977). In turn, sustainable harvests of tropical wildlife populations will depend on relationships between rate of recruitment and population size. The stock-recruitment model predicts the riskiness of harvests for different populations sizes (McCullough 1987). The greatest base population is at carrying capacity (K) and the smallest at extirpation (0). A sustainable harvest can be realized at any base population size, but there is only one point at which the sustained harvest is at the maximum, or MSY (Caughley 1977).

A species population in a hunted area can be compared to a predicted K and MSY. This is accomplished by comparing the density of the hunted population (N) to an estimated K as N/K. MSY is also denoted as a proportion of K. In turn, the hunted population is positioned in relation to MSY, and this position is used to evaluate the riskiness of hunting in the sense that populations hunted at MSY or below are at greater risk of overhunting than populations that are hunted above MSY (fig. 19.2).

Harvesting species at the MSY is a risky management strategy and should be avoided. If attempts are made to manage a population at the theoretical MSY and small misjudgments occur, this slight overhunting would result in a decreased base population the following year. If this overhunting goes unnoticed and the population is again harvested in the same numbers, the effect of overhunting would be even more dramatic and would quickly lead to extirpation (McCullough 1987) (fig. 19.2).

Similarly, harvesting species with small base populations (to the left of MSY) is a risky management strategy and should be avoided. Again, if small misjudgements occur in calculating the sustainable harvest, this slight overhunting would result in a deceased base population the following year and would quickly lead to overexploitation and extirpation (McCullough 1987).

Harvesting species with large base populations (to the right of MSY), on the oth-

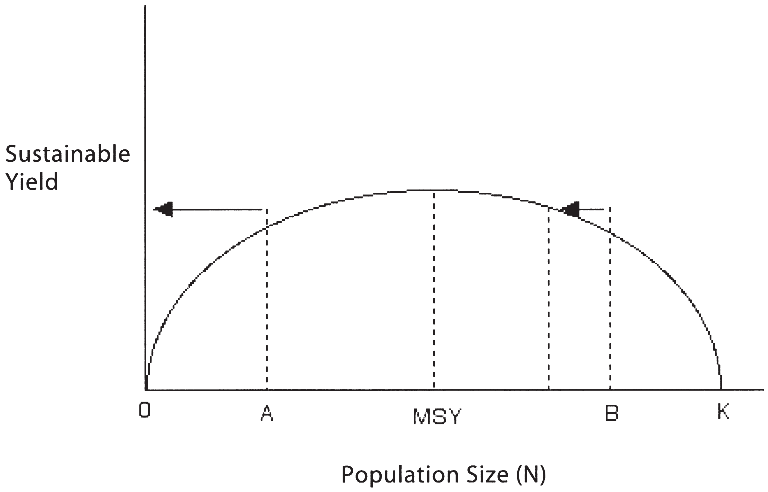

FIGURE 19.2 Representation of the stock-recruitment model, showing K and MSY. Overhunting at point A would drive the population to extirpation, whereas overhunting at point B would lead to a sustainable harvest at a lower population size.

er hand, is a safe management strategy that can be used for long-term sustainable use of a species (fig. 19.2). If small misjudgments occur with harvesting with a large base population, this slight overhunting would result in a decreased base population the following year. If this overhunting goes unnoticed and the population is again harvested in these same numbers, the population would stabilize at this new sustained harvest level and would not decrease further. Harvesting a species with a large base populations is a safer management strategy, since it is less likely to result in extirpation (McCullough 1987).

The stock-recruitment model used here does not actually evaluate the sustainability of current hunting. Rather, it is a powerful way to examine the potential for long-term sustainability. If animals are hunted in a risky manner, then there is less potential for long-term sustainability. In turn, if animals are hunted safely, then there is a much better potential for long-term sustainability.

In the stock-recruitment model a safe harvest is one that occurs to the right of the MSY point. MSY is species specific and is predicted to be at 50% of K for very short-lived species, 60% of K for short-lived species, and 80% of K for long-lived species. These differences derive mainly from variance in reproduction and the way in which this variance changes as the species approaches K in accordance with density-dependent interactions (Kirkwood, Beddington, and Rossouw 1994). Very short-lived species have the greatest variance in reproduction and show density dependent changes in reproduction as a normal distribution as their densities progress from low numbers to K. Short-lived species show slightly skewed changes in their reproduction with maximum production occurring at slightly greater population levels, usually at 60% of K. Long-lived species show little density-dependent responses to reproduction until their populations are actually quite large (Kirkwood, Beddington, and Rossouw 1994). Therefore the MSY is further to the right and is predicted to be at 80% of K.

The stock recruitment model was used to evaluate the riskiness of hunting of mammals in the Peruvian Amazon. For example, ungulates, rodents, and primates were studied in the Pacaya-Samiria National Reserve, in both hunted subsistence sites within the reserve and nonhunted fully protected areas (Bodmer 2000). Densities of these mammals in nonhunted areas were used to estimate K. MSY was set at 60% of K for peccaries, deer, and large rodents and 80% of K for lowland tapir (*Tapirus terrestris*) and primates. Lowland tapir was the only species for which hunting was risky. The tapir population in the subsistence zone was at 60% of the estimated K, a value that is below the predicted MSY of 80%. White-lipped peccary (*Tayassu pecari*), red brocket deer (*Mazama americana*), agouti (*Dasyprocta fulinosa*), woolly monkey (*Lagothrix lagothricia*), and white capuchin (*Cebus albifrans*) populations in the subsistence use zone were all above the predicted MSY's (table 19.1). Collared peccaries (*Tayassu tajacu*), brown capuchin (*Cebus apella*), howler monkey (*Alouatta seniculus*), and monk saki monkey (*Cacajao calvus*) populations in the subsistence use zone were actually above the estimated

TABLE 19.1 Examples of the Stock-recruitment Analysis in the Pacaya-Samiria National Reserve

SPECIES	MSY	N/K	STRATEGY
White-Lipped peccary	60%	84% ± 50%	safe
Collared peccary	60%	171% ± 28%	safe
Red brocket deer	60%	86% ± 28%	safe
Lowland tapir	80%	60% ± 80%	risky
Agouti	60%	83% ± 16%	safe
Woolly monkey	80%	92% ± 20%	safe
Brown capuchin	80%	130% ± 10%	safe
White capuchin	80%	81% ± 40%	safe
Howler monkey	80%	168% ± 15%	safe
Monk saki monkey	80%	136% ± 19%	safe

Note: MSY is maximum sustainable yield; N, density in the subsistence use zone; and K, carrying capacity. K was estimated from densities at the fully protected site. MSY is given as the percent of K. Strategies were either risky or safe.

K and thus were more abundant in the hunted area than the nonhunted area. This finding would obviously signify a safe hunting strategy.

Some concerns with this method are that estimating K from nonhunted populations represents an equilibrium population, not really K. An equilibrium population is the observed size of a population within the ecosystem and might be an underestimate of the real K (Caughley and Sinclair 1994). This danger is especially true for predator-limited species in which prey densities are held below K by predator mortality. An underestimate of K would lead to an underestimate of MSY and a misrepresentation in the relationship between N and the actual MSY.

Standard error in density estimations and hunting pressure calculations can be incorporated in the results. The riskiness of hunting can then be evaluated along a range of MSY estimates and a range of sizes for hunted populations.

The stock-recruitment model in this form is an important conservation strategy, since species will only be harvested sustainably in the long-term if their base populations are large. As previously mentioned, faster-reproducing species, such as peccaries, deer, and large rodents, are less vulnerable to overhunting. These faster-reproducing species have a predicted MSY at 60% of K. Thus base populations of these species must be above 60% of K to be considered sustainably harvested over the long term. Slow reproducing species such as tapir and primates are more vulnerable to overhunting. Because these species have less variance in their reproduction, they have a predicted MSY at 80% of K. Thus the base population of these species must be above 80% of K to be considered sustainably harvested over the long term and means that they almost have to be at K to be considered for harvesting.

EFFORT MODELS

Effort models examine relationships between hunting effort and hunting yield and commonly use catch per unit effort (CPUE). These models usually require extensive information about the daily activities of hunters to measure effort. Therefore most of the yield/effort models of Neotropical hunting have been conducted by anthropologists (Vickers 1991). Differences in the catch (or harvest) per unit effort are assumed to reflect differences in actual density or abundance. A decrease in the catch per unit effort suggests overuse (a decreasing population); a constant catch per unit effort, a stable population; and an increase in catch per unit effort, an increasing population. Catch per unit effort analysis can either use a comparative design that looks at nonhunted, slightly hunted, or heavily hunted areas, or it can be used to monitor an area over time.

Hunting registers were used to obtain hunting offtakes and effort (time spent hunting) to develop catch per unit effort relationships in the Tamshiyacu-Tahuayo Community Reserve (Puertas 1999; Puertas and Bodmer this volume). Catch per unit effort was tested by examining a hunted site during the high- and low-water seasons. During high water, access to hunted sites by canoe is relatively easy. During low water access is difficult. Abundance and CPUE of large mammals did not change between the two seasons (Puertas and Bodmer this volume), whereas hunting pressure and effort were considerably different between the seasons, being much greater during high water. Thus, catch per unit effort successfully reflected abundances of animal populations, and changes in catch per unit effort would therefore reflect changes in abundance and give an indication of overhunting.

Catch per unit effort relies on several conditions and assumptions. First, effort must be measurable, even though the choice of measures is somewhat arbitrary. In the Peruvian Amazon, effort was recorded as the number of days a person spent hunting (hunter-days) (Puertas and Bodmer this volume). Second, effort must be constant. If hunters change from bow and arrow to guns. the measure of off-take per effort would not be constant, and the comparison would be suspect (Robinson and Bodmer 1999). The activities of hunters during hunting trips might not always be constant, so assumptions are be made about the average activity of hunters during hunting trips. Third, the catch, or hunting pressure, must be accurately recorded. If animals are omitted from the catch, this will alter the catch per unit effort calculation and render the analysis suspect.

AGE MODELS

Age models examine the age structure of wildlife populations to see if changes in demography indicate overuse. There are two types of analysis that depend on whether hunting is selective or random (Caughley 1977). Type 1 models are used when hunting is selective and hunters harvest only certain age classes, such as the larger or older individuals of a species. If older or larger individuals are selectively hunted, the age distribution of the population will be skewed toward younger or smaller animals. A stable age distribution in a selectively hunted population indicates that the animals are probably not overhunted. In contrast, if the age distribution continues to decline toward younger or smaller animals, then the population is likely overhunted.

Age distributions from hunted samples can be used to evaluate whether animals are overhunted in a selectively hunted situation. Samples collected from individuals in a selectively hunted population will not reflect the age distribution of the population but will reflect the age distribution of the harvest. If the age distribution of the hunted sample decreases, becoming more biased toward younger ages, this finding would reflect a shortage in the preferred age or size classes and suggest overhunting.

Type 2 models apply when hunting is random with respect to age classes. Random hunting occurs when hunters have no choice of the individuals they are selecting and hunt individuals randomly with regard to age. This commonly happens with snaring or trapping. If hunting is truly random, then samples from randomly hunted populations should reflect the age distribution of the population, and changes in the age distribution of the hunted samples should directly reflect changes in the demography of the population.

However, the interpretation of overhunting from changes in the age distribution is problematic. Changes in age distribution in randomly hunted populations might be caused by (a) recruitment rates increasing with density declines, resulting in proportionally more younger animals; (b) behavioral shifts (i.e., more wariness) in certain age classes, making them less vulnerable (so hunting actually becomes selective); (c) a reduction of natural predators in hunted areas, which in turn results in less infant or young mortality and skews the population toward older animals; or (d) immigration of young individuals into overhunted sites from source areas.

Age distribution can be compared between slightly or nonhunted sites and heavily hunted sites, or it can be monitored in the same site over time. Nonhunted sites can only be included if there is the possibility of obtaining age data of animals from nonhunted samples (i.e., live trapping or capture).

Age distributions are instantaneous samples of individuals. Survival and mortality relationships can only be inferred if one assumes a stable age distribution (Caughley and Sinclair 1994). This stable age distribution assumes that there are no variations in the age distribution between cohorts, an unlikely situation in free-ranging animals. In addition, survival relations can only be inferred from a randomly hunted sample (Caughley and Sinclair 1994).

A variety of techniques are used to age wild animals. The most common technique for mammals is tooth wear. In the Tamshiyacu-Tahuayo reserve skulls from hunted animals were used to determine age through tooth wear and in turn to evaluate the age distributions of populations (Gottdenker and Bodmer 1998). Results are not easy to interpret in terms of overhunting. For example, age models would predict that randomly hunted populations of collared peccaries and white-lipped peccaries are different between persistently hunted and slightly hunted populations. However, within-site, interyear variability in age distribution is significant and overrides differences between hunting sites, masking any effect of hunting (fig. 19.3). On the other hand, obviously overhunted species, such as lowland tapir, show skewed age distributions between slightly hunted and heavily hunted sites, with age distributions being younger in the overhunted sites (fig. 19.4).

Age models have conditions and assumptions that must be considered. First, studies must determine whether a population is randomly or selectively hunted. Second, interpreting what causes changes in age distribution can be problematic in randomly hunted species. Third, it is difficult to determine whether a species is overhunted from the degree of change in age distribution. Indeed, it is possible for a randomly hunted population to show little variance in age distribution even if the population is being overhunted. This observation is especially true for species, such as primates, that have little variation in density-dependent reproduction and do not migrate between areas.

Our understanding of how hunting affects age structure of tropical forest species remains in its infancy. Evaluating sustainable use by understanding age structure has enormous potential because data collection agrees with the activities of local hunters. Hunters can easily collect skulls from animals they hunt with only a minimum of extra labor, thus creating large skull collections (Bodmer and Puertas 2000). Still, it is not advisable to make management decisions using only age data on randomly hunted populations with our current lack of understanding of the relationship between age distribution and sustainability of hunting.

HARVEST MODELS

Animal populations can theoretically be sustainably harvested at any population level, except at carry capacity (K) and extirpation (0) (Caughley 1977). Thus one way to evaluate the sustainability of hunting would be to know the actual production at the population size being harvested. The harvest can then be compared to production in order to obtain a measure of the percent of production harvested at the time hunting is being assessed, as well as determining whether this percent is within sustainable limits. This analysis is known as the harvest model (Bodmer 1994).

The harvest model uses production estimates derived from reproductive productivity and population density. Reproductive productivity is determined from data on reproductive activity of females and uses information on (a) litter size and (b) gross reproductive productivity (number of young/number of females). Population density is determined from field censuses of wildlife species. Animal densities are then multiplied by reproductive productivity to give an estimate of production, measured as individuals produced/km^2 as:

$$P = (0.5D)(Y^{*}g),$$

where Y is gross reproductive productivity, g is the average number of gestations per

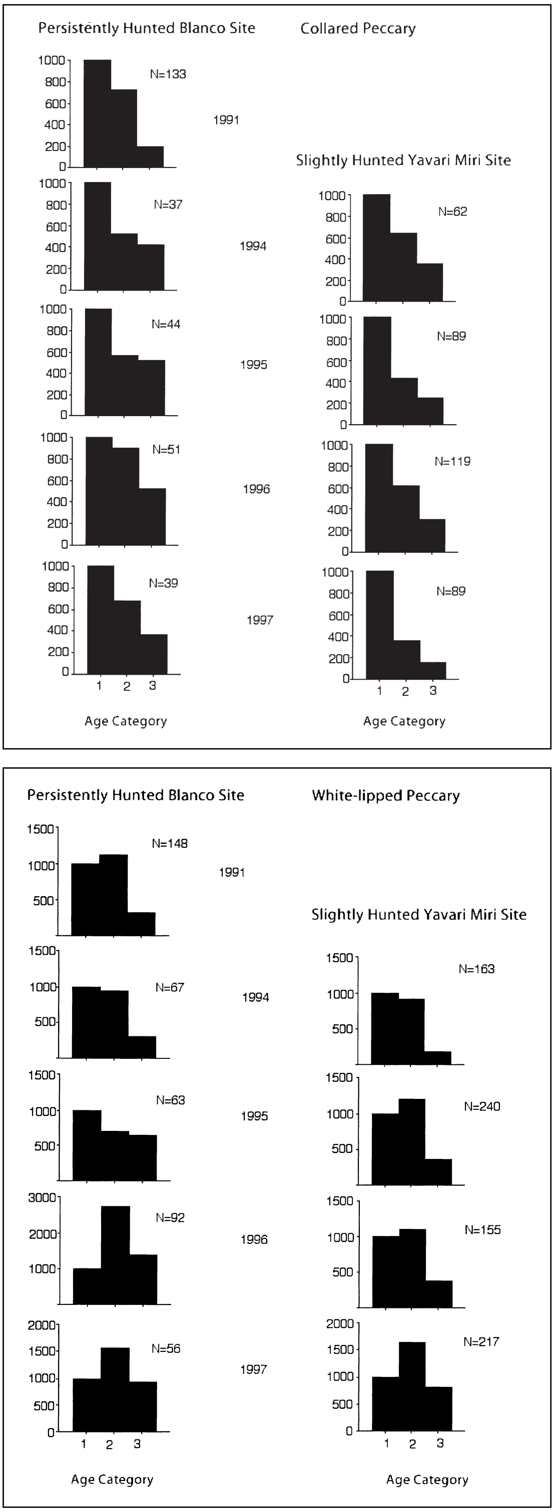

FIGURE 19.3 Annual age distribution of collared peccary and white-lipped peccary in the persistently and slightly hunted areas of the Tamshiyacu-Tahuayo Community Reserve.

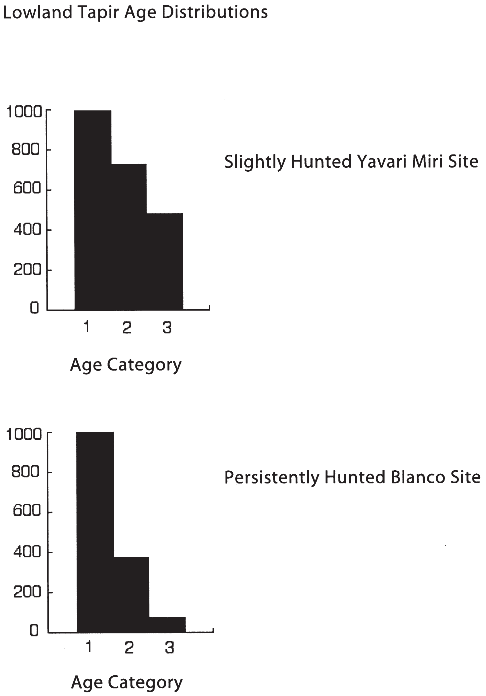

FIGURE 19.4 Age distribution of lowland tapir in the persistently and slightly hunted areas of the Tamshiyacu-Tahuayo Community Reserve.

year, and *D* is the population density (discounted by 50% under the assumption that the population sex ratio is 1:1). Of course sex ratios are often not 1:1, and animal populations often vary in sex ratio for numerous reasons. Our current understanding of sex ratios in Neotropical mammals is still very incomplete. Thus we usually assume a 1:1 sex ratio. Hunted sex ratios probably do not reflect actual sex ratios, and with our current understanding, it is better to assume a 1:1 sex ratio than use hunted sex ratios.

The sustainability of hunting is determined by comparing harvest with production. Harvest data and catchment areas give an estimate of hunting pressure (individuals harvested/km^2). This calculation of production assumes no prereproductive or adult mortality. Therefore an estimate of population growth rate must be incorporated in order to estimate the proportion of production that can be harvested sustainably.

Robinson and Redford (1991) suggest that the average lifespan of a species can be used as an index of population growth. Animals with longer lifespans have slow population growth and in turn a smaller percent of production should be harvested to maintain a sustainable hunt (Kirkwood, Beddington, and Rossouw 1994). Likewise, animals with shorter lifespans have a faster population growth and in turn a larger percent of production can be harvested to maintain a sustainable hunt.

Robinson and Redford (1991) propose that hunters can take 60% of the production of very short-lived animals (those whose age of last reproduction is less than five years) to maintain a sustainable hunt, 40% of the production of short-lived animals (those whose age of last reproduction is between five and ten years), and 20% of the production of long-lived animals (those whose age of last reproduction is greater than ten years).

An example using the subsistence zone of the Pacaya-Samiria National Reserve will illustrate the harvest model. Examination of the reproductive condition of female red brocket deer shot by hunters revealed that the gross productivity (total number of young examined/total number of females examined) was 0.44. Collared peccaries have an average of 2.0 gestations per year (two birthing periods) (Gottdenker and Bodmer 1998). This number resulted in an annual reproductive productivity of 0.88 young/female-year. The reproductive productivity was multiplied by one-half of the density of red brocket deer (0.6 ind./km^2) since it was assumed that one-half of the population of red brocket deer were females. The product, annual production (0.5 ind. produced/km^2), was then divided into the annual hunting pressure of 0.06 red brocket deer hunted per km^2. This calculation yielded the percentage of production taken by hunters, which in this case was 12% of red brocket deer production. This figure is below the 40% maximum for a short-lived species, suggesting that harvests of red brocket deer in the subsistence zone probably are sustainable. As mentioned above the 40% maximum accounts for mortality due to factors other than hunting.

Sensitivity analyses can be used to see whether the error in estimating the different variables, such as density, hunting pressure, and reproduction, will influence the results. For example, the harvest model used to evaluate sustainability of hunting in the Pacaya-Samiria National Reserve incorporated standard error calculations. Red brocket deer in the subsistence use zone had error margins that did not exceeded the 40% limit, providing greater confidence in the conclusion (table 19.2). Over 100% of lowland tapir production was harvested in the subsistence use zone, clearly showing that this species is overhunted and that the base population was being depleted (table 19.2).

The harvest model is a useful way to evaluate the sustainability of hunting in an area because it uses information on production and harvests from the field sites. However, the model is a closed population model and does not take into account immigration or emigration of animals from adjacent areas. For example, the lowland tapir population is clearly overhunted according to the harvest model, and the harvest model predicts its extirpation. However, tapirs still occur in the subsistence use zone of the reserve. This presence suggests that individuals are immigrating to the area from adjacent nonhunted forests.

THE UNIFIED-HARVEST MODEL

The unified harvest model combines the stock-recruitment and harvest models into a unified analysis that evaluates both the sustainability of current hunting and

TABLE 19.2 Percent of Production Taken by Hunters in the Subsistence Zone of the Pacaya-Samiria National Reserve

	PERCENTAGE OF PRODUCTION TAKEN BY HUNTERS		
SPECIES	Subsistence Zone	Proportion of Production Analysis That Can Be Harvested Sustainably	Sustainability
White-Lipped peccary	19 ± 17	40	Appears sustainable
Collared peccary	4.7 ± 2.2	40	Appears sustainable
Red brocket deer	12% ± 6	40	Appears sustainable
Lowland tapir	>100	20	Overhunted
Agouti	2.5 ± 0.6	40	Appears sustainable
Brown capuchin monkey	3.0 ± 0.5	20	Appears sustainable
White capuchin monkey	5.0 ± 2.4	20	Appears sustainable
Woolly monkey	15.0 ± 4.0	20	Appears sustainable
Howler monkey	36 ± 9	20	Overhunted
Monk saki monkey	3.3 ± 0.7	20	Appears sustainable

the potential for long-term sustainable use. The unified harvest model uses a modified population growth curve. As with stock-recruitment curves, the horizontal axis is the population size from extirpation (0) to carrying capacity (K) and the vertical axis is the sustainable limit of exploitation expressed as sustainable yield (SY). The SY mirrors the growth of the population dN/dt and has a maximum point of growth or a maximum sustainable yield (MSY).

The major difference between the unified harvest model and the population growth curve is that the vertical axis in the unified harvest model uses the percentage of production harvested as a measure of SY rather than population growth. Thus the harvest model can be used to evaluate the sustainability of offtake, and the line (known as the SY line) is in fact the 20%, 40%, or 60% limit to the percentage of production that can be harvested.

For example, a maximum of 40% of collared peccary production can be harvested sustainably according to the harvest model. Therefore the SY line in the unified harvest model is the 40% limit. If the harvest of collared peccary exceeds the 40% limit, then it is deemed unsustainable. If, however, the harvest is lower than the 40% limit, then the harvest appears to be sustainable. Thus sustainable harvests can occur at any collared peccary population size, as long as the harvest is less than 40% of production. In the case of the lowland tapir, the maximum level of harvest is 20% of production and in turn, the SY line represents the 20% limit for lowland tapir (table 19.3).

The unified harvest model also analyzes the riskiness of harvests in terms of the potential for long-term sustainability by incorporating the stock-recruitment analy-

TABLE 19.3 The Limits of Sustainability of the Unified Harvest Model

LIFE HISTORY STRATEGY	MAXIMUM % OF PRODUCTION HARVESTABLE	ESTIMATED MSY AS A % OF K
Short-lived	60%	50%
Medium-lived	40%	60%
Long-lived	20%	80%

Note: The limits reflect live history strategies of species and are of two types: (1) limits of the maximum percent of production that can be harvested before a species is overhunted, and (2) the estimated MSY (maximum sustainable yield) of species that is used to determine the proximity of harvested populations to MSY and in turn the riskiness of hunting. K is carrying capacity.

sis. This procedure is done by determining the proximity of the current harvest to carrying capacity (K) and to the estimated maximum sustained yield (MSY). The unified harvest model is used to evaluate whether a harvest level is risky or safe depending on the population size relative to the predicted MSY.

The unified harvest model can then combine the percentage of production of a harvested population with its position relative to MSY in order to give both a measure of the current sustainability and the long-term riskiness of the harvest. This result can be very useful since it can be represented by a single line, which denotes both the percent of production harvested in relation to both the SY line and the species estimated MSY.

The unified harvest model was used to evaluate the sustainability of hunting in the subsistence use zone of the Pacaya-Samiria National Reserve by combining results from the stock-recruitment and harvest models. In the case of the white-lipped peccary, 19% of production was harvested, which is below the 40% limit, and the harvested population was at 83% of K, well above the estimated MSY at 60% of K (fig. 19.5A). Thus, harvests of white-lipped peccary appeared sustainable and the harvested population was being safely hunted in terms of its long-term sustainability. Similarly, in the case of the red brocket deer, 12% of production was harvested, well below the 40% limit, and the harvested population was at 86% of K (fig. 19.5B). Thus harvests of red brocket deer also appeared sustainable. The case of the woolly monkey was similar to the white-lipped peccary and red brocket deer, but the SY line represents 20% of production harvested, and the MSY is set at 80% of the estimated K (fig. 19.5C).

In the case of the lowland tapir, well over 100% of production was harvested, above the sustainable limit of 20% and obviously not sustainable. Similarly, the tapir population was harvested at 60% of K, which was below the predicted MSY of 80% K. Thus lowland tapir were both hunted at unsustainable levels and at risk in terms of long-term sustainability (fig. 19.5D).

Sensitivity analysis can be incorporated into the model on both the SY and riski-

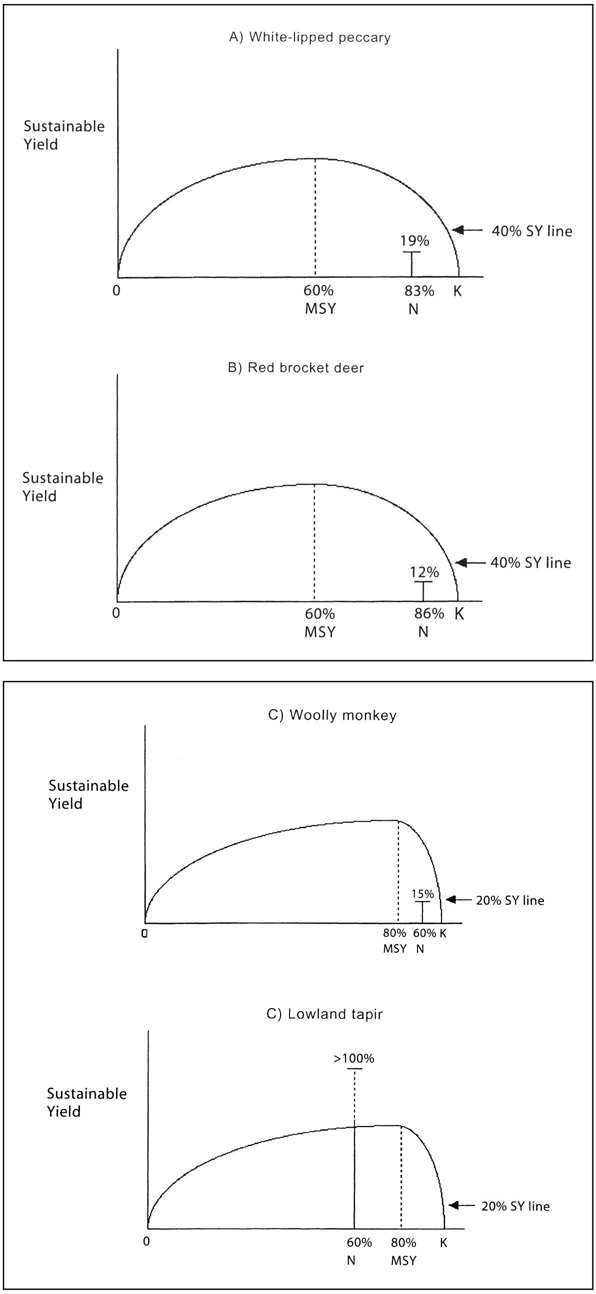

FIGURE 19.5 Diagram of the unified harvest model. This example evaluates the sustainability of hunting in the subsistence zone of the Pacaya-Samiria National Reserve. The height of the solid vertical line represents the percent of production harvested, whereas the position of the vertical line represents the proximity of the harvested population to K and MSY. The SY line is the estimated limit of sustainable harvests, which for white-lipped peccary (A) and red brocket deer (B) is 40% of production, and for woolly monkey (C) and tapir (D) is 20% of production.

ness calculations. The possibility of misjudging the sustainability of hunting can be evaluated by looking at the error margins of density, hunting pressure, and reproductive variables.

The unified harvest model reflects the conservation requirements of species by setting SY limits and MSY levels in accordance to species vulnerability to overhunting. Species susceptibility to overhunting is correlated to life history characteristics, including reproduction, longevity, and generation time. Species with greater vulnerability to overhunting have higher bars in the unified harvest model, as with tapir whose SY limit is set at 20% of production and whose predicted MSY is set at 80% of K. In contrast, species that are less vulnerable to overhunting have lower bars, as with collared peccary whose SY limit is set at 40% of production and whose predicted MSY is set at 60% of K (table 19.3).

The unified harvest model combines both the stock-recruitment analysis and the harvest model; therefore it relies on the same assumptions and carries the same concerns and potential weaknesses as these models. Some concerns with the unified harvest model are that estimating K from nonhunted populations might be an underestimatation of the real K. The SY calculation in the unified model assumes a closed population and does not take into account immigration or emigration of animals from adjacent areas.

PRODUCTION MODEL

The most commonly used model for evaluating sustainability of hunting in tropical wildlife is Robinson and Redford's population-growth model (Robinson and Redford 1991, 1994; Robinson 2000), termed here the production model. The sustainability of hunting can be evaluated by calculating maximum possible production of a species and comparing this figure to actual harvests in the absence of detailed information about species density and reproduction at a specific site. The model evaluates whether an actual harvest is unsustainable, but it can not evaluate whether an actual harvest is sustainable.

The production model assumes that populations of wildlife are density dependent, with maximum production at 0.6 K. As with the other models, K is estimated from nonhunted, undisturbed populations. Maximum production ($P_{\max}$) is calculated by multiplying the density at maximum production (estimated as 0.6 K) by the finite rate of population increase ($\Gamma_{\max}$) and subtracting it from the previous year's density (also estimated at 0.6 K), using:

$$P_{\max} = (0.6K^{*}\Gamma_{\max}) - 0.6\mathrm{K},$$

where $\Gamma_{\max}$ is the exponential of $\tau_{\max}$, being the intrinsic rate of population increase (highest rate of population increase when a species is not limited by food, space, resource competition, or predation). The intrinsic rate of population increase can be calculated using Cole's 1954 equation:

$$1 = e^{-r}{}_{\max} + be^{-r}{}_{\max(a)} - be^{-r}{}_{\max(w+1)},$$

where a is the species-specific age of first reproduction, w is the age of last reproduction, and b is the annual birth rate of female offspring. These reproductive parameters are available in the literature from captive and wild individuals for commonly hunted species. Cole/s equation is actually a measure of maximum reproductive productivity.

As with the harvest model, the production model assumes no prereproductive or adult mortality. Hence, the average lifespan of a species is used as an index of an animal/s population growth. As with the harvest model, the harvest limits are set at 60% of productionfor very short-lived species, 40% of production for short-lived species, and 20% of production for long-lived species. This modification of $\Gamma_{\max}$ by a factor of f_{rr} of 0.6, 0.4, or 0.2 means that the effective rate of population growth, Γ_{rr} is

$$\Gamma_{rr} = 1 = (\Gamma_{\max}{}^{-1})\, f_{rr}$$

and the maximum possible production available to hunters is:

$$P_{rr} = (\Gamma_{rr}{}^{-1})0.6K$$

(Slade, Gomulkiewicz, and Alexander 1998). Γ_{rr} has been used to show maximum possible harvests for a number of species (Robinson and Bodmer 1999).

Collared peccary harvests in the Tamshiyacu-Tahuayo Community Reserve were evaluated using the production model. The maximum production rate of collared peccary is 1.99 (Robinson and Redford 1991). The density of collared peccary at the nonhunted site was 1.6 individuals/km^2, yielding a maximum sustainable harvest (0.4$P_{\max}$) of 0.38 ind/km^2, which was above the actual harvest of 0.33 ind./km^2 at the hunted Blanco site. In contrast, the maximum sustainable harvest of lowland tapir was well below the observed harvest at the hunted site. The density of lowland tapir at the nonhunted site was 0.21 individuals/km^2, yielding a maximum sustainable harvest (0.2$P_{\max}$) of 0.0055 ind/km^2, which was well below the actual harvest of 0.07 ind./km^2 at the hunted Blanco site.

The production model does not tell us much about collared peccary hunting in the Blanco site, only that it is not obviously overhunted. It does not tell us whether the hunting is sustainable or not because the model does not use density data from the Blanco site. In contrast, the model clearly implies that lowland tapir harvests are not sustainable at the Blanco site.

The production model can help determine if a species is overhunted when harvests exceed maximum levels, but it cannot determine whether a harvest is sustainable if levels are below the maximum. One concern of the model is that it includes many parameters without using data from the actual site of harvesting. This failing can result in estimations that are not appropriate for a particular site.

SOURCE-SINK MODELS

The models described above are useful indicators of the sustainable use of populations, but they do not embody the complexities of natural ecosystems and the unpredictable fluctuations of wildlife populations. Some of the models, such as abundance comparisons, stock-recruitment model, age structure analysis, and effort models, are open models that intrinsically incorporate immigration and emigration from neighboring areas. Others, such as the harvest model and production model, are closed population models that do not take into account immigration or emigration.

One promising way to include concerns of complexity, unpredictable fluctuations, and animal movements into management strategies for tropical wildlife is to adjoin nonhunted source populations to hunted (or sink) areas (McCullough 1996; Townsend 1996b; Hill et al. 1997; Fragoso, Silvius, and Prada 2000; Novaro, Redford, and Bodmer 2000). Both intact habitats with continuous animal populations or fragmented habitats with a metapopulation structure can be used with a source-sink strategy (Novaro, Redford, and Bodmer 2000).

Source-sink models require information on the status of source and sink populations and movements of animals between sources and sinks. Analyses of source-sink systems in the tropics have usually used information on the populations of wildlife in source and sink areas but have generally not known the degree of movement between sources and sinks (Novaro, Redford, and Bodmer 2000).

For example, the unified harvest model can incorporate source and sink areas by estimating the percentage of production harvested and the riskiness of harvests in heavily hunted sinks, slightly hunted sources, and nonhunted sources. In nonhunted sources the percentage of production harvested is zero. It is then possible to combine source and sink areas in order to reach an approximation of the percentage of production harvested and the riskiness of the harvest throughout the entire source-sink area.

It is important also to appreciate the importance of landscape features and the spatial relationship between source and sink populations. In the example above, it is assumed that animals will disperse from the source to the sink. This case might be true for the fully protected area of the Pacaya-Samiria National Reserve since it is situated in the center of the reserve and surrounded by the subsistence use zone. In other areas, however, this might not be the case and consideration must be given to the spatial assumptions.

The Tamshiyacu-Tahuayo Community Reserve and its surroundings can demonstrate how source-sink analysis can be combined with the unified harvest model. The Tamshiyacu-Tahuayo Community Reserve was divided into three hunting zones: (a) a persistently hunted area of 1,700 km^2, (b) a slightly hunted areas totaling 4,000 km^2, and (c) a nonhunted areas totaling 5,300 km^2. The nonhunted and slightly hunted areas were potential source populations for the persistently hunted area. The size of hunting zones were estimated from data on harvests and catchment area collected from hunters over an eight-year period (Novaro, Redford, and Bodmer 2000)

The effectiveness of the source-sink strategy was examined for lowland tapir, peccary, and deer populations. The unified harvest model showed that, in the persistently hunted Blanco site, 140% of lowland tapir production was hunted; the harvest was ruled risky. This region is clearly a sink area for lowland tapir. The slightly hunted site had an estimated 16% of lowland tapir production hunted, a figure that is below the 20% limit; the hunting was deemed safe. Thus the slightly hunted sites can be considered part of the source area. The nonhunted sites had 0% of production hunted, and the slightly hunted plus nonhunted site together made up the aggregate source area.

Hunters were taking an estimated 8% of the lowland tapir production from this aggregate source area, which is within sustainable levels. Within the entire source-sink area, including the persistently hunted, slightly hunted, and nonhunted sites, hunters were taking an estimated 18% of lowland tapir production. This figure suggests that hunting of lowland tapir in the entire source-sink area appears to be sustainable and that the sustainability of hunting in the persistently hunted area depends largely on immigration (or replenishment) rates from adjoining source areas.

But are lowland tapir actually moving between the hunting zones? Continued persistence of tapir in the Blanco site suggests that recruitment via immigration from the source area is important. In addition, tapir populations in the Blanco site are considerably younger than tapir population in the slightly hunted area, suggesting that younger animals might be moving from the source to the sink (see age model above).

The effectiveness of the source-sink strategy was also examined with peccary and deer populations (table 19.4). The risky harvesting levels of white-lipped peccary hunting in the Blanco site and the proximity of collared peccary and brocket deer

TABLE 19.4 Results of the Harvest Model for Ungulates in Source and Sink Areas in and Around the Tamshiyacu-Tahuayo Community Reserve

	PERCENTAGE OF PRODUCTION HARVESTED		
SPECIES	Sink	Source	Source-Sink
Lowland tapir	140%	8%	18%
Collared peccary	31%	3.3%	6%
White-lipped peccary	11%	1.5%	2%
Red brocket deer	38%	2.1%	9%

harvests to the sustainable limits suggests that these animals might be at risk of overhunting during some years. However, if a management strategy includes the slightly hunted and nonhunted source areas, this risky strategy is more acceptable because source areas could replenish overhunting in the persistently hunted site.

METHODS

All of the models described above require the input of data collected from field studies. Thus the level of accuracy of the models depends largely on the data collected from the field. Weak data sets will yield inaccuracies, and the results of the models will be suspect. It is important to acknowledge the importance of collecting reliable data with sufficient sample sizes. All of the models require information on hunting pressure, and the comparative and monitoring designs themselves require a knowledge of hunting pressure.

Hunting pressure is usually collected by involving hunters in the study, and many studies have involved local hunters and their families in data collection (Vickers 1991; Bodmer 1994; Alvard 1998; Jorgenson 2000; Townsend 2000; among others). This participatory approach has several advantages over nonparticipatory methods, which do not involve local people in the design and implementation of data collection:

1. The participatory approach permits researchers to collect information on hunting pressure.
2. It allows researchers and hunters to work together and better understand each other's needs.
3. It sets the stage for local involvement in future management of wildlife resources.
4. It teaches hunters how to collect data so that in the future they will be directly involved with analyzing the sustainability of their own hunting.
5. Hunters can easily collect animal parts such as skulls, reproductive tracts, kidney fat, and genetic material, among other biological material.

These participatory methods are useful for collecting catch per unit effort data. They are also useful for collecting skull samples that can be used for age structure analysis and reproductive samples that are needed to determine gross reproductive productivity.

Many of the models require information on density (stock-recruitment model, harvest model, production model, and unified harvest model), while others can use measures of abundance (abundance comparisons). In the Neotropics most studies have used line transect censuses to estimate large mammal densities. These census data have usually been analyzed using the computer program DISTANCE (Buckland et al. 1993). The major drawback to this method is that a large sample size of direct observations is required, whereas small sample sizes are usually obtained in the field. Large distances using numerous transects are necessary to obtain sample sizes sufficient to estimate densities. For example, in the Tamshiyacu-

Tahuayo Reserve there has been about 1,000 km of censuses conducted in each of the sampled areas (nonhunted, slightly hunted, and heavily hunted) for a total of around 3,000 km censused. In the Pacaya-Samiria National Reserve there has been around 2,300 km censused. Many of the rarer species have not been sighted sufficiently to estimate density, even with these efforts of censusing.

DISCUSSION

Over the past decade many studies have begun to evaluate the sustainable use of wildlife (Robinson and Bennett 2000b). The most common model that is used is the production model developed by Robinson and Redford (1991). However, other models outlined in this article are also regularly used, and when information is available, these models may be preferable.

One of the major findings is that almost all of the sites examined had some species that were overhunted, while others were used more sustainably (Robinson and Bennett 2000b). In the Neotropics it was usually the rodents and faster-reproducing ungulates, such as collared and white-lipped peccaries and deer, that were hunted more sustainably, and the primates and slower-reproducing ungulates that were overhunted.

If hunting is to be sustainable, then overhunting should be stopped or reduced. In almost all areas studied a reduction in overhunting would entail a decrease in the hunting of certain species. Some authors have suggested that this reduction in harvests can be supplemented by increasing the harvests of sustainably used species (Alvard 1998). However, this is a very risky strategy that should not be used at the current time because of our incomplete understanding of tropical wildlife, the simplicity of the models used, and the limited accuracy of evaluating the sustainability of hunting.

The models described in this article are useful tools with which to evaluate whether measured hunting appears to be sustainable, but they are not sufficiently precise to determine exact hunting quotas or to recommend increases in harvests. The models can suggest whether current hunting pressures appear sustainable and whether this hunting can be continued at the measured levels. The models are also useful at revealing overhunting and in turn if hunting levels should be reduced. These models are not precise enough to suggest increases in hunting or to initiate hunting in nonhunted areas. The models are not population projections; rather, they are analysis of population size, harvest rates, and demography.

Evaluating the sustainability of hunting is only the first step toward converting unsustainable hunting to more sustainable hunting. It is important to evaluate sustainability as part of a process in order to manage hunting in a more sustainable manner. In many areas this assessment can be best done by including hunters in the evaluation through participatory approaches. Hunters, either local or sport, are often the people who use the wildlife most and who are the most interested in the continued well-being of the wildlife populations. They are the ones who visit and spend time in remote areas where wildlife abounds. Hunters are also often willing to contribute actively toward wildlife management. Thus, if hunters have a better understanding about wildlife management, they will be better suited to implement wildlife management actions.

Involving hunters and their families in the collection of data has some very important ramifications for conservation. First, such involvement produces a common ground in order to discuss wildlife issues among wildlife extension personnel, researchers, and the hunters. But more importantly, it persuades the hunters to become involved in analyzing the impact of their own hunting. They can then better understand the consequences of hunting, which in turn helps them think about ways of managing harvests in a way that agrees with their own realities. This self-monitoring process will be essential to the long-term implementation of sustainable wildlife harvests, and it frequently begins with participatory research techniques.

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20

Hunting Sustainability of Ungulate Populations in the Lacandon Forest, Mexico

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Wildlife has been and continues to be an important resource for the subsistence of rural people worldwide, providing food, hides, tools, medicine, income, and many other benefits (Redford and Robinson 1991; Shaw 1991; Freese 1998; Robinson and Bennett 2000b). There are many documented cases of continuous use of vertebrate species by native people in the tropics. Three good examples are the hunting of white-tailed deer (*Odocoileus virginianus*) by Mayan Indians of the Yucatan Peninsula, Mexico (Mandujano and Rico-Gray 1991; Jorgenson 1995), the use of duikers (*Cephalophus* spp.) by Mbuti tribes in the Ituri Forest of Central Africa (Hart 2000), and the harvest of Celebes pigs (*Sus celebensis*) by the Wana people of Central Sulawesi, Indonesia (Alvard 2000). However, the persistence of these harvested ungulate populations does not necessarily mean that local hunting systems have been sustainable in the past or that they are sustainable today (Robinson and Bodmer 1999).

On the basis of the arguments of Caughley and Sinclair (1994) and Prescott-Allen (1996), we define sustainable hunting as occurring when the number of animals taken does not exceed their production rates for a given period and when their long-term viability is not impaired. In this study we rely on five currently available models to evaluate the sustainability of hunting of ungulate populations in the Lacandon tropical rain forest of Mexico. Ungulates (Mammalia: Artiodactyla and Perissodactyla) are usually ranked as one of the most important groups of game mammals in Latin America because of their high yield, the good taste of their meat, and the usefulness of their skins (Ojasti and Dallmeier 2000).

Five ungulate species were included in this study: (a) Baird's tapir (*Tapirus bairdii*), which is endangered throughout its range (INE 2000; IUCN 2000); (b) white-lipped peccary (*Tayassu pecari*), whose populations and range seem to be declining in Mexico; (c) collared peccary (*Tayassu tajacu*); (d) white-tailed deer; and

(e) red brocket deer (*Mazama americana*). The last three species are still locally abundant and constitute an important source of protein for subsistence hunters in southeastern Mexico and Central America (March et al. 1996; Reid 1997; Bolaños 2000; Escamilla et al. 2000; Naranjo 2002). The objectives of this study were to evaluate the hunting sustainability of ungulate populations around Montes Azules Biosphere Reserve (MABR) in the Lacandon Forest of Chiapas, Mexico; and to determine if hunting sustainability of ungulates is affected by spatial scale in the study area.

MODELS OF HUNTING SUSTAINABILITY

Hunting sustainability in tropical forests has been assessed using a diversity of methods and models. The simplest methods consist of evaluations of the effects of hunting on game populations. These effects have been estimated by comparing hunting effort, densities, and age structure of game populations in unhunted and hunted areas (Robinson and Bodmer 1999). For hunting effort the measurement of catch per unit effort (i.e., prey killed/100 man hours) allows one to infer whether the abundance of game populations has changed over time as a result of hunting (Puertas 1998; Puertas and Bodmer this volume). An evident decline in catch per unit effort between two periods may suggest that the population has been overhunted. For densities the assumption is that hunting provokes a decline in population density. Therefore, habitats being equal, hunted areas would maintain lower densities than unhunted areas (Robinson and Bennett 2000b). For age structure one may expect that hunted areas would sustain populations with higher proportions of young individuals than unhunted areas because of the selectivity of hunters for the largest (and older) animals (Bodmer et al. 1997a).

These three methods may be helpful in assessing the effects of hunting on game populations. However, they also have potential biases: The differences in population densities or age structures between hunted and unhunted areas may not be due to hunting pressure but to such natural factors as variations in soils, primary productivity, availability of water, and demographic stochasticity, among many others. Similarly, a decay of catch per unit effort through time could be a result of changes in the livelihood of local hunters more than an effect of population decline.

The two most widely used models of hunting sustainability rely on comparisons of production rates and actual harvest rates of game populations (Robinson and Redford 1994; Robinson and Bodmer 1999). Robinson and Redford's 1991 production model works with estimations of maximum production rates (n animals produced/km^2/year; P_{max}) that are compared to actual harvest rates (n animals taken/km^2/year). This model is particularly useful in the absence of data on densities and actual production rates of hunted populations; it allows the detection of overharvest but not of sustainable hunting (Robinson and Bodmer 1999).

The harvest model proposed by Bodmer (1994) uses calculations of actual density, reproductive productivity (number of young/female/km^2/yr), and harvest rates of hunted populations. This model can be used to estimate whether hunting is sustainable or not at a given site (Robinson and Bodmer 1999).

Both the production and the harvest models assume that production, maximum potential harvests, and growth rates of game populations are density-dependent. Likewise, both models assume that Maximum Sustainable Yield (MSY) of Neotropical rain-forest mammals may be achieved at about 0.6 K in species with relatively high reproductive productivity (e.g., deer and peccaries), but the same MSY is reached at up to 0.8 K in slowly reproducing animals (e.g., tapirs; Bodmer and Robinson this volume). Therefore, sustainable harvest rates should not exceed 20%, 40%, or 60% of the production rates of long-lived species (i.e., tapir), short-lived species (i.e., peccaries and deer), and very short-lived species (i.e., spiny rats), respectively (Robinson and Bodmer 1999).

Evaluation of sustainability of hunting systems has frequently involved the model of Maximum Sustained Yield (Bennett and Robinson 2000a). MSY is conceived as the maximum possible number of animals harvested without driving the population into decline (Caughley 1977; Eltringham 1984). Theoretically, MSY is achieved when the harvest rate equals the population's recruitment rate by reproduction and it may occur at about 50 to 60 % of carrying capacity (K) for density-dependent populations in a given habitat (Caughley 1977; Riney 1982; McCullough 1987). However, MSY has suffered criticism as a management goal because under its guidance many wild populations seemed to have been depleted (Larkin 1977; Freese 1998). One of the problems of using MSY as a goal is that sustainable yields eventually may be obtained at densities well below 0.5 or 0.6 K (Caughley 1977; Caughley and Sinclair 1994). This implies that it is not possible to obtain the MSY of a wild population in an unhunted area because its density is already at carrying capacity (Eltringham 1984). In such cases there is a great risk of driving the population to local extinction when harvests are mistakenly higher than they should be (Caughley and Sinclair 1994).

Two more models that have recently been applied to evaluate hunting sustainability in tropical forests are the stock-recruitment model and the unified harvest model (Bodmer 2001). The stock-recruitment model (logistic model) can help forecast sustainable harvests for any population size between two moments in time (McCullough 1987). It has been used to evaluate the status of a harvested population by analyzing the distance between its actual size (N) and K (Bodmer et al. 1997a). The model assumes that MSY is reached at about 0.5 K (Caughley 1977).

The unified harvest model proposed by Bodmer and Robinson (this volume) integrates the information needed to evaluate hunting sustainability through both the harvest and the stock-recruitment models: productivity, harvest rates, and density at hunted and unhunted sites. In addition to its usefulness in assessments of hunting sustainability, the model can be applied to predict the potential of populations for sustainable use (Bodmer and Robinson this volume).

METHODS

STUDY AREA

The Lacandon Forest of Mexico comprises the southwestern sector of the Greater Maya Forest. The area is located in the northeastern portion of the state of Chiapas (from 16°05 to 17°15′ N, and from 90°30′ to 91°30′ W) and is delimited by the Guatemalan border on the east, north, and south and by the Chiapas Highlands on the west. Average monthly temperatures range from 24°C to 26°C with maximum and minimum values in May (28°C) and in January (18°C), respectively. Mean annual rainfall is 2,500 to 3,500 mm, with roughly 80% of the rains falling between June and November. The area was originally covered by over a million hectares of rain forest, of which about half remain today. Among the protected areas extant in the Lacandon Forest, Montes Azules Biosphere Reserve (MABR) is the largest with over 3,300 km^2, harboring some of the largest Mexican populations of precious hardwood trees and large vertebrate species, harvested by both Indian and mestizo residents (Vasquez and Ramos 1992; Medellín 1994; March et al. 1996).

ABUNDANCE AND DENSITY

From May 1998 through December 2000, two of the authors (EJN and JEB), assisted by two trained biologists and three local hunters, recorded individuals, tracks, and fecal groups of large- and medium-sized species along 1,908 km of line transects established at two slightly hunted (n = 8 transects) and two persistently hunted (n = 7 transects) sites of the Lacandon Forest. Slightly hunted sites were located within MABR, while persistently hunted sites were both within MABR and in community lands contiguous to the protected area (table 20.1; fig. 20.1). Line transects

TABLE 20.1 Hunting Intensity and Distance Traveled by the Authors in Four Sampling Sites of the Lacandon Forest, Mexico (1998–2000)

SITE	HUNTING SIGNS* /100 KM (N)	HUNTING INTENSITY	DISTANCE TRAVELED (KM)
MABR-Chajul	0.42 (2)	Light	478.2
MABR-Playón de la Gloria	0.55 (5)	Light	905.3
MABR-Reforma Agraria	3.10 (11)	Persistent	355.6
Lacanjá-Bonampak	5.33 (9)	Persistent	169.0
Total			1,908.1

*Hunting signs included direct sightings of hunters, used cartridges, and animal carcasses with clear signs of shots or cuts made by humans.

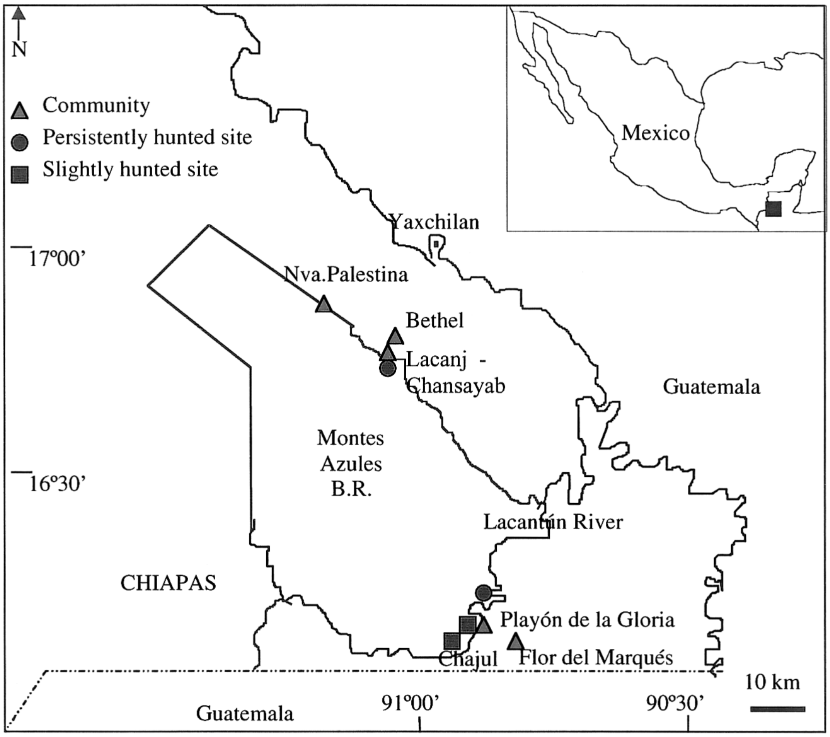

FIGURE 20.1 Study sites and communities visited in the Lacandon Forest, Mexico.

were 1 to 5 km long, and each of them was walked at least six times during the study. We walked the transects quietly and slowly (1 to 1.5 km/h), searching for individuals and other ungulate signs during the first and the last hours of daylight.

Perpendicular distances between the centerlines of the transects and ungulate individuals or groups seen were recorded. Peccary group size was assessed whenever possible. We only counted fresh tracks (clean, neat, and very contrasting to surrounding soil) observed within a 1-m strip along every transect. We erased all tracks found after every count. Encounter rates (number of individuals/100 km), indices of abundance (number of tracks or fecal groups/km; Conroy 1996), and density (number of individuals or groups/km^2) of each ungulate species were calculated for all sites, years, and seasons using the DISTANCE computer software (Buckland et al. 1993; Thomas et al. 1998).

HUNTING RATES

From September 1999 through August 2000, two of the authors (MMG and EJN), assisted by local hunters, obtained systematic records of hunting in five communities adjacent to MABR: (a) Bethel and (b) Lacanjá-Chansayab, populated by La-

TABLE 20.2 Population Size, Number of Hunters, and Number of Interviews Carried Out in Five Communities of the Lacandon Forest, Mexico (1999–2000)

	BETHEL	LACANJÁ-CHANSAYAB	NUEVA PALESTINA	FLOR DEL MARQUÉS	PLAYÓN DE LA GLORIA
Ethnic group	Lacandon	Lacandon	Tzeltal	Mestizo	Mestizo
Population	210	350	15,000	200	300
Hunters	30	50	850[*]	25	35
Interviews	44	43	45	44	56
% of population interviewed	21.0	12.3	0.3	22.0	18.7
Catchment area (km^2)	113.1	201.1	452.4	28.3	28.3
Number of species used	35	37	32	42	37

[*] Only the fifty most active hunters were monitored during the study.

candon Indians; (c) Nueva Palestina, inhabited by Tzeltal Indians; and (d) Playón de la Gloria and (e) Flor del Marqués, whose residents are mestizo (table 20.2; fig. 20.1) We conducted a total of 232 formal interviews (range = 40–56/community) through structured questionnaires to both men and women of age fifteen and older. With the help of hunters from each community, we further recorded the species, sex, approximate age category (young, juvenile, or adult), weight, site and date of capture, and hunting method used for each animal consumed during the study.

We were also assisted by the hunters from all communities in estimating their catchment areas through the calculation of the radius of hunting around the villages. We used data on catchment areas and hunting frequencies to calculate specific annual harvest rates in each community (individuals hunted/ km^2; Robinson and Redford 1991; Robinson and Bodmer 1999).

HUNTING SUSTAINABILITY MODELS APPLIED

We applied five different methods to evaluate hunting sustainability of ungulate populations in the Lacandon Forest.

Density Comparisons To assess hunting effects on population density, estimated densities of each ungulate species were contrasted between slightly and persistently hunted sites, between seasons, and among localities and years of study using chi-square analysis and t-tests (Sokal and Rohlf 1995). The hypothesis tested was that densities are lower in persistently hunted than in slightly hunted sites of the study area.

Production Model We compared actual estimates of harvest rates (H) obtained from visual records of hunting at the five communities visited and also the theoretical maximum production rates ($P_{\max}$) of each species (Robinson and Redford 1991). We calculated $P_{\max}$ through an equation combining maximum finite rates of increase ($\Gamma_{\max}$) and values of 60% of population density at carrying capacity (0.6 K):

$$P_{\max} = (\Gamma_{\max} - 1)\ 0.6D \tag{1}$$

where $P_{\max}$ is maximum production rate; $\Gamma_{\max}$, maximum finite rate of increase; and D, density.

$\Gamma_{\max}$ was in turn derived from the iterative solution of Cole's equation (Cole 1954; Robinson and Redford 1986b):

$$1 = e^{-r_{\max}} + b\, e^{-r_{\max(a)}} - b\, e^{-r_{\max(w+1)}} \tag{2}$$

where e is base of natural logarithms (2.71); $r_{\max}$, maximum intrinsic rate of increase; b, fecundity rate; a, age at first reproduction; and w, age at last reproduction. We assumed that hunting was not sustainable if harvest rates exceeded 20% of $P_{\max}$ estimated for tapirs or 40% of $P_{\max}$ estimated for deer and peccaries (Robinson and Redford 1991, 1994).

Harvest Model We used data on annual production rates (n individuals produced/km^2) calculated from population densities in persistently hunted areas of the Lacandon Forest, coupled with annual fecundity rates (n female young produced/female) estimated by Bodmer (1994) and Bodmer, Eisenberg, and Redford (1997) in the Peruvian Amazon (Equation 3):

$$P = (Y * G)\ 0.5D \tag{3}$$

where P is production rate (number of individuals produced/km^2/year); Y, annual number of young born per female; G, annual number of gestations; and P, population density at hunted sites (number of individuals/km^2).

Since sex ratios were not significantly different from the expected 1:1 for all species in the study area (Naranjo 2002), we used 50% of total density (the density of females) at hunted sites for calculations of production. We considered that hunting was sustainable if a harvest rate (H) was well below 40% of production (P) of deer and peccaries and if H was well below P of tapirs (Bodmer 1994; Robinson and Bodmer 1999).

Stock-Recruitment Model We used this model to evaluate the status of ungulate populations at persistently hunted sites through the analysis of the distance between actual population size (N) and its environmental carrying capacity (K) (McCullough 1987; Robinson and Bodmer 1999). We assumed that (a) carrying capacity (K) was represented by population density of each species at slightly/unhunted sites within MABR (Bodmer et al. 1997a); and (b) maximum sustained yield (MSY) is achieved at about 0.6 K in deer and peccary populations and at roughly 0.8 K in tapir populations (McCullough 1987; Bodmer et al. 1997a; Robinson and Bennett 2000b). We considered that a population was in safe condition for sustainable hunting if N was at or over 60% of K in deer and peccary populations or was equal to or greater than 80% of K in tapir populations (Robinson and Redford 1994; Bodmer et al. 1997a).

Unified Harvest Model This model constitutes an integration of the harvest and the stock-recruitment models, combining data on actual productivity, harvest rates, and population densities in slightly and persistently hunted sites (Naranjo 2002; Bodmer and Robinson this volume). We used the information on population densities, harvest rates, and reproductive productivity mentioned above to construct a graph that displays a vertical bar representing the status of hunted populations with respect to their K (x-axis), and with respect to their corresponding MSY (y-axis). Following the criteria applied in the harvest and the stock-recruitment models, we assumed that a population was being sustainably harvested and in safe condition if its vertical bar was well under its corresponding curve representing MSY (the harvest did not exceed production), and on the right side of the graph (N approached to K; Bodmer 2001).

RESULTS

ABUNDANCE AND DENSITY

We observed 411 individuals and 1,153 tracks of tapirs, peccaries, and deer during the study (tables 20.3 and 20.4).). We saw tracks, but not individuals, of white-tailed

TABLE 20.3 Comparative Encounter Rates (ER) and Densities of Ungulate Populations in Slightly Hunted and Persistently Hunted Sites of the Lacandon Forest, Mexico (1998–2000)

	SLIGHTLY HUNTED SITES			PERSISTENTLY HUNTED SITES		
SPECIES	N (ind.)	ER[a] (ind/100 km)	Density (ind/km^2 ± SE)	N (ind.)	ER[b] (ind/100 km)	Density (ind/km^2 ± SE)
Tapirus bairdii	14	1.07	0.24 ± 0.09	3	0.50	0.05 ± 0.04
Tayassu pecari	211	16.15	7.93 ± 5.95	52	8.65	1.08 ± 0.87
Tayassu tajacu	87	6.66	1.53 ± 0.39	25	4.16	1.15 ± 0.47
Mazama americana	13	0.99	0.20 ± 0.07	6	1.00	0.33 ± 0.19
Odocoileus virginianus	P[c]	—	—	P	—	—
Total	325	$\bar{x}$ = 6.22	$\bar{x}$ = 2.48 ± 1.63	86	$\bar{x}$ = 3.58	$\bar{x}$ = 0.65 ± 0.39

[a] Distance traveled = 1306.7 km.

[b] Distance traveled = 601.4 km.

[c] Present but not seen during transect sampling.

TABLE 20.4 Frequency of Ungulate Tracks in Slightly Hunted and Persistently Hunted Sites of the Lacandon Forest, Mexico (1998–2000)

	SLIGHTLY HUNTED SITES		PERSISTENTLY HUNTED SITES		OVERALL	
SPECIES	Tracks	Tracks/ 100 km[a]	Tracks	Tracks/ 100 km[b]	Tracks	Tracks/ 100 km[c]
Tapirus bairdii	307	23.49	90	6.89	397	20.81
Tayassu pecari	72	5.51	41	3.14	113	5.92
Tayassu tajacu	312	23.88	119	9.11	431	22.59
Mazama americana	145	11.10	64	4.90	209	10.95
Odocoileus virginianus	1	0.08	2	0.15	3	0.16
Total	837	$\bar{x}$ = 12.81	316	$\bar{x}$ = 4.84	1,153	$\bar{x}$ = 12.09

[a] Distance traveled = 1306.7 km
[b] Distance traveled = 601.4 km
[c] Distance traveled = 1908.1 km

deer during transect samplings; they were eventually sighted in the study area. Average group sizes of the four ungulate species seen were 20.2 for white-lipped peccary (5–60 ind., n = 13 groups); 2.3 for collared peccary (1–15 ind., n = 49 groups); 1.1 for red brocket deer (1–3 ind., n = 18 groups); and 1.1 for Baird's tapir (1–2 ind., n = 17 groups). The rank order of group densities was collared peccary > red brocket deer > tapir > white-lipped peccary. Average densities of the four species were 1.34 (0.6 individuals/km^2 and 0.38 (0.17 groups/km^2 (table 20.3).

Seventy-nine percent of all deer, peccaries, and tapirs sighted during the study were found at slightly hunted sites within MABR, easily explained by a greater sampling effort in these areas compared to persistently hunted sites (table 20.3). Our sampling effort was not the same in both kinds of sites because forest patches with similar structure and composition (and consequently the length of transects) were smaller outside MABR. To reduce this bias in the contrast of ungulate abundance, we used population density (number of individuals/km^2). In this comparison we found a significantly higher density of ungulates at slightly hunted sites than at persistently hunted sites (χ^2 = 177.2; df = 3; $P < 0.0001$), which suggests that heavy hunting pressure probably has had an effect on local ungulate populations.

However, such an effect did not appear to be the same for all species. Individual densities of the white-lipped peccary and Baird's tapir were almost seven and five times greater at slightly hunted than at persistently hunted sites, respectively. In contrast, the densities of the collared peccary were similar at both sites, while the red brocket deer was slightly more abundant at persistently hunted sites (table 20.3).

These results suggest that Baird's tapirs and white-lipped peccaries are more vulnerable to hunting pressure than collared peccaries and red brocket deer in the Lacandon Forest. Bodmer, Eisenberg, and Redford (1997) observed a similar pattern in the Peruvian Amazon, where the abundance of peccaries was similar, but the abundance of tapirs was very different between hunted and unhunted areas.

We performed an additional analysis of ungulate abundance using data on track frequencies recorded in the Lacandon Forest (table 20.4). In this analysis, we detected a higher relative abundance of collared peccary and tapir tracks compared to white-lipped peccary and red brocket deer tracks (Kruskal-Wallis; $H = 159.9$; $df = 4$; $P < 0.0001$). The higher abundance of collared peccary tracks may be explained by their actual higher density and relative tolerance to human disturbance compared to other ungulates in the study area (Fragoso, Silvius, and Villa-Lobos 2000). We found considerably more ungulate tracks per 100 km in slightly hunted than in persistently hunted sites ($\chi^2 = 9.48$; $df = 3$; $P = 0.044$; table 20.5). This result supports the hypothesis that hunting has reduced the abundance of ungulate populations in the study area.

HUNTING SUSTAINABILITY

We obtained an overall annual harvest rate of 0.77 ungulates per km^2 (table 20.5). Collared peccaries were more frequently harvested than the rest of the ungulate species in the Lacandon Forest ($P < 0.05$). Collared peccaries accounted for 55% of overall harvest rates, followed by red brocket deer (28%), white-tailed deer (11%), white-lipped peccaries (5%), and Baird's tapirs (1%). In contrast, red brocket deer ranked first in biomass extracted (1469 kg, or 27%) to total ungulate biomass extracted in the five communities, followed by white-tailed deer (21%), collared peccaries (21%), Baird's tapirs (19%), and white-lipped peccaries (12%; table 20.6).

TABLE 20.5 Numbers of Hunters, Ungulates Taken, Biomass Harvested, and Catchment Areas of Three Ethnic Groups in the Lacandon Forest, Mexico (1999–2000)

	LACANDON		TZELTAL		MESTIZO		ALL COMBINED	
VARIABLE	n	%	n	%	n	%	n	%
Number of hunters monitored	80	42.1	50	26.3	60	31.6	190	100
Number of ungulates hunted	93	48.2	53	27.5	47	24.3	193	100
Ungulate biomass extracted (kg)	2,308	42.5	2,219	40.8	906	16.7	5,433	100
Catchment area (km^2)	314	38.2	452	54.9	57	6.9	823	100
Overall ungulate harvest rate (individuals/10 km^2/year)	1.7	21.9	0.9	12.3	5.1	65.8	7.7	100

TABLE 20.6 Evaluation of Hunting Sustainability of Ungulate Populations in the Lacandon Forest Through the Production and the Harvest Models

SPECIES	DENSITY (IND/KM^2)	P_{MAX}[a] (IND/KM^2)	P[b] (IND/KM^2)	H[c] (IND/KM^2)	P_{MAX}	P	MFP[d]	SUST?
Tapirus bairdii	0.05	0.007	0.007	0.003	0.40[e]	0.44[e]	0.2	No
Tayassu pecari	1.08	0.853	0.508	0.013	0.02	0.03	0.4	Yes
Tayassu tajacu	1.15	1.718	0.874	0.140	0.08	0.16	0.4	Yes
Mazama americana	0.33	0.097	0.109	0.072	0.74[e]	0.66[e]	0.4	No
Odocoileus virginianus	0.29[f]	0.187	0.218	0.027	0.15	0.12	0.4	Yes
Total	2.61	2.862	1.716	0.255				

[a] Maximum production rates based on r_{max}.

[b] Production rates based on actual densities estimated in the Lacandon Forest and reproductive data from R. E. Bodmer (pers. comm.).

[c] Harvest rates obtained from visual hunting records in five communities.

[d] Maximum fraction of production that can be sustainably harvested (Robinson and Redford 1991).

[e] Unsustainable hunting under Robinson and Redford's criteria (1991).

[f] Estimated from track frequency using data for red brocket deer.

The results, pooling data from all communities visited (table 20.7), obtained through the production model (Robinson and Redford 1991) suggest that the harvests of Baird's tapir and red brocket deer were unsustainable on a "regional" scale. Following Robinson and Redford's criteria, an unsustainable harvest consists of taking more than 20% of the maximum annual production (0.2 of $P_{\max}$) of long-lived mammals, such as tapirs, and over 40% of $P_{\max}$ of short-lived mammals, such as deer and peccaries. The average fraction of Baird's tapir $P_{\max}$ harvested in the study area was 40%, which denotes an overhunting of this species. Nonetheless, this overharvest was actually concentrated in the Tzeltal community of Nueva Palestina, where 105% of $P_{\max}$ was taken. In contrast, the Lacandon communities of Bethel and Lacanjá-Chansayab harvested only 15% of tapir $P_{\max}$, while mestizos from Playón de la Gloria and Flor del Marqués did not hunt tapirs (table 20.8). An analogous situation was observed for the red brocket deer, which was overharvested by Lacandon and mestizo hunters, who took over 100% of $P_{\max}$, but not by Tzeltal hunters, who took only 9% of $P_{\max}$ (table 20.8).

Under this model the harvests of the remaining three ungulate species (both peccaries and the white-tailed deer) were not high enough to be regarded as unsustainable. However, this model does not allow for the verification of the hypothesis that such harvests are actually sustainable (Robinson and Bodmer 1999).

The harvest model (Bodmer 1994) was helpful in confirming a similar pattern of unsustainable offtake at a landscape scale in the Lacandon Forest: Hunters took an estimated 44% and 66% of production (P) of tapirs and red brocket deer, respectively (table 20.8). The overharvest of tapirs was again located in Nueva Palestina,

TABLE 20.7 Hunting Sustainability of Ungulates Taken by Three Ethnic Groups in the Lacandon Forest Through the Production Model

SPECIES	DENSITY (IND/KM²)	P_{MAX}[a] (IND/KM²)	LACANDON		TZELTAL		MESTIZO	
			H[b]	H/P_{max}	H	H/P_{max}	H	H/P_{max}
Tapirus bairdii	0.05	0.007	0.001	0.15	0.007	1.05[c]	0	0
Tayassu pecari	1.08	0.853	0.020	0.02	0.009	0.01	0.009	0.01
Tayassu tajacu	1.15	1.718	0.029	0.02	0.038	0.02	0.354	0.21
Mazama americana	0.33	0.097	0.111	1.14[c]	0.009	0.09	0.097	1.00[c]
Odocoileus virginianus	0.29[d]	0.187	0.007	0.04	0.031	0.17	0.044	0.24
Total	2.61	2.862	0.168		0.094		0.504	

[a] Maximum production rates based on r_{max}.
[b] Harvest rates obtained from visual hunting records in five communities.
[c] Unsustainable harvest under Robinson and Redford's criteria (1991).
[d] Estimated from track frequency using data for red brocket deer.

TABLE 20.8 Hunting Sustainability of Ungulates Taken by Three Ethnic Groups in the Lacandon Forest Through the Harvest Model

SPECIES	DENSITY (IND/KM²)	P[a] (IND/KM²)	LACANDON		TZELTAL		MESTIZO	
			H[b]	H/P	H	H/P	H	H/P
Tapirus bairdii	0.05	0.007	0.001	0.15	0.007	1.04[c]	0	0
Tayassu pecari	1.08	0.508	0.020	0.04	0.009	0.02	0.009	0.02
Tayassu tajacu	1.15	0.874	0.029	0.03	0.038	0.04	0.354	0.41[c]
Mazama americana	0.33	0.109	0.111	1.02[c]	0.009	0.08	0.097	0.89[c]
Odocoileus virginianus	0.29[d]	0.218	0.007	0.03	0.031	0.14	0.044	0.20
Total	2.61	1.716	0.168		0.094		0.504	

[a] Production rates based on actual densities estimated in the Lacandon Forest and reproductive data from R.E. Bodmer (pers. comm.).
[b] Harvest rates obtained from visual hunting records in five communities.
[c] Unsustainable harvest under Robinson and Redford's criteria (1991).
[d] Estimated from track frequency using data for red brocket deer.

where Tzeltal hunters extracted an estimated 104% of P. In the same way Lacandon and mestizo hunters took an estimated 102% and 89% of P of red brocket deer in their respective communities. A noteworthy difference in the evaluation of sustainability through the harvest model compared to the production model was the detection of unsustainable hunting of collared peccaries in mestizo communities. Mestizo hunters obtained about 41% of collared peccaries' P, barely exceeding the limits of sustainability proposed by Robinson and Redford (1991) for this species.

Since the harvest model works with actual data on population densities, production rates, and harvest rates of local populations, it allows the inference that offtakes may be sustainable when they are well below the maximum fractions of P (0.2, 0.4, or 0.6, depending on species longevity) that can be taken without driving the population into decline (Robinson and Redford 1991). Consequently, this model suggests that the hunting of collared peccaries, white-lipped peccaries, and white-tailed deer appears sustainable, while tapirs and red brocket deer are being overhunted on a landscape scale in the Lacandon Forest. On a local scale Tzeltal hunters seem to be overhunting tapirs, Lacandon hunters are probably overharvesting red brocket deer, and mestizo hunting rates of collared peccaries and red brocket deer are beyond the limits of sustainability.

The stock-recruitment model has been used to assess the status of populations and to predict their potential for sustainable harvests (Caughley 1977; McCullough 1987; Bodmer et al. 1997a). The data on densities of ungulates at unhunted, slightly hunted, and persistently hunted sites in the Lacandon Forest indicate that the populations of collared peccary and red brocket deer are in safe condition, while tapir and white-lipped peccary populations seem to be in risky condition (table 20.9; fig. 20.2).

At 75% of its carrying capacity (0.75 K), the hunted collared peccary population is well above its respective point of MSY (0.6 K; Robinson and Redford 1991), implying that this species probably has a good potential to support sustainable harvests at a landscape scale. The red brocket deer is an interesting case because its density was higher at persistently hunted sites than at slightly hunted sites. Thus it is likely that the hunted population of this species (N) is at its carrying capacity (1.0 K) and so it is in safe condition to allow sustainable hunting. On the other hand, the hunted populations of Baird's tapir and white-lipped peccary apparently have been negatively affected by hunting at the study area, since they were at only 0.21 K and 0.14 K, respectively (table 20.9; fig. 20.2).

Bodmer (2001) has recently proposed the unified harvest model, so its use is still incipient. This model provides an integrated and graphical view of the results ob-

TABLE 20.9 Status of Ungulate Populations in Persistently Hunted Sites of the Lacandon Forest, Mexico

SPECIES	K (IND/KM^2)	D$_{PH}$ (IND/KM^2)	D$_{PH}$/K	STATUS
Tapirus bairdii	0.24	0.05	0.21	Risky
Tayassu pecari	7.93	1.08	0.14	Risky
Tayassu tajacu	1.53	1.15	0.75	Safe
Mazama americana	0.20	0.33	1.65	Safe?
Odocoileus virginianus	?	0.29	?	?

Note: Density estimates from persistently hunted sites (D$_{ph}$) were compared to density estimates from unhunted sites (assumed as carrying capacity K).

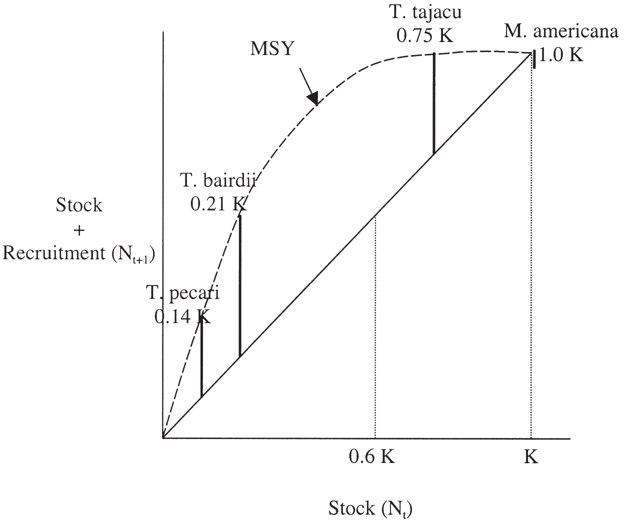

FIGURE 20.2 Stock-recruitment model comparing the status of persistently hunted populations of ungulates with respect to their carrying capacity (K) in the Lacandon Forest, Mexico.

tained through the harvest and the stock-recruitment models, showing that the hunting systems of ungulates are not producing equal effects on different species in the Lacandon Forest (figs. 20.3 and 20.4). The apparently sustainable harvest and safe condition of the hunted collared peccary population, as well as the unsustainable hunting and risky condition of the tapir population estimated through the other models was confirmed with the unified harvest model (figs. 20.3 and 20.4).

Both the production and the harvest models indicated that the hunted white-lipped peccary population was sustainably harvested on both local and landscape scales in the Lacandon Forest. The unified harvest model provided a different view: hunting of white-lipped peccaries in fact seems to be within the theoretical sustainability limits but this result is actually a consequence of the species' very low density in persistently hunted areas. This finding concurs with the information provided by interviewed hunters, as well as with our own visual records of hunting in the communities visited during the study.

The unified harvest model offered a clear view of this situation: the white-lipped peccary population was at a very low density and it was harvested at a low rate (fig. 20.3). The analysis of hunting sustainability for the red brocket deer population is particularly interesting by means of this new model. The red brocket deer had a higher density at persistently hunted than at slightly hunted but still was apparently overharvested (fig. 20.3). An explanation of this contradictory result may be based on the hypothesis that the red brocket deer population maintains a relatively high density at persistently hunted sites via immigration of individuals from slightly hunted areas of MABR (a source-sink dynamics; Pulliam 1988).

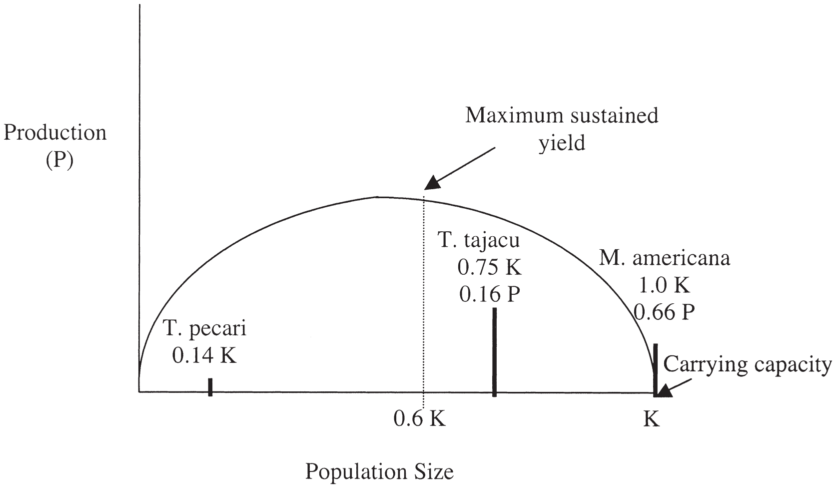

FIGURE 20.3 Unified harvest model showing the sustainability of hunting and status of red brocket deer, collared peccary, and white-lipped peccary populations at persistently hunted sites of the Lacandon Forest, Mexico. Bar position on the x-axis indicates population status with respect to carrying capacity (K). The height of the bar denotes the harvested fraction of population production (P) in relation to the maximum sustained yield curve.

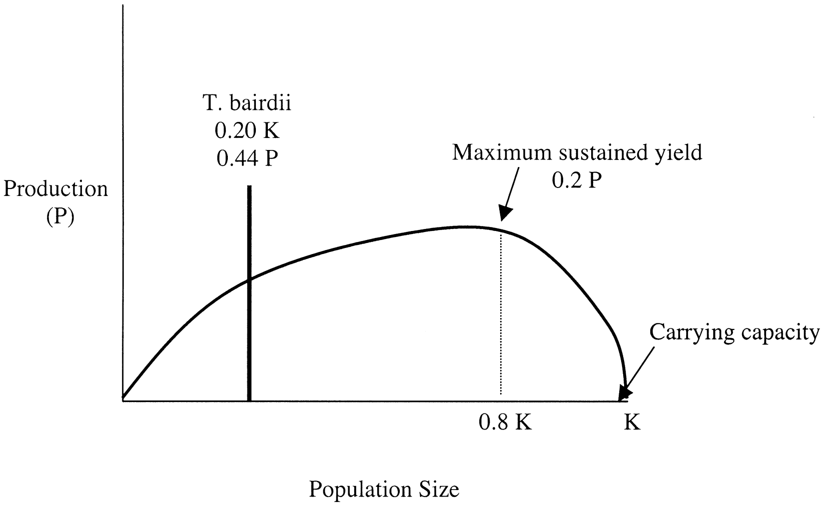

FIGURE 20.4 Unified harvest model showing the sustainability of hunting and status of Baird's tapir populations at persistently hunted sites of the Lacandon Forest, Mexico. Bar position on the x-axis indicates population status with respect to carrying capacity (K). The height of the bar denotes the harvested fraction of population production (P) in relation to the maximum sustained yield curve.

Finally, given the lack of reliable data on white-tailed deer densities in the study area, we cannot draw conclusions about the sustainability of its hunting. However, considering the harvest rates obtained for this species, as well as the information provided by local hunters, it is likely that its populations benefit by habitat transformation outside existing protected areas in the Lacandon Forest.

DISCUSSION

POPULATION DENSITY AND ABUNDANCE

The abundance and density of ungulate populations at slightly hunted sites of Montes Azules Biosphere Reserve (MABR) are within the range observed in other Neotropical rain forests. Baird's tapir encounter rates estimated in MABR were similar to those obtained by Cruz (2001) and Naranjo and Cruz (1998) in La Sepultura Biosphere Reserve, Mexico. However, the density of tapirs was lower in MABR than in Corcovado National Park (CNP), Costa Rica (Naranjo 1995; Foerster 1998), and Barro Colorado Island (BCI), Panama (Glanz 1982).

We attribute these differences largely to a lower hunting pressure in the latter two areas compared to MABR and a substantial difference of size between MABR (> 3,000 km^2) and the other two areas (< 500 km^2). Furthermore, Baird's tapir abundance was higher in slightly hunted sites of the Lacandon Forest than in an unhunted area of Chiquibul Reserve, Belize (Fragoso 1991), and northeastern Honduras (Flesher 1999), where there was relatively high hunting pressure on this species.

Population densities of collared peccaries, white-lipped peccaries, and red brocket deer estimated in slightly hunted areas of the Lacandon Forest were not very different than the densities obtained in several Central and South American localities (Glanz 1982; Bodmer et al. 1997a; Fragoso 1998a). This finding suggests that local populations of the three species are in good condition at unhunted and slightly hunted sites of our study area. However, the situation seems notably different for tapirs and white-lipped peccaries at persistently hunted sites of the Lacandon Forest. The clear differences in the density of these two species between slightly and persistently hunted sites may be a combined effect of overhunting and habitat transformation. Human density and activity has dramatically increased in the study area during the last twenty-five years (INEGI 2002), and the concomitant need for land, timber, and food has caused forest fragmentation and overexploitation of many wildlife populations outside extant protected areas (Naranjo 2002).

Both the tapir and the white-lipped peccary are vulnerable to heavy hunting pressure in different ways: The first has a very low reproductive productivity (Eisenberg 1989), and its populations often cannot recover from an intense or even a moderate harvest rate (Bodmer 1995b). In addition, because of its habitat requirements, the tapir is sensitive to habitat fragmentation and other effects of human activity (e.g., noise, odors, dogs, and cattle; Matola, Cuarón, and Rubio-Torgler 1997; Naranjo and Cruz 1998).

The white-lipped peccary is similarly sensitive to habitat fragmentation because of its extensive home range and its feeding strategies (Fragoso 1998a). Moreover, hunters capitalize on its social behavior and very large herd size to decimate their populations in the study area (Naranjo 2002). The impact of these factors was evident in many communities adjacent to MABR (e.g., Nueva Palestina, Bethel, and Playón de la Gloria), where both tapirs and white-lipped peccaries appear to be close to local extinction outside the protected area.

Estimations of wildlife population densities and abundances in tropical rain forests are almost always complicated by factors such as the natural rarity of the species, the restricted visibility within the forest, and the high sensitivity of these mammals to human noises and odors. In spite of these difficulties, the use of density and abundance comparisons between areas with different hunting pressure should not be discarded as a useful technique in evaluating the effects of hunting on populations of Neotropical ungulates, especially if they are combined with other kinds of informationm such as production and harvest rates, that allow running models of hunting sustainability.

HUNTING SUSTAINABILITY

Evaluation of hunting sustainability of ungulate populations in the Lacandon Forest benefited from the simultaneous application of several models. The production and the harvest models gave similar results on a landscape scale, but there were some differences on a local scale. Both models suggested unsustainable hunting of tapirs and red brocket deer in the study area. However, these species were not overharvested in all communities. In most cases the harvest/production ratios (H/P) obtained through the harvest model tended to be higher than H/P ratios estimated with the production model, primarily because the first is based on actual data of population productivity and the second uses theoretical calculations of $P_{\max}$. This trend made it possible to detect unsustainable offtake of collared peccaries by mestizo hunters through the harvest model only.

It was remarkable that the production model did not indicate overhunting of white-lipped peccaries, while the harvest model in fact suggested sustainable hunting of this species in the study area. However, synergic effects of habitat fragmentation, heavy hunting pressure, and extensive home ranges of herds seem to have driven this mammal to local extinction in most of the rain-forest patches remaining around MABR. In this sense both the stock-recruitment model and the unified harvest model provided a reasonable answer to this apparent incongruity: Hunting of white-lipped peccaries is within sustainability limits largely because the group density of this species is very low at persistently hunted sites. Hence, hunters of the Lacandon Forest have a smaller chance of finding a white-lipped peccary herd than any other ungulate group when they go out to search for prey. This fact was particularly evident in mestizo communities, in which the interviewees themselves explained the extremely low harvest rate of this species because of its scarcity in the small catchment areas within their communities. In addition, most of the oldest hunters interviewed during the study concurred in the perception that white-lipped peccary populations have severely declined or even disappeared near their villages in the last two decades.

All these observations lead to the conclusion that current hunting on the remaining white-lipped peccary populations outside MABR should be lowered to facilitate their recovery through local reproduction and immigration from slightly hunted areas of MABR. Forest management to improve connectivity between large forest fragments in community lands would also help to facilitate migration of white-lipped peccaries from MABR.

There were some similarities but also some differences between the results of the evaluations of hunting sustainability of tapirs and white-lipped peccaries in the study area. The analysis of interviews with residents of the Lacandon Forest revealed that hunting pressure on tapirs has been relatively low in the last three years. In fact, this mammal does not appear within the most frequently hunted species in the study area (Naranjo 2002). However, tapirs were overhunted in Nueva Palestina, where Tzeltal hunters took a little more than 100% of P. Meanwhile, Lacandon hunters extracted only 15% of P, and mestizo hunters did not take tapirs at all.

The causes of these variations may be related to the geographical, cultural, and socioeconomic contexts of hunters and their communities. Tzeltal hunters of Nueva Palestina (n = 850) outnumbered by far the Lacandon and mestizo hunters combined (n = 140) and used a larger catchment area than the latter two. These differences imply that Tzeltal hunters had a higher probability of finding a tapir in their home ranges than Lacandon and Tzeltal hunters. On the other hand, as noticed by March (1987), most Lacandon hunters interviewed in this study said that they did not like to hunt tapirs because they are too heavy and too bulky to be carried back to their homes. Consequently, it would be a waste of time and effort to hunt one of these large mammals. The reason why mestizo hunters did not harvest tapirs during the study was simple: the species is rarely found in their *Ejidos*.

As in the case of white-lipped peccaries, the stock-recruitment and the unfiied harvest models were helpful in recognizing that the tapir population has been depleted in the most persistently hunted sites, maintaining extremely low densities (around 0.05 ind/km^2) in a few localities outside the protected areas of the Lacandon Forest. Under these circumstances a few animals hunted per year can constitute an unsustainable offtake, as was observed on both local (Nueva Palestina) and landscape scales.

Red brocket deer seemed to be regionally and locally overhunted by two ethnic groups (Lacandon and mestizo). Nevertheless, its populations at persistently hunted sites were at its carrying capacity (1.0 K; figs. 20.2 and 20.3). The production, harvest, and stock-recruitment models provided partial arguments for understanding the whole situation of red brocket deer hunting in the study area. In contrast, the unified harvest model was the only one that showed the complete scenario at once: The persistently hunted population of red brocket deer is being overharvested, but at the same time it is in safe condition compared to the slightly hunted population (fig. 20.3).

This result suggests that the red brocket deer population may be functioning in a source-sink system in the area, where MABR would be the source of individuals and the surrounding communal lands would be the sinks. A similar case was observed by Bodmer (2000), who found that a source-sink system seemed to be maintaining a constant overhunting of lowland tapirs recorded in persistently hunted areas of the Peruvian Amazon. In this condition the overharvest appears less risky for red brocket deer than for tapirs and white-lipped peccaries in the Lacandon Forest. However, a decrease of current harvest rates of red brocket deer in Lacandon and mestizo communities should benefit both the hunters and their prey.

CONCLUSION

Using several models to evaluate hunting sustainability was a first step toward understanding the current status of ungulate populations harvested in the Lacandon Forest. It must be recognized, however, that the results of models applied in this study do not constitute exact measurements of reality but rather offer an overview of the general trends of the hunting systems present in the study area.

Estimates of hunting sustainability may be affected by scale factors (Wiens 1989; Novaro, Redford, and Bodmer 2000). Novaro, Redford, and Bodmer (2000) found that most evaluations of hunting sustainability did not consider the potential effects of animal migration from large protected areas to hunted areas (a source-sink system; Pulliam 1988; Pulliam and Danielson 1991). In consequence, local hunting systems that apparently are unsustainable may actually be sustainable at a much larger, regional scale, as shown recently by Novaro (1997); Bodmer (2000); Fragoso, Silvius, and Villa-Lobos (2000); and Hill and Padwe (2000). Migration of animals between slightly hunted and persistently hunted areas of the Lacandon Forest has not been measured, but the evidence gathered over the three years of this study suggests that the movement of individuals from large protected areas (i.e., Montes Azules and Lacantún Biosphere Reserves) into nonprotected community lands is an important variable in the functioning of regional ungulate hunting systems. However, much more field evidence is needed to support the hypothesis of source-sink dynamics in this and other hunting systems (Clutton-Brock 1997; Novaro, Redford, and Bodmer 2000).

A common recommendation derived from this kind of evaluation is that hunting should be controlled where it seems to be unsustainable (Robinson and Redford 1991; Bodmer et al. 1997a, 1997b; Robinson and Bennett 2000b). The process of steering unsustainable hunting systems toward sustainability is complex. Comprehensive and detailed assessments of the status of game populations and their harvest rates are certainly very important but not sufficient to predict and encourage sustainability. A realistic strategy to promote hunting sustainability must not only address the biology of game species but also the cultural and socioeconomic context of local people along with the needs and interests of local hunters (Western, Wright, and Strum 1994; Bennett and Robinson 2000a; Bodmer 2000). Residents of the Lacandon Forest will not participate in programs of wildlife conservation and sustainable use unless they are convinced that they can share the benefits of hunting regulation in their own lands. Research and education can help to boost this process.

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21

Human Use and Conservation of Economically Important Birds in Seasonally Flooded Forests of the Northeastern Peruvian Amazon

JOSÉ A. GONZÁLEZ

Wildlife plays a key role for people inhabiting the Amazonian rain forest (Terborgh, Emmons, and Freese 1986; Redford and Robinson 1991; Vickers 1991). Subsistence hunting has been very significant for the economy of the Amazon region and, in particular, for the well-being of thousands of rural families (Dourojeanni 1972). Indeed, in many parts of the northeastern Peruvian Amazon, wildlife provides most of the animal protein consumed by local households (Pierret and Dourojeanni 1967; Ríos, Dourojeanni, and Tovar 1973; Bodmer et al. 1994). Although mammals are always the most important prey for susbistence hunters, birds may comprise a significant amount of the total biomass intake (Ayres et al. 1991; Vickers 1991; Zent 1997). Birds are especially important in terms of the number of animals taken and may account for up to 27% of captures (Ojasti 1993). Bird eggs are also an important source of food for local people in many areas of the Peruvian Amazon (González 1999a). Several Amazonian ethnic groups also hunt birds for ornamental, medicinal, or magical purposes (Redford and Robinson 1991).

Finally, birds such as parrots and macaws are popular as pets and are heavily targeted by the pet market (Thomsen and Brautigam 1991). The resultant international trade in psittacines is of great concern to conservation biologists (WCI 1992; Wright et al. 2001). Until 1973 more than a hundred species were exported regularly from the Peruvian Amazon, with psittacines and other ornamental birds comprising more than 40% of this trade (Dourojeanni 1972). Nowadays, despite being banned by national laws, the harvesting and trade of parrots and macaws is still a common practice in many parts of the region (González 1999b).

Notwithstanding the importance of subsistence hunting and the pet-bird trade in the Neotropics for both human welfare and wildlife conservation, most of the field data required to develop sustainable management programs is still lacking (Peres 1997). Some recent studies have focused on assessing the sustainability of ungulate harvests in the Peruvian Amazon (Bodmer et al. 1994, 1999), but there are still few reports that deal with the sustainability of bird hunting (Begazo 1997). Even though the sustainability and implications of the bird trade have been extensively analyzed in recent years (Beissinger and Bucher 1992; Thomsen and Mulliken 1992; WCI 1992), figures that quantify illegal trade at the national level and its impact on the populations of the exploited species are still lacking (Beissinger 1994). In this paper I document the patterns of harvesting of wild birds in the Ucayali-Puinahua floodplain (northeastern Peruvian Amazon), evaluate the relative importance of each species in social and economic terms, and finally assess the effects of harvesting on bird populations as a first step in developing sound management strategies for bird conservation.

STUDY AREA AND METHODS

Field work was conducted in the southern part of the Pacaya-Samiria National Reserve (PSNR), a protected area located in the Department of Loreto between the Marañón and Ucayali/Puinahua rivers (from 04° 26′ 36″ to 06° 08′ 01″ S and from 73° 26′ 59″ to 75° 34′ 33″ W). The reserve covers an area of 2,150,770 ha, being one of the largest conservation units in Latin America (fig. 21.1).

The climate is tropical with a mean annual temperature around 27°C and a mean annual rainfall over 2,900 mm, most falling between October and May, when much of the land becomes flooded. Rivers reach their highest levels from

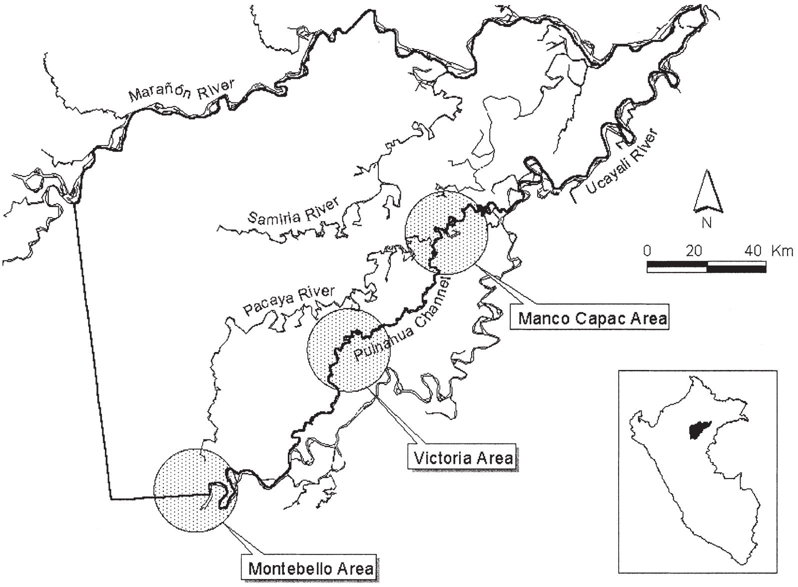

FIGURE 21.1 Location of the study sites at Pacaya-Samiria National Reserve.

March to May and their lowest in August and September (Soini 1995). The floodplain ecosystem consists of varied landforms and aquatic surfaces sculptured by the river. These features include natural levees (*restingas*), mud and sand bars (*barreales* and *playas*), backswamps (*tahuampas*), palm swamps (*aguajales*), lakes (*cochas* and *tipishcas*), side channels (*caños*), and rivers (Hiraoka 1995). Most of the study area is occupied by palm swamps (37%) and seasonally flooded forests (34%). A detailed description of vegetation communities present at PSNR is provided by Rodríguez, Rodríguez, and Vásquez (1995).

Within the reserve and the surrounding areas, humans live in 173 rural settlements, most of which (89%) are small villages with fewer than 500 inhabitants located on the borders of the Marañón and Ucayali/Puinahua rivers. The last population census recorded 32,241 persons living in the southern part of the reserve (Ucayali/Puinahua basin), 27% inside the boundaries of the protected area, and 73% in the buffer zone (Rodríguez, Rodríguez, and Vásquez 1995). The inhabitants of the study area include people of mixed origins (*mestizos*), as well as detribalized natives from the ethnic groups Cocama-Cocamilla and Shipibo-Conibo.

Major economic activities include fishing, agriculture, extraction of forest products, and game hunting, with the relative importance of each of these activities varying in different parts of the reserve. Although the population is mainly engaged in subsistence production, the growing need to integrate into the market economy has forced some inhabitants to distance themselves from the traditional systems of production, threatening the ecological sustainability of the area as well as the human population's opportunities for survival and development (Junglevagt for Amazonas 1995).

ESTIMATES OF BIRD USE

Between January and April 1997 I conducted interviews with local families in a total of 194 households in seventeen communities located in the southern part of the PSNR (fig. 21.1). This sample represents 23.3% of the households in the visited villages and 2.9% of the population in the whole study area. Since 1992 the selected communities have been part of two large development projects financed by USAID/TNC/FPCN (Project Employment and Natural Resources Sustainability No. 527-0341) and AIF-WWF/DK (Juglevagt for Amazonas: Programa Integral de Desarrollo y Conservación Pacaya Samiria). I was always accompanied by well-known managers of these projects in order to increase trust between myself and local people. However, as interviews and questionnaires may bias the estimation of the total number of animals harvested (Wright 1978), I included several crossquestions to assess the credibility of the answers. Six households (3.1%) were excluded from the analyses because of incoherent responses or hostile atmospheres. Several especially designed booklets, containing pictures of the most commonly taken game birds (Begazo 1997), were distributed among twenty-six selected hunters to keep a record of the number of birds they harvested monthly. Even so, the calculations of hunting pressure should be considered as estimates because of biases inherent in the interview and participatory methods of data collection (Silva and Strahl 1991; Townsend this volume).

ESTIMATES OF BIRD ABUNDANCE AND DENSITY

I also estimated the abundance and density of the most important game birds in three heavily hunted areas close to the villages Urarinas, Montebello, and Victoria and three areas of low/absent hunting pressure inside the protected area, close to ranger stations Alfaro, Santa Cruz, and El Dorado. A total of 143.5 km of transect lines (82.4 inside the reserve, 61.1 outside) and 67.8 km of streams (40.8 inside and 27.1 outside) were surveyed following the methodology proposed by Strahl and Silva (1997). Nineteen, twelve, and ten transects were surveyed at each of the protected sites, respectively, and nine, eleven, and eleven at each of the hunted sites near villages. Transects were walked along streams and preexisting trails and were variable in length, ranging from 1.1 to 8.8 km. Each transect was surveyed only once between January and May 1998, between 7:00 and 11:00 A.M. or between 4:00 and 6:00 P.M. Both visual and auditory sightings were recorded, but only visual sightings were used for abundance estimates. The perpendicular distance between the bird and the transect was measured using steps. Birds sighted on the trail or over the stream were assigned a distance of 1 m. Results are expressed as number of birds per 10 km surveyed and for terrestrial birds as number of birds per km^2. Density was calculated using the King method (Overton 1971).

Differences in bird abundance are not likely to be attributable to habitat type since the censused areas were very similar. I used the harvest model proposed by Robinson and Redford (1991) to evaluate the sustainability of subsistence hunting of terrestrial birds in the study area, employing reproductive and demographic data recorded during the study, as well as unpublished information provided by A. Begazo. Conservative parameters were used for estimating the maximum production and the size of the catchment area.

ESTIMATES OF EGG-HARVESTING

During the heron nesting seasons of 1997–1998 (March to May), I monitored the total number of eggs harvested from two heronries located close to the villages of Padre López and Nueva Cajamarca. I visited the heronries with two groups of egg-collectors to assess the impact of egg-harvesting on nesting success.

ESTIMATES OF PARROT AND MACAW HARVESTING

Between 1996 and 1999, during the nesting season of parrots and macaws (February to April), I monitored the total number of nestlings collected in two Mauritia palm swamps (total area: 3,890 ha) located close to the village of Victoria, where most of the parrot trade took place. During the nesting seasons of 1998 and 1999, I also estimated nest density and chick productivity of the seven most commonly harvested species in this area.

Density of parrot and macaw nests was estimated in variable-sized plots, ranging from 20 to 47 ha, randomly placed along two transect lines that crossed the most frequently used Mauritia palm swamps. Eight plots were set in 1998 (total: 268 ha) and nine in 1999 (total: 278 ha). Each plot was surveyed during two consecutive days by the researcher and two experienced poachers looking for parrot and macaw nests. Nest density estimates were done before the harvesting season began. However, at one of the swamps in 1999, it is possible that some undetected harvesting had occurred in two of the plots before our arrival in the area. Productivity (fledglings/nest) was calculated with the information provided by poachers and by means of the nests opened during the harvesting process. Only those nests containing fully fledged young were considered. The total area of harvest was mapped using aerial photographs and GPS data gathered during our visits. Sustainability was assessed by comparing the recorded annual harvesting rates with the estimated annual production of nestlings in the whole area.

RESULTS

BIRDS AS A SOURCE OF FOOD

At least forty-one bird species were hunted for food in the southern part of PSNR and its surroundings during 1996 (table 21.1); the use of other six additional bird species was recorded during our visits to the study site in 1997–1998. However, only eight species were hunted regularly by more than 25% of the households, with these species accounting for 75% of the total number of birds harvested in the study area (table 21.2). Undulated tinamous (*Crypturellus undulatus*), anhingas (*Anhinga anhinga*), razor-billed curassows (*Mitu tuberosa*), muscovy ducks (*Cairina moschata*), and olivaceous cormorants (*Phalacrocorax olivaceus*) were the most-frequently hunted species. The razor-billed curassow and the muscovy duck, because of their larger size, were the most important species in terms of biomass. The white-eyed parakeet (*Aratinga leucophthalmus*) and the dusky-headed parakeet (*Aratinga weddellii*), locally considered as agricultural pests, were also killed in large numbers using nets in corn and rice fields but were not considered in our analyses because they were not eaten.

Subsistence hunting showed a marked seasonality in the study area related to the scarcity of fish and agricultural products during the flood season, which forced local people to dedicate more time and effort to hunting activities. Furthermore, hunting is much easier when waters reach their highest levels because wildlife is concentrated in the few small areas that remain unflooded (restingas).

In general, subsistence hunters took significantly more birds during the flood season (November to May) than during the dry season (June to October) (Mann-

TABLE 21.1 Birds Consumed in Seventeen Rural Settlements of the Ucayali/Puinahua Floodplain During 1996

		HOUSEHOLDS		BIRDS	
LATIN NAME	COMMON NAME	N	%	N	%
Mitu tuberosa	Razor-billed curassow	129	66.49	382	5.75
Cairina moschata	Muscovy duck	107	55.15	481	7.24
Anhinga anhinga	Anhinga	106	54.63	484	7.28
Crypturellus undulatus	Undulated tinamou	89	45.87	740	11.14
Pipile cumanensis	Blue-throated pipin-guan	71	6.59	269	4.05
Phalacrocorax olivaceus	Olivaceous cormorant	68	35.05	657	9.89
Ardea cocoi	Cocoi heron	61	31.44	266	4.00
Tinamus major	Great tinamou	55	28.35	181	2.72
Aratinga leucophthalmus	White-eyed parakeet	54	27.83	832	12.52
Ortalis guttata	Speckled chachalaca	35	18.04	110	1.65
Ara spp.	Macaws	27	13.91	177	2.66
Columbidae[a]	Pigeons	26	13.40	139	2.09
Penelope jacquacu	Spix's guan	26	13.40	95	1.43
Ara severa	Chestnut-fronted macaw	25	12.88	266	4.00
Aratinga weddellii	Dusky-headed parakeet	23	11.85	933	14.04
Amazona spp.	Parrots	23	11.85	138	2.08
Aramus guarauna	Limpkin	22	11.34	54	0.81
Aramides cajanea	Gray-necked wood-rail	21	10.82	107	1.61
Crypturellus cinereus	Cinereous tinamou	15	7.73	52	0.78
Tigrisoma lineatum	Rufescent tiger-heron	11	5.67	31	0.47
Psophia leucoptera	Pale-winged trumpeter	8	4.12	21	0.32
Ramphastos spp.	Toucans	7	3.60	13	0.19
Pteroglossus spp.	Aracaris	7	3.60	7	0.11
Ceryle torquata	Ringed kingfisher	5	2.57	51	0.77
Anhima cornuta	Horned screamer	5	2.57	8	0.12
Cochlearius cochlearius	Boat-billed heron	4	2.06	40	0.60
Agamia agami	Agami heron	4	2.06	17	0.26
Icteridae[b]	Oropendolas	3	1.54	18	0.27
Odontophorus gujanensis	Marbled wood-quail	3	1.54	8	0.12
Crax globulosa	Wattled curassow	2	1.03	4	0.06
Graydidascalus brachyurus	Short-tailed parrot	1	0.51	20	0.30
Butorides striatus	Striated heron	1	0.51	15	0.23
Gymnomystax mexicanus	Oriole blackbird	1	0.51	15	0.23
Busarellus nigricollis	Black-collared hawk	1	0.51	3	0.05
Rosthramus sociabilis	Snail kite	1	0.51	2	0.03
Buteo magnirostris	Roadside hawk	1	0.51	2	0.03
Nothocrax urumutum	Nocturnal curassow	1	0.51	2	0.03

TABLE 21.1 Continued

LATIN NAME	COMMON NAME	HOUSEHOLDS N	HOUSEHOLDS %	BIRDS N	BIRDS %
Mesembrinibis cayennensis	Green ibis	1	0.51	2	0.03
Casmerodius albus	Great egret	1	0.51	2	0.03
Jabiru mycteria	Jabiru	1	0.51	1	0.01

Note: Sample size was 194 households. The number and percentage of households that consumed each species and the total number of individuals of each species consumed during the year are presented in the table. During our visits to the study area in 1997 and 1998, we recorded the use for food of six additional bird species: *Tinamus tao*, *Tinamus guttatus*, *Crypturellus soui*, *Porphyrula martinica*, *Jacana jacana*, and *Opisthocomus hoazin*.

[a] Includes *Leptotila rufaxilla* and *Columba* spp.

[b] Includes *Psarocolius angustifrons* and *Cacicus cela*.

TABLE 21.2 Estimate of the Number and Biomass of the Most Important Game Birds Consumed During 1996 in Seventeen Rural Settlements of the Ucayali-Puinahua Floodplain

	NUMBER		BIOMASS (KG)[a]	
	$\bar{x}$	C.I. 95%	$\bar{x}$	C.I. 95%
Mitu tuberosa	976	801–1,168	2,942	2,415–3,521
Cairina moschata	926	726–1,151	2,199	1,724–2,733
Anhinga anhinga	992	784–1,226	1,339	1,058–1,655
Crypturellus undulatus	1,059	792–1,368	601	449–777
Pipile cumanensis	559	417–709	712	531–903
Tinamus major	375	267–492	408	290–535
Phalacrocorax olivaceus	759	542–1,009	1,376	983–1,830
Ardea cocoi	475	342–625	1,077	775–1,417

Note: Only the eight species that were consumed by more than 25% of the 834 households (6,622 inhabitants) during 1996 are represented (see table 21.1 for the complete list of birds consumed). The $\bar{x}$ is mean, and C.I. the confidence interval.

[a] Masses (males and females averaged) reported for these species in Ayres et al. (1991), Ojasti (1993), and Peres (1997) were averaged and used in the calculations.

Whitney *U*-test, *U* = 0, P < 0.05). However, this seasonal pattern was not statistically significant in the case of waterbirds alone (Mann-Whitney *U*-test, *U* = 14.5, P > 0.05). The average number of terrestrial birds harvested monthly per hunter was 7.8 ± 2.5 (mean ± sd.) during the flood season and only 2.2 ± 1.7 in the dry season. In the case of waterbirds only 1.4 ± 1.2 and 1.1 ± 0.9 birds were harvested monthly per hunter in the flood and dry seasons, respectively.

All the species, except the olivaceous cormorant, were more abundant in the surveys conducted inside the protected area than in heavily hunted areas outside the reserve (table 21.3). However, the abundances (number of birds/10 km) of the most commonly hunted birds did not show significant differences between heavily hunted areas and areas where hunting pressure is low or even absent, except for the great tinamou (Kolmogorov-Smirnov tests, $P > 0.05$; table 21.3). The harvest model of Robinson and Redford (1991), applied to the most commonly hunted terrestrial birds, suggests that only the razor-billed curassow is being hunted at the maximum sustainable harvest rate (20% of the production), whereas current harvest rates of the other species are under the estimated maximum sustainable level (table 21.4).

BIRDS AS A SOURCE OF EGGS

Bird eggs are frequently consumed in the study site, especially in villages located close to breeding colonies. During 1996 I recorded the use of eggs of twenty-two species, of which the great egret (*Casmerodius albus*), cocoi heron (*Ardea cocoi*), boat-billed heron (*Cochlearius cochlearius*), and agami heron (*Agamia agami*) were the most commonly harvested. Eggs of these species were consumed in 11% of the households monitored (table 21.5). The greater ani (*Crotophaga major*), striated heron (*Butorides striatus*), great tinamou (*Tinamus major*), hoatzin (*Opisthocomus hoazin*), and horned screamer (*Anhima cornuta*) were also important sources of eggs for local people.

The use of heron eggs was monitored in the villages of Padre López and Nueva Cajamarca, where most of the egg harvesting took place. The collection of eggs is practiced almost every year by some households from these villages during the

TABLE 21.3 Abundance (Number of Birds/10 Km; x ± SD) of the Eight Most Commonly Hunted Bird Species in Heavily HUNTED Areas (Outside PSNR) and Lightly Hunted Areas (Inside PSNR)

		HEAVILY HUNTED	LIGHTLY HUNTED
Razor-billed curassow	*Mitu tuberosa*	1.77 ± 1.34	1.80 ± 0.97
Muscovy duck	*Cairina moschata*	1.43 ± 2.48	4.44 ± 6.35
Anhinga	*Anhinga anhinga*	2.84 ± 2.73	3.26 ± 3.89
Undulated tinamou	*Crypturellus undulatus*	2.67 ± 1.92	3.87 ± 2.17
Blue-throated pipin-guan	*Pipile cumanensis*	1.01 ± 0.97	2.32 ± 1.02
Great tinamou	*Tinamus major*	1.06 ± 1.12	5.23 ± 2.82
Olivaceous cormorant	*Phalacrocorax olivaceus*	25.40 ± 42.95	14.37 ± 13.25
Cocoi heron	*Ardea cocoi*	7.86 ± 8.95	10.70 ± 1.34

TABLE 21.4 Maximum Production and Maximum Sustainable Yield for the Most Important Terrestrial Game Birds

	DENSITY[a] (#/KM^2)	MAXIMUM PRODUCTION (#/KM^2)	MAXIMUM SUSTAINABLE HARVEST (#/KM^2)	CURRENT HARVEST (#/KM^2)	% OF PRODUCTION HARVESTED
Mitu tuberosa	5.28	1.88	0.38	0.38	20.05
Pipile cumanensis	4.43	1.97	0.39	0.21	10.52
Penelope jacquacu	2.69	1.20	0.24	0.07	6.13
Ortalis guttata	3.17	1.82	0.36	0.08	4.39
Tinamus major	25.28	39.06	7.81	0.14	0.36
Crypturellus undulatus	25.80	46.41	9.28	0.41	0.89
Crypturellus cinereus	1.35	2.43	0.49	0.04	1.57
Psophia leucoptera	2.03	0.63	0.13	0.01	2.02

Note: Estimates done using a conservative harvest model, compared with current harvest rates in the study area.

[a] The observed densities in areas of low/absent hunting pressure were used as a conservative estimation of densities at carrying capacity, except for *P. leucoptera* and *P. jacquacu* for which the maximum observed density was used.

TABLE 21.5 Bird Eggs Consumed in 101 Households of the Study Area in 1996

LATIN NAME	COMMON NAME	NO. OF EGGS	NO. OF HOUSEHOLDS
A. agami/C. Cochlearius	Agami/Boat-Billed Herons[a]	489	7
C. albus/A. cocoi	Great egret/cocoi heron[a]	360	4
Crotophaga major	Greater ani	167	9
Butorides striatus	Striated heron	94	4
Tinamus major	Great tinamou	86	7
Opisthocomus hoazin	Hoatzin	84	9
Anhima cornuta	Horned screamer	68	6
Crypturellus undulatus	Undulated tinamou	37	6
Pitangus sulphuratus	Great kiskadee	36	1
Cairina moschata	Muscovy duck	32	2
Other birds[b]		59	4

[a] Eggs of *Agamia agami/Cochlearius cochlearius* and *Casmerodius albus/Ardea cocoi* are collected, consumed, and sold together, so they were placed in the same category.

[b] Includes *Phaetusa simplex*, *Mitu tuberosa*, *Crypturellus cinereus*, *Leptotila rufaxilla*, *Crotophaga ani*, *Aramus guarauna*, *Aramides cajanea*, *Mesembrinibis cayennensis*, and *Ortalis guttata*

month of April in two large mixed-species heronries (an activity that is locally known as *garceada*).

The exploitation of eggs in the heronry at Padre López began in 1986. Since then, the heronry has moved three times from its position but has always remained close to its previous location. Local people report that up to six species of waterbirds bred in the heronry during the first years of exploitation (great egret, cocoi heron, boat-billed heron, agami heron, olivaceous cormorant, and anhinga), but only great egrets and cocoi herons were present during our study.

Eleven households of the village (33.3%) have participated at least once in the harvesting of heron eggs. The number of eggs taken during the study period ranged from 5,400 in 1996 to only a dozen in 1998 (table 21.6). Some of the eggs were consumed by the collectors and their families, but most were sold in the neighboring villages of Victoria and Obreros (ca. US$ 1 per dozen). The occasional hunting of chicks and adults from this colony was also reported by local people but did not occur during our study period.

At Nueva Cajamarca (inhabited by natives from the ethnic group Shipibo), nine households (52.9%) have participated in the collection of heron eggs in recent years. The number of eggs taken ranged from 780 in 1996 to 210 in 1998 (table 21.6). Most of these eggs were consumed by the collectors and their families. When harvesting eggs, Shipibo Indians practiced a traditional management technique of leaving at least one egg in each nest in the belief that this guarantees the permanence of the heronry in the same site the following year.

TABLE 21.6 Number of Heron Eggs Harvested in the Heronries at Padre López and Nueva Cajamarca Between 1996 and 1998

		HARVESTING GROUPS[a]	EGGS/TRIP/GROUP $\bar{x} \pm$ SD	TOTAL EGGS HARVESTED
Nueva Cajamarca	1996	7	77.9 ± 69.1	780
	1997	6	55.6 ± 30.7	445
	1998	4	52.5 ± 61.0	210
Padre López	1996	3	1,800.0 ± 1,039.2	5,400
	1997	3	700.0 ± 264.5	2,100
	1998	1	12	12

Note: $\bar{x}$ = mean.

[a] Each harvesting group was usually formed by two to three people.

MAGICAL, MEDICINAL, AND OTHER USES OF BIRDS

Several bird species were sometimes used in the study area for medicinal, magical, ornamental, or domestic purposes (table 21.7). The use of the crimson-crested woodpecker's beak (grated and macerated in alcohol) to strengthen virility and the use of macaw feathers as ornaments were the most frequently recorded practices. However, none of these uses is very widespread in the region since only three of the households (1.5%) stated that they hunt birds regularly for medicinal, ornamental, or other related purposes.

BIRDS AS PETS

At least thirty-three species of birds were kept as pets by local households in the study area. The most popular were the canary-winged parakeet (*Brotogeris versicolorus*), cobalt-winged parakeet (*B. cyanoptera*), tui parakeet (*B. sanctithomae*), orange-winged parrot (*Amazona amazonica*), festive parrot (*A. festiva*), yellow-crowned parrot (*A. ochrocephala*), and blue-and-yellow macaw (*Ara ararauna*).

There is also an important trade of these birds to neighboring large cities. Globally, 77.2% of the nestlings harvested by local collectors in 1996 were sold to middlemen, who brought them to the big markets of Pucallpa, Iquitos, or Lima. Of the households in the study area, 26.3% sold parakeets (*Brotogeris* spp.) in 1996, 18.5% sold parrots (*Amazona* spp.), 8.8% sold macaws (*Ara* spp.), and 4.1% sold other bird species. A total of 934 birds of fourteen species were sold during 1996 in the 194 households visited (table 21.8). Although parakeets were the most frequently sold pets, the orange-winged parrot, festive parrot, and blue-and-yellow macaw were the most important species in terms of gross profit.

Most of the harvesting and trade of parrots and macaws in the study area took place in the village of Victoria and its surroundings because of the near presence of

TABLE 21.7 Wild Bird Species Used for Ornamental, Medicinal, Magical, or Domestic Purposes in the Study Area

LATIN NAME	COMMON NAME	TYPE OF USE	PARTS USED
Eurypyga helias	Sunbittern	Magical (pusanga)[a]	Wing bone
Daptrius americanus	Red-throated caracara	Magical (pusanga)	Eye fluid
Campephilus melanoleucos	Crimson-crested woodpecker	Medicinal (virility)	Beak
Opisthocomus hoazin	Hoatzin	Medicinal (cough)	Meat
		Medicinal (virility)	Coccyx
Coragyps atratus	Black vulture	Medicinal (epilepsy)	Heart/Blood
Ara spp.	Macaws	Ornamental (adornment)	Feathers
Mitu tuberosa	Razor-billed curassow	Domestic (feather duster)	Feathers
Ramphastos spp.	Toucans	Magical (pusanga)	Tongue
Trogon spp.	Trogons	Medicinal (depilatory)	Fat
		Magical (pusanga)	Heart/brain
Herpetotheres cachinnans	Laughing falcon	Medicinal (snake bites)	Fat
Nyctidromus albicollis	Pauraque	Medicinal (birth)	Eggs

[a] Pusanga is a potion or an amulet used to attract the love of another person.

TABLE 21.8 Birds Traded as Pets in 194 Households of the Study Area During 1996

		NO. OF BIRDS SOLD		TOTAL INCOME[a]	
SPECIES	NO. OF SELLERS	N	%	S/.	%
Brotogeris versicolorus	45	497	53.2	507	9.6
Brotogeris cyanoptera	14	73	7.8	85	1.6
Brotogeris sanctithomae	20	151	16.2	382	7.2
Ara ararauna	10	40	4.3	981	18.5
Ara macao	6	12	1.3	343	6.5
Ara chloroptera	5	8	0.8	307	5.8
Amazona festiva	20	52	5.6	1,013	19.1
Amazona amazonica	11	52	5.6	883	16.6
Amazona ochrocephala	11	30	3.2	658	12.4
Amazona farinosa	4	6	0.6	90	1.7
Other species[b]	5	13	1.4	52	1.0

[a] Using the average prices paid by middlemen to local collectors (US$ 1 = S/. 3.5).
[b] Includes *Aratinga weddellii*, *Aratinga leucophthalmus*, *Graydidascalus brachyurus*, and *Mitu tuberosa*.

a large area of Mauritia palm swamps in which these species concentrate in large numbers to breed every year. We estimated that 79% of the macaws and 58% of the parrots traded to towns came from this part of the reserve. The harvesting of parrot and macaw nestlings is a major economic activity (locally called *loreada*) practiced by many people from Victoria every year between the months of February and April.

Between 1996 and 1999 I monitored the harvesting of parrots and macaws in two large Mauritia palm swamps (1,230 and 2,660 ha), located close to the village. Three species of parrots and four species of macaws were collected by local poachers (*loreros*) in these sites, the orange-winged parrot (61.1% of the captures) and the blue-and-yellow macaw (25.9%) being the most commonly harvested. The total number of nestlings taken during the four-year study period was 1,718, ranging from 680 birds harvested in 1996 to 166 in 1998. The number of households that took part in the loreada ranged from forty-two (45.2%) in 1996 to eighteen (19.3%) in 1998. The reasons for these changes probably relate to the presence of the researcher in the harvesting area and to the increasing number of birds confiscated by regional authorities, causing a reduction in the demand of nestlings (González 1999b).

Two methods were generally used to collect nestlings in the study site: cutting down the nesting tree (for species like macaws that nest very high) or hacking open the nest cavities in order to remove the chicks. Both methods are very destructive because nests become useless and the next generation is completely removed. Mortality during the harvesting process is another matter of great concern, especially when the collectors cut down the nesting trees. Overall, 229 of 1,142 nestlings died during the harvesting process (20.1%) in the study site. Mean mortality rates varied between parrots (3.2%) and macaws (29.2%). Figures were particularly high for the blue-and-yellow macaw (48.4% of the nestlings died during the harvest).

The red-bellied macaw, orange-winged parrot, and blue-and-yellow macaw were the most abundant species breeding in the studied swamps (mean of 19.1, 14.8, and 6.4 nests/100 ha, respectively). The nestling production (number of fledglings/successful nest) ranged from 1.35 fledglings/nest for the scarlet macaw to 2.33 fledglings/nest in the festive parrot. Overall productivity in the swamps was estimated with these data and compared with the average annual harvest rate for each species (table 21.9). Following the categories of Robinson and Redford (1991), parrots and macaws should be considered as long-lived species, for which a maximum sustainable harvest rate of 20% of the production can be assumed (Robinson and Redford 1991). In this case our data suggest that some species, like the red-bellied or the chestnut-fronted macaws, which have little demand, are being harvested under the maximum sustainable level, while other species, like the scarlet macaw, the blue-and-yellow macaw, and the orange-winged parrot are being overharvested and may be seriously threatened in the long term.

TABLE 21.9 Estimate of the Number of Nests, Total Number of Nestlings Produced, and Current Number of Birds Harvested Annually in the Mauritia Palm Swamps Located Close to the Village of Victoria

	ESTIMATED NO. NESTS[a]	PRODUCTION (NO. NESTLINGS)[a]	MAXIMUM HARVEST RATE (20%)	CURRENT ANNUAL HARVEST[b]
A. ararauna	249	379	75.8	111.5
A. macao	35	47	9.4	15.0
A. severa	89	169	33.8	7.8
A. manilata	742	1,485	297.0	10.5
A. amazonica	576	1,014	202.8	262.5
A. festiva	78	181	36.2	16.8
A. ochrocephala	17	31	6.2	3.5

[a] Average values recorded during the 1998 and 1999 nesting seasons.
[b] Average values recorded in the village of Victoria from 1996 to 1999.

DISCUSSION

HUNTING OF BIRDS FOR FOOD

The PSNR and its buffer zone provide local people with most of the resources they need to survive, including medicines, building materials, and food. Hunting in the study area is practiced mainly for subsistence. Game is used to satisfy the food needs of the hunter and his family, although sometimes the surplus may be sold in the village (Rodríguez, Rodríguez, and Vásquez 1995). The commercialization of game meat to large cities is banned. Peruvian laws (D.S. No. 934-73-AG/DGFF and D.S. No. 158-77-AG/DGFF) only permit subsistence hunting of some species of the Cracidae, Columbidae, and Tinamidae families. Despite the laws, our data shows that the range of birds used by local people in the study area is much wider and includes some species that may be endangered at the national level (CDC-UNALM 1993).

Soini et al. (1996) reported that people living in the PSNR or its surroundings use more than sixty animal species for subsistence hunting, including thirty mammals, twenty-five birds, and five reptiles. In this study we recorded the use of more than forty bird species, cracids, tinamous, and waterbirds being the most commonly hunted groups.

Cracids are traditionally considered the most important birds for subsistence hunting in tropical forests, and they are always present in the diet of all Amazonian rural settlements (Pierret and Dourojeanni 1967; Vickers 1991; Ojasti 1993). However, management of cracid populations is difficult because of their low capacity to recover from losses caused by hunting. As a consequence, cracids do not tolerate high harvesting rates, and their populations usually decline under continuous hunting (Silva and Strahl 1991; Vickers 1991). Some authors have pointed out that the best way to conserve these species is to give them total protection, at least until we have precise demographic information to determine the optimum harvesting rates (Dobson 1997). Others, however, argue that most of the cracid populations might tolerate some level of extraction, especially if hunting is in extensive areas surrounded by unhunted buffer populations (Silva and Strahl 1991; Begazo 1997).

Tinamous are the second most important group of game birds, the undulated tinamou being the most commonly hunted species in the study area. Tinamous are easily located by their sounds, which are imitated by hunters to attract the birds. Many undulated tinamous are also captured using a slip knot trap (*tuclla*) close to villages and agricultural fields.

Among waterbirds, the most important species in terms of biomass consumed is the muscovy duck. The hunting of this species is frequently associated with rice fields, where ducks concentrate to feed during the months of October and November when waters begin to rise and shallowly inundate these areas. Soini et al. (1996) reported a sharp decline suffered by whistling ducks (*Dendrocygna autumnalis* and *D. bicolor*) in the study area, suggesting that this decline may be related to the extensive use of pesticides in the rice fields where these birds forage. The effect of pesticides on muscovy ducks is unknown as there are no long-term data on this species. Experimental studies to assess this point are urgently needed. Olivaceous cormorants and anhingas are usually hunted with shotguns during fishing activities. Because of their foraging habits, these species are also frequently trapped in fishing nets.

The comparative method of assessing hunting sustainability, in which abundances or densities of species are compared between hunted and unhunted sites, depends on many problematic and often untested assumptions, such as similarity of habitat and constancy of all variables except hunting pressure (Robinson and Redford 1994; Bodmer and Robinson this volume). However, when long-term monitoring data are not available and an assessment must be made of hunting sustainability, the comparative method can be used as a good initial diagnosis of the effect of hunting on animal populations (Silva and Strahl 1991; Bodmer et al. 1994; Peres 1997).

My data suggest that most of the game birds are not being overharvested in the southern part of PSNR, although sample size may be too small and variances too high to extract definitive conclusions. The harvest model of Robinson and Redford (1991) also indicates that none of the terrestrial game birds are being overhunted in the study area, although the current harvest rate of razor-billed curassows is at the maximum sustainable level.

Vickers (1991) pointed out that, when human population density is low and rural settlements are dispersed, subsistence hunting can be practiced on a sustainable basis for most of the species used by Amazonian people. Furthermore, the effects of hunting may be reduced if the hunting occurs over extensive areas surrounded by unhunted buffer populations (Begazo 1997; Bodmer et al. 1997a).

Several reasons may contribute to the sustainability of bird hunting in the study site. First, in the southern part of PSNR hunting is only a secondary activity compared with fishing and agriculture, which are the main sources of food for local people (González 1999c). Second, hunting pressure in not continuous throughout the year and shows a clear seasonal pattern, increasing during the months of maximum flooding (February to April) but decreasing sharply during the rest of the year. Finally, because of the presence of a huge protected area, it is likely that unhunted populations from inside PSNR serve as a source of new individuals to repopulate overhunted areas, maintaining relatively stable populations of game birds in spite of hunting.

HARVESTING OF BIRD EGGS

Bird eggs are an important source of food in some areas (Cott 1954; Redford and Robinson 1991). Flamingo eggs are eaten in certain areas of the Andes of Bolivia and Chile (Campos 1986), collection of seabird eggs is a traditional practice in the Caribbean islands that dates back several centuries (Haynes 1987), and harvesting eggs by indigenous peoples from beach-nesting birds in the Peruvian Amazon is common (Redford and Robinson 1991). However, there are very few reports on the harvesting of eggs from mixed-species colonies of wading birds (heronries), and the impact of this harvest has rarely been evaluated (Feare 1976).

Thomas (1987) reports on the consumption of maguari stork (*Ciconia maguari*) nestlings in the llanos of Venezuela, and Luthin (1987) reports that wood stork (*Mycteria americana*) nestlings are consumed in Central America. Soini et al. (1996) observed the harvesting of cocoi heron nestlings from heronries in a small village in northeastern Peru. My data suggest that collection of heron eggs is a common activity, traditionally practiced by several native communities in some parts of the Peruvian Amazon.

While the harvesting of eggs of noncolonial nesting birds in the study area can be considered as occasional and probably has little effect on wild bird populations, the harvesting of eggs in heronries may have severe consequences because any negative impact to a breeding colony may affect a large proportion of the local population. Human activities are a major factor in the disturbance of colonial waterbirds (Ellison and Cleary 1978; Tremblay and Ellison 1979; Frederick and Collopy 1989). In some cases birds may abandon the site because of frequent human disturbance; in other cases the colony may persist but with lower reproductive success (Parnell et al. 1988).

The impact of human disturbance on local heronries is analyzed in González (1999a). All the evidence suggests that heronries in the study area are highly sensitive to human disturbance during early stages of nesting and that this disturbance may represent a major threat to local wading bird populations. In 1998 a group of hunters entering the colony at Padre López during egg laying caused the total abandonment of the heronry. Egg harvesting during early stages of nesting probably caused the abandonment of the colony at Nueva Cajamarca by agami herons.

Management of large water bird colonies for egg harvesting has proven problematic, and outright protection of the colonies may be the only way to prevent depletion (Feare 1976; Haynes 1987). Subsistence egg harvesting practiced on a small scale by people of Nueva Cajamarca for their own consumption seems to be less detrimental to herons than commercial egg harvesting practiced in Padre López. However, because of the great sensitivity of breeding herons to human disturbance during early stages of nesting, it is my opinion that heronries in the study area cannot be properly managed for long-term harvesting of eggs on a sustainable basis.

HARVESTING OF NESTLINGS FOR THE PET TRADE

The tradition of keeping wild animals as pets is quite common among people inhabiting the Amazon region (Redford and Robinson 1991). There is also a thriving export trade in wild animals for pets. No less than 150 animal species have been regularly exported as pets from the Amazon region, parrots and primates being the most important groups (Dourojeanni 1972).

In Peru a total of 1,958,000 animals were legally exported from Iquitos between 1965 and 1973 (before a national law banned the trade of Amazonian wildlife); 39% of these animals were psittacines and 4.9% other birds (Dourojeanni 1985). Prior to the enactment of the Wild Bird Conservation Act in 1992, documented U.S. imports of live birds since 1900 totaled nearly thirty million birds (WCI 1992). Although significant, these figures represent only a small fraction of the total number of birds removed from the wild because they do not include smuggled birds, birds dying during the capture and holding process prior to export, and birds sold in domestic pet markets (Iñigo-Elías and Ramos 1991; Thomsen and Mulliken 1992). Although there is a strong tradition in Neotropical countries of keeping birds in captivity, we lack detailed studies on the magnitude of the domestic cage-bird trade (Thomsen and Brautigam 1991)

My data show that, despite being banned by national laws since 1973, the harvesting and domestic trade of psittacines is still a common practice in the Peruvian Amazon. It is a matter for concern that large numbers of long-lived species (*Amazona* spp. and *Ara* spp.) are harvested every year in some parts of the PSNR. Because of their low reproductive rates, large, long-lived species cannot sustain high levels of exploitation (Munn 1988; Thomsen and Brautigam 1991; WCI 1992). The comparison of estimated production and current harvest rates in the village of Victoria showed that at least three species are being harvested over sustainable levels.

Several authors have explored in recent years the feasibility of sustainable harvest of wild parrot populations (Munn et al. 1991; Thomsen and Brautigam 1991;

Beissinger and Bucher 1992). As discussed by Beissinger and Bucher (1992), the sustainable harvest of certain species of parrots is biologically possible and could contribute to both habitat protection and the local economy. The social, political, and economic feasibility of sustainable parrot harvests, however, is still in question. As there are no documented examples of any sustainable harvesting project for the pet trade, Snyder, James, and Beissinger (1992) and WCI (1992) strongly recommended the implementation of pilot sustainable management projects, designed to test how different management techniques benefit the local communities and how effectively these techniques can be controlled. Because of the amount of information available and the willingness of collectors to participate, the palm swamps located close the village of Victoria offer a good opportunity to develop one such experimental project, intended to evaluate the biological, social, and economic sustainability of the harvesting of wild parrot and macaw nestlings.

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Patterns of Use and Hunting of Turtles in the Mamirauá Sustainable Development Reserve, Amazonas, Brazil

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Turtles have been, and continue to be, one of the principal sources of protein from the wild for indigenous and riverine populations in Amazonia. Pressure on the resource increased with the arrival of the first European colonizers, who exploited almost all species of Amazonian quelonians (Ayres and Best 1979). The most heavily exploited species was *Podocnemis expansa*, sought after for its size, its eggs, and the quality of its meat.

Several authors have reported on the exploitation of female turtles and their eggs, especially those in the genus *Podocnemis* (Bates 1863; Smith 1979a; Fachín-Terán 1994; Fachín-Terán, Chumbe, and Taleixo 1996; Rebêlo and Lugli 1996; Landeo 1997). Turtles are more vulnerable during their annual reproductive period than at other times, and the protection of eggs and nesting areas is considered a high priority. Turtle exploitation levels have been quantified and recorded through research projects of short duration (Bates 1863; Smith 1979a; Moll 1986; Polisar 1995; Fachín-Terán Chumbe, and Taleixo 1996; Thorbjarnarson, Perez, and Escalona 1997; Landeo 1997), but few studies have monitored the capture of Amazonian turtles (Rebêlo and Lugli 1996; Fachín-Terán, Vogt, and Thorbjarnarson 2000). In combination with data on harvest levels, long-term research projects describing the characteristics of turtle populations will enable us to evaluate the biological impact of current harvests.

Historically, populations of three species of *Podocnemis* that occur in the Mamirauá Sustainable Development Reserve (Reserva de Desenvolvimento Sustentável Mamirauá, or RDSM) were abundant. Bates (1863) reports that from this section of the Solimões River, in the neighborhood of Ega (present-day Tefé), and from the Madeira River, approximately forty-eight million *P. expansa* eggs were collected annually between 1848 and 1859 for exportation to Pará.

Pressure on the resource continues to this day, bringing *P. expansa* to the brink of extinction in this part of the Amazon. Interviews with the oldest inhabitants of the area indicate that populations of two other species in the genus, *Podocnemis unifilis* and *Podocnemis sextuberculata*, have also diminished drastically because of the continuous hunting pressure to which they have been subjected. In a recent assessment by the IUCN Freshwater Turtle and Tortoise Specialist Group, *P. unifilis*, *P. sextuberculata*, and *Geochelone denticulata* were placed on Appendix I of CITES as endangered species and *P. expansa* on Appendix II as a species at low risk but dependent on conservation (IUCN 1996).

Podocnemis expansa was placed on Appendix II rather than Appendix I because for the past twenty years it has been under an intensive conservation program by the Brazilian government. The program includes nesting beach protection and the release of over two million hatchlings per year into the wild. However, there is no scientific proof that this program is working, and in fact populations are diminishing within some of the protected reserves, notably Rio Trombetas. Throughout the remainder of its range in other countries, *P. expansa* populations have been drastically reduced (e.g., Peru; Soini 1997) and remain at high risk of local extinction.

The present study examined turtle hunting patterns in the RDSM. These patterns include species, number and size of individuals extracted, hunting methods and season, and habitats where turtles are most frequently captured.

METHODS

The study was carried out in the Jarauá sector of the RDSM. The reserve covers 1,124,000 ha between the Japurá, Solimões, and Auti-Paraná rivers, near the city of Tefé, Amazonas state, Brazil (03° 08′ S, 64° 45′ W, and 2° 36′ S, 67° 13′ W). Crampton et al. (this volume) give a detailed description of the reserve.

Information on species, number, sex, weight, method, habitat, and use of turtles was gathered in the communities of São Raimundo de Jarauá (2° 51′ S, 64° 55′ W), Nova Colômbia (2° 54′ S, 64° 54′ W), Novo Pirapucu (2° 53′ S, 64° 51′ W), and Manacabi (2° 50′ S, 54° 52′ W) through both interviews and direct observations. These communities were selected because they are located near turtle-nesting beaches and near lakes designated for preservation, personal use, or commercialization on the Japurá river and the Jarauá Paraná. Fifty families were interviewed on two occasions in these four communities, the first time between September 22 and October 12, 1996, and the second between November 17–18, 1997. All communities had few households and were therefore completely sampled. Data on turtle captures were collected from September 1996 to April 1998.

The consumption of turtles during the study period was identified based on the presence of ectodermal shields (Thorbjarnarson, Perez, and Escalona 1993). Species were identified using external shell characteristics. Carapace length was measured in a straight line at the point of greatest separation between the anterior and posterior edges (Medem 1976). Sex was determined by size, head color, carapace length, plastron shape, invagination of the anal plate, precloacal length, and thickness of the tail (Ponce 1979; Pritchard and Trebbau 1984) and in some cases by asking the interviewee if he had noted the gonads of the turtle before it was consumed. Turtles were weighed with spring scales.

Várzea ecosystems comprise a diversity of aquatic features and habitat types, many of which appear only seasonally. Often there are no direct, concise translations for the names of these unique habitats, and we use the local Portuguese language terms in the text. Here we give a brief description of these habitat types and also of terms that refer to changes in the hydrological cycle:

Enchente: rising water phase in the annual hydrological cycle

Vazantei dropping water phase in the annual hydrological cycle

Repiquete: temporary rises in the water level (oscillating water levels) that usually precede the main enchente. In the Central Amazon these oscillations usually occur around December and January; from February to April the water usually rises steadily.

Remanso: an eddy that occurs in little curved inlets along the edge of main river channels. These curved inlets are usually caused when a chunk of forest falls into the river (*terra caida*); the water flows into the new inlet and forms an eddy.

Restingas: levees in the floodplain.

Poças: ponds or static pools of water in the forest or sometimes on beaches, created by rainwater or when water is stranded in floodplain when water levels drop

Paraná: side branch of a main river channel that winds its way through the várzea floodplain. It is always connected at both ends to whitewater river.

Canos: channels that drain lakes in the várzea

Lagos: floodplain lakes

Enseada: outer curve of a meander or curve in a river where erosive processes are at their strongest. Remansos often form along the enseadas.

Ressaca: an inlet or branch to any water body (usually lake or channel) that dead-ends

RESULTS

COMMUNITIES STUDIED

São Raimundo de Jarauá is the largest and most important community in the Jarauá sector. It comprises eighteen houses with twenty families, who engage primarily in commercial fishing and who also practice subsistence farming. Turtles are captured in the Japurá river and in the paranás, ressacas, canos, and floodplain lakes of the Paraná do Jarauá Hydrological System. The high number of *P. sextuberculata* (n = 386) and *P. unifilis* (n = 177) registered for this community reflects the knowledge that community dwellers have of turtle behavior and of the areas where turtles occur.

Novo Pirapucu comprises nine houses and ten families. The community engages in both subsistence and commercial fishing activities and in subsistence agriculture. Its location near a *P. sextuberculata* nesting beach on the Japurá river explains the high consumption of females of this species (n = 37) by community members. During the 1996 nesting season, community members agreed to preserve 50% of the area of the beach in order to allow turtle researchers from the Mamirauá project to study the species reproductive biology (protection of the beach continued through 2002). This protection reduced the rate of capture of reproductive females in the area. In 2003 this community has offered to preserve 75% of the beach.

The community of Manacabi comprises nine families in nine houses and relies primarily on subsistence agriculture and subsistence fishing. Small turtle nesting beaches emerge during the dry season in the paraná that provides access to the community. In 1996 four *P. sextuberculata* and one *P. unifilis* females were captured there.

Nova Colômbia, with ten houses and eleven families, relies primarily on agriculture and less intensively on subsistence fishing. Of the eleven *G. denticulata* registered for this community, eight were captured in the restingas of the Paraná do Jarauá and three in the restingas of Nova Colômbia.

Through interviews and direct observations in the field, we were able to locate the carapaces of dead turtles. Members of the communities eat four species of quelonians (table 22.1), in the following order of importance: *P. sextuberculata* (66.6%, n = 447), *P. unifilis* (30.0%, n = 201), *G. denticulata* (2.8%, n = 19), and *Chelus fimbriatus* (0.6%, n = 4). Of 671 quelonians captured by community members, 655 (97.6%) were consumed, ten (1.5%) were sold, and six small individuals (0.9%) were kept to be raised in captivity.

TABLE 22.1 Species, Sex, and Number of Quelonians Consumed in Four Communities of the Jarauá Sector of the RDSM

	Podocnemis sextuberculata			***Podocnemis unifilis***			***Geochelone denticulata***		***Chelus fimbriatus***		
SITE	**M**	**F**	**N/D**	**M**	**F**	**N/D**	**M**	**F**	**M**	**F**	**TOTAL**
São Raimundo de Jarauá	210	130	46	84	85	8	3	3	1	1	571
Novo Pirapucu	12	37	0	0	10	0	0	0	0	0	59
Manacabi	4	6	0	0	7	0	2	0	0	1	20
Nova Colômbia	0	2	0	3	4	0	6	5	0	1	21
Total	226	175	46	87	106	8	11	8	1	3	671

Note: M is male; F, female; and N/D, not determined.

SPECIES AND SIZE

Two members of the Pelomedusidae family (*Podocnemis sextuberculata* and *P. unifilis*), one of the Chelidae (*Chelus fimbriatus*), and one of the Testudinidae (*Geochelone denticulata*) were recorded. There was variation in size and number of animals captured in each species. *Podocnemis sextuberculata* and *P. unifilis* showed sexual dimorphism in size, males being smaller than females (table 22.2).

CAPTURE METHODS AND SEASON

Of the 447 *P. sextuberculata* registered in the study, 363 were captured with gill nets in different aquatic habitats of the Paraná do Jarauá, and 45 females at nesting beaches. Of the 301 *P. unifilis* registered, 51 were captured with gill nets and 74 females were captured by probing in the mud of shallow lakes with a wooden pole. The eleven *G. denticulata* were captured by hand. One male and two female *C. fimbriatus* were captured with gill nets and one female with a harpoon (table 22.3).

Podocnemis sextuberculata is captured primarily during the dry season and when water levels begin to rise (start of the enchente) (fig. 22.1). Almost all size classes are captured during this period (fig. 22.2). During the nesting season in August, September, and October, individuals are captured by hand when they emerge to lay eggs on the beaches. Gill nets are used in the paranás and ressacas during temporary oscillations in the water levels in October and November and at the start of the flood season from December/January through March.

The size of the mesh influences the size classes of turtles captured with nets. Mid-sized males and females are most frequently caught with gill nets. This size

TABLE 22.2 Statistical Summary of Measurements of Quelonians Captured in the Jarauá Sector of the RDSM

		CARAPACE LENGTH (CM)				WEIGHT (KG)			
SPECIES	SEX	X	S.D.	Range	N	X	S.D.	Range	N
P. sextuberculata	M	20.7	1.9	11.1–24.4	162	0.9	0.2	0.17–1.4	160
	F	20.9	4.7	12.4–31.2	90	1.1	0.7	0.2–3.8	78
P. unifilis	M	21.6	5.8	7.6–31.0	68	1.5	0.8	0.06–3.3	46
	F	32.9	10.2	8.7–46.0	74	4.4	3.5	0.105–14	16
G. denticulata	M	44.4	3.6	39.3–50.3	9			9	1
	F	42.3	3.9	36.6–46.5	9	8.9	1.0	7.55–10	4
C. fimbriatus	M			29.2	1			3.3	1
	F			40.5–43.0	2			13	1

Note: M is male; F, female; X, mean; S.D., standard deviation; and N, sample size.

TABLE 22.3 Methods Used to Capture Four Quelonian Species in the Jarauá Sector of the RSDM

	Podocnemis sextuberculata			*Podocnemis unifilis*			*Geochelone denticulata*		*Chelus fimbriatus*		
METHODS	**M**	**F**	**N/D**	**M**	**F**	**N/D**	**M**	**F**	**M**	**F**	**TOTAL**
Gill net	217	106	40	31	20	1	0	0	1	2	418
By hand	0	45	0	2	31	1	11	8	0	0	98
Jaticá	1	15	0	0	3	0	0	0	0	0	19
Wooden pole	0	0	0	46	23	5	0	0	0	0	74
Harpoon	4	7	0	2	16	0	0	0	0	1	30
Diving	0	2	1	0	0	0	0	0	0	0	3
Drag nets	3	0	0	0	0	0	0	0	0	0	3
Unknown	1	0	5	6	13	1	0	0	0	0	26
Total	226	175	46	87	106	8	11	8	1	3	671

Note: M is male; F, female; N/D, not determined.

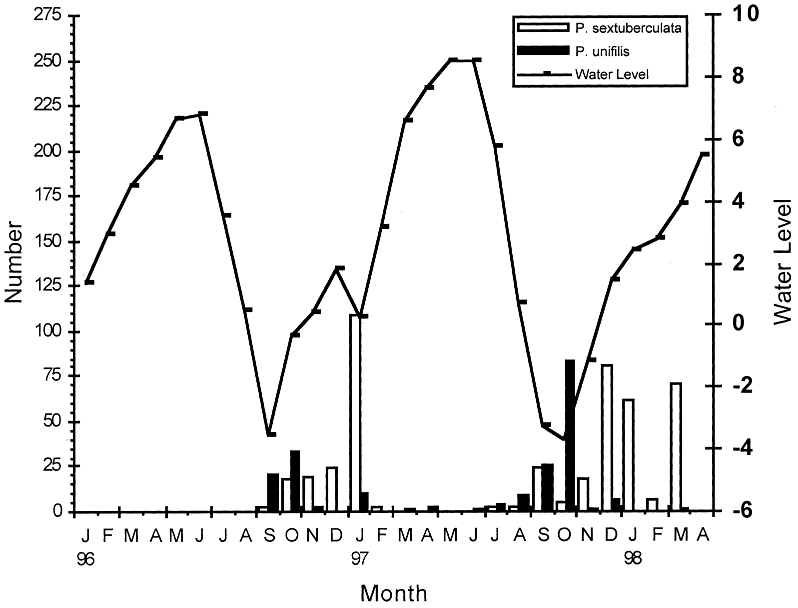

FIGURE 22.1 Capture of two species of *Podocnemis* in the Jarauá sector of the RDSM (Mamirauá Sustainable Development Reserve) with respect to water levels.

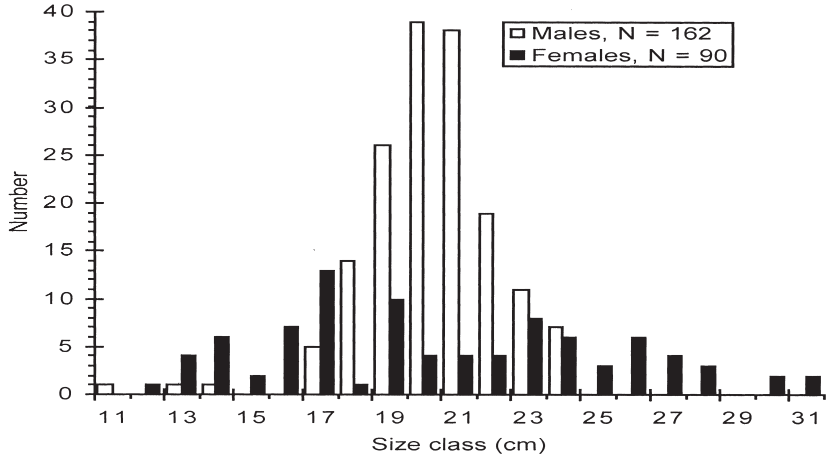

FIGURE 22.2 Size-Class distribution for *P. sextuberculata* captured in the Jarauá sector of the RDSM (Mamirauá Sustainable Development Reserve).

bias in net captures, which also occurs with the drag nets used in the remansos, has led to the popular local belief that the population contains many males and few females. Studies using Trammel nets indicated that gill nets used by fishermen are not efficient enough to capture the larger females, which are found in the deeper sections of the water channel where the current is weaker. As a result, a large portion of the adult population escapes capture.

During the dry season the *P. unifilis* population is concentrated in the canos and poças of the ressacas and lakes. In the 1996 dry season, adult males and females were the most common age class captured (fig. 22.3). Because of the concentration of the population in these habitats during the dry season, however, the potential exists for fishermen to capture animals of all sizes and of both sexes, as they did in October of 1997 (fig. 22.4).

Podocnemis unifilis is captured primarily with wooden poles (see below), with gill nets, by hand, and with harpoons. Capture with gill nets is occasional and occurs primarily when fishermen are seeking tambaqui fish (*Colossoma macropomum*). These nets have a stretched mesh size of 22 cm and do not capture hatchlings and juveniles.

Following the nesting season, *P. unifilis* females remain in canos and small pools with abundant macrophytes, burying themselves to a depth of about 20 cm in the mud until the water level rises again. Inhabitants of São Raimundo de Jarauá know this behavior, as well as the sites where *P. unifilis* can be found in the dry season from September to October. They have developed a searching technique that involves the use of a three-meter long wooden pole. They locate the buried turtle by the characteristic sound produced when the stick impacts on its carapace, then

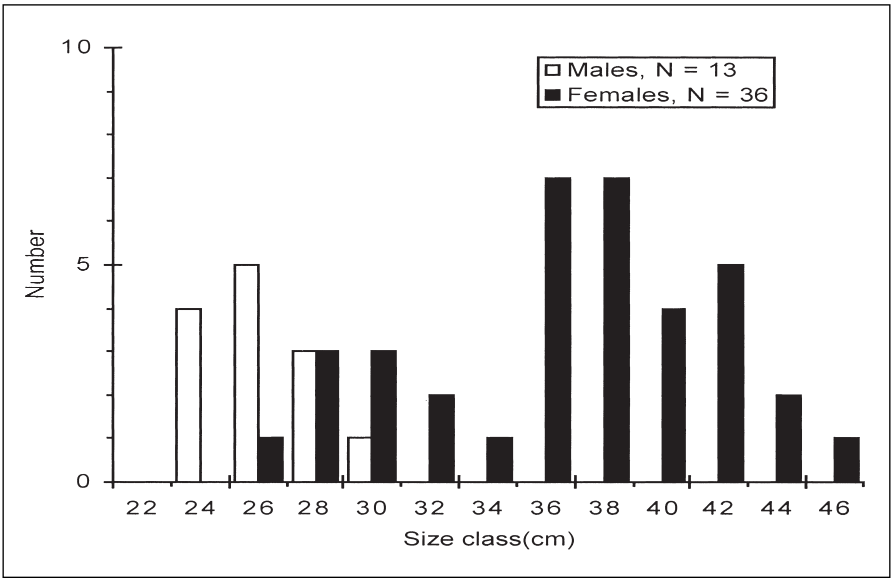

FIGURE 22.3 Size-Class distribution for *P. unifilis* captured in the Jarauá sector of the RDSM (Mamirauá Sustainable Development Reserve) from September 1996 through April 1997.

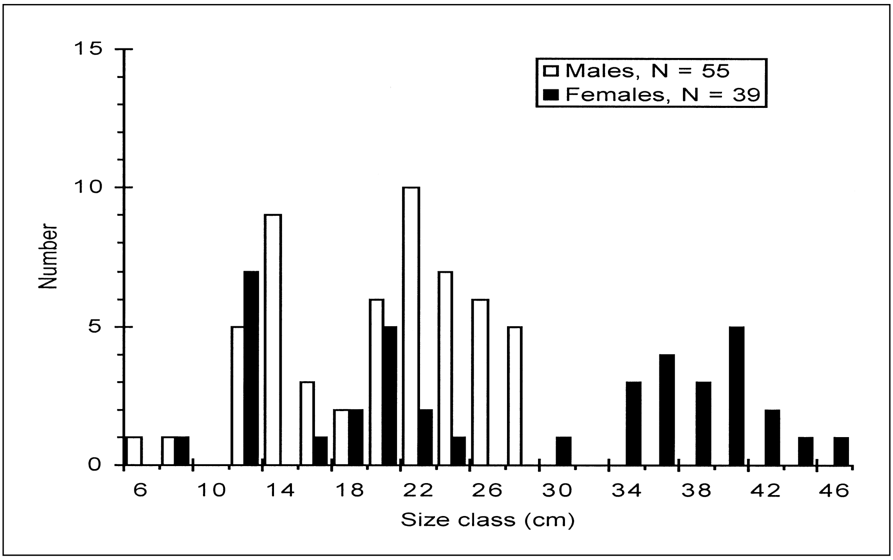

FIGURE 22.4 Size-Class distribution for *P. unifilis* captured in the Jarauá sector of the RDSM (Mamirauá Sustainable Development Reserve) from May 1997 through April 1998.

capture it by hand. Using this method, one community member captured twelve females in one day.

Additionally, individuals of *P. unifilis* swimming just under the surface of the water are identified by the size and shape of air bubbles visible at the surface and then captured with harpoon, *jaticá*, or by diving. A harpoon consists of a long pole with an iron tip secured to a strong line. The tip of the harpoon releases when it enters the prey but remains attached to the line, allowing the animal to be captured. The strike causes a small wound in the carapace but does not kill the animal. Harpoons with smooth, unbarbed tips are known as jaticás.

HABITATS WHERE QUELONIANS WERE CAPTURED

Podocnemis sextuberculata was captured primarily in ressacas (54.8%) and paranás (28.6%), while *P. unifilis* was captured most frequently in canos (37.8%), lakes (20.4%), and ressacas (18.9%). *Chelus fimbriatus* was also captured in three habitat types: paranás, ressacas, and canos. *Geochelone denticulata* was captured only in restingas (table 22.4).

DISCUSSION

HUNTING OF TURTLES

The three most sought-after genera of quelonians in Amazonia are *Podocnemis*, *Peltocephalus*, and *Kinosternon*. The genus *Podocnemis* includes six species, all ex-

TABLE 22.4 Habitats Where Quelonians Were Captured in the Jarauá Sector of the RDSM

	P. sextuberculata		*P. unifilis*		*Chelus fimbriatus*		*G. denticulata*	
HABITAT	N	%	N	%	N	%	N	%
Unknown			15	7.5			2	10.5
Ressaca	245	54.8	38	18.9	1	25.0		
Paraná	128	28.6	7	3.5	2	50.0		
River-Beach	43	9.6	12	6.0				
River-Remanso	15	3.4						
River-Enseada	7	1.6	8	4.0				
Lake	9	2.0	41	20.4				
Cano			76	37.8	1	25.0		
Restinga							17	89.5
Island			4	2.0				
Total	447	100.0	201	100.0	4	100.0	19	100.0

Note: Enseada is the outer edge of a meander or curve in the river.

ploited to varying degrees depending on local preference, but *P. expansa* and *P. unifilis* are the most favored for the preparation of several dishes considered to be delicacies (Alho 1986).

The capture of quelonians in the RDSM primarily provides food for local consumption. When *P. sextuberculata* and *P. unifilis* are captured in large quantities by professional fishermen outside of RDSM, however, it is always for commercial (illegal) purposes. These two species are also eaten in appreciable quantities in Itacotiara and other cities near Manaus, the capital of Amazonas State, with *P. unifilis* the most frequently consumed species (Smith 1979a; Santos 1996).

In the RDSM unsustainable exploitation of the Amazonian turtle (*P. expansa*) has virtually eliminated the species from the area. Quelonian hunting therefore focuses primarily on two species, *P. sextuberculata* and *P. unifilis*, which make up 96.6% of captures. Similarly, quelonian extraction in Jaú National Park focuses on three species: *Peltocephalus dumerilianus*, *Podocnemis unifilis*, and *P. erythrocephala*, which represent 95% of captures (Rebêlo and Lugli 1996). In Cinaruco-Capanaparo National Park, Venezuela, 100% of captures are of three species, *P. unifilis*, *P. vogli*, and *P. expansa* (Thorbjanarson, Perez, and Escalona 1997). In all three locations, populations of *P. expansa* are small, with isolated females nesting only when river levels are low. According to Rebêlo (1985), the 261 quelonians confiscated in Manaus and on the Purus, Negro, and Uatumâ rivers included four commercial species: *P. expansa*, *P. unifilis*, *P. sextuberculata*, and *Peltocephalus dumerilianus*. Of these four *P. sextuberculata* was the species most frequently sold on the Purus river (50%) and *P. unifilis* the most frequently sold in Manaus (63%).

SIZES OF CAPTURED TURTLES

All size classes of *P. sextuberculata* are affected by fishing because fishermen use a mesh size 10 or 15 cm in length. Furthermore, the entire animal is cooked, so consumption is independent of the size of the animal. On the other hand, capture of *P. unifilis* focuses primarily on adults, with females being the most affected. A similar pattern was observed by Thorbjarnarson, Perez, and Escalona (1993) on the Capanaparo River, Venezuela, where adult males and females are the most frequently captured size classes.

The smallest reproductive female *P. sextuberculata* recorded in this study, captured while egg laying at a beach on the Paraná do Manacabi, measured 26 cm. Vanzolini (1977) examined eleven *P. sextuberculata* from three rivers in the Brazilian Amazon and found that the smallest female containing eggs measured 27.1 cm. If 26 cm is the minimum reproductive size for the species, then 19% (n = 17) of the ninety females for which we obtained a carapace length were sexually mature. The proportion of adult females in samples is probably higher, given that we were unable to measure carapace length in 49% (n = 95) of the 175 captured females.

The mean size of *P. unifilis* females captured within the RDSM was smaller (X = 32.9 + 10.2 cm [mean ± sd.], n = 74) than that reported by Smith (1979) for Itacoatiara, Amazonas, Brazil, (X = 35.5 + 5.5 cm, n = 15) or by Thorbjarnarson, Perez, and Escalona (1993) for the Capanaparo River in Venezuela (X = 33.1 + 3.3 cm, n = 109). The largest sizes documented by any study for captured females are those reported by Fachín-Terán, Chumbe, and Taleixo (1996) for Pacaya-Samiria National Reserve in Peru (X = 41.0 + 3.0 cm, n = 145).

Of ten individuals of *P. unifilis* examined by Vanzolini (1977) in Brazil, the smallest female with eggs measured 33 cm. If this is the minimum reproductive size for the species, then 64% (n = 47) of the seventy-four females captured during this study for which carapace length was measured were above this size. This proportion may be somewhat larger because we could not measure carapace length for 30% (n = 32) of the 106 females captured. This number is still a smaller proportion than that reported by Thorbjarnarson, Perez, and Escalona (1993), who found that 82.6% of 109 females measured on the Capanaparo River in Venezuela were of reproductive age. An even higher value was obtained by Fachín-Terán, Chumbe, and Taleixo (1996) for Pacaya-Samiria in Peru, where 95% of females eaten in the communities that border the reserve were of reproductive age. These differences are due to the fact that animals of all sizes were captured at RDSM, while in the other studies, which report only large individuals of reproductive size, the turtles were apparently captured at the nesting beaches.

Mean carapace lengths of *Geochelone denticulata*, both for males (X = 44.4 + 3.65 cm, n = 9) and females (X = 42.3 + 3.97 cm, n = 9), were larger than those reported by Fachín-Terán, Chumbe, and Taleixo (1996) for Pacaya-Samiria in Peru, where mean carapace length for ten males was 36.5 + 5.6 cm and for nine females 32.4 + 11.3 cm. Capture of *G. denticulata* in the RDSM is occasional and can occur at any time of year.

CAPTURE METHODS AND SEASON

Podocnemis sextuberculata is primarily captured with gill nets. Fishermen near Itacoatiara use the same method, leaving their nets up overnight and capturing turtles as well as the targeted fish (Smith 1979a). In the dry season reproductive females are captured at night on the beaches of the Japurá and Solimões rivers in the RDSM. The same occurs near Itacoatiara (Smith 1979a).

Podocnemis unifilis is captured during the dry season in canos, lakes and ressacas, primarily using the wooden pole method and gill nets. A different pattern was reported for this species in the Itacoatiara area, where it is captured year round with *espinhel* (long line with multiple baited hooks) and with harpoons. Most captures occur during the season of rising water levels (May and June) when *P. unifilis* moves into the flooded forest to feed on flowers and fruits (Smith 1979a). The long line was also the method most frequently used to capture turtles on the Capanaparo river in Venezuela (Thorbjarnarson, Perez, and Escalona 1997). Harpoons are also used on the Orinoco river, Venezuela, to capture *P. expansa* during the rainy season (Ojasti 1971) and in Belize to capture *Dermatemys mawei* while it floats on the surface of the water (Moll 1986).

Podocnemis unifilis is also captured by hand at night when the females emerge to lay eggs on islands and lake margins (Smith 1979a). In the RDSM capture by hand is also accomplished at night during the egg-laying season when females emerge on the beaches of the Japurá and Solimões rivers.

Data gathered from twenty-one *extrativistas* (subsistence forest dwellers) from the lower and middle Jaú river, who capture primarily *Peltocephalus dumerilianus*, *Podocnemis unifilis*, and *P. erythrocephala*, suggest that 64% of stocked turtles were attracted with a bait of fish and captured with jaticá, 20% were caught with several types of baited hooks (float line, rod and line, and long line), and 15% were captured on land by ambushing (*viração*). *Geochelone denticulata* was captured during incidental encounters (Rebêlo et al. 1996). Polisar (1995) reported three techniques used to capture *Dermatemys mawei* in Belize: harpoon, net, and diving. Free diving is the most efficient of these techniques. When well organized, diving can lead to the almost complete removal of turtles from an area.

Although *Geochelone denticulata* is a preferred diet item, this species is captured only occasionally because, not nesting communally, they are usually hard to find. Santos (1996), however, reported an unusual incident whereby in one flood season one person captured about sixty animals at a small settlement in the Barroso sector of the RDSM. The water level that year was extremely high and the normally terrestrial tortoise was easy to spot floating in the flooded forest.

Chelus fimbriatus is only occasionally captured and is of less importance in the local diet than are *Podocnemis* turtles (Smith 1979a). Fachín-Terán, Chumbe, and Taleixo (1996) observed the same ranking in Pacaya-Samiria National Reserve in Peru, and this finding was confirmed for the RDSM in this study, in which *C. fimbriatus* was the least captured species. *Chelus* is uncommon in RDSM. Additionally, because of its strong musky odor, most people do not find it an attractive food item.

HABITATS WHERE QUELONIANS WERE CAPTURED

In the RDSM *P. unifilis* uses several microhabitats for reproduction but relies on the beaches of the Japurá River less than on reproductive sites on the margins of its lakes, ressacas, and canos. The majority of the population remains in these habitats until the next flood, making them vulnerable to predation by humans. In other portions of its range, such as Pacaya-Samiria in Peru and the Guaporé and Trombetas Biological Stations in Brazil, the species nests primarily on sand beaches that emerge along river edges, and for this reason females are captured more frequently than males (Fachín-Terán 1992; Soini and Coppula 1995; Soini and Soini 1995; Fachín-Terán, Chumbe, and Taleixo 1996).

Podocnemis unifilis uses lakes, ressacas, and the flooded forest during the enchente, while in the dry season the majority of the population remains buried in the mud of canos and pools that form in the ressacas. Such estivation behavior has not previously been reported for the species. One of us (RCV) observed this same behavior in December of 1990 when he collected forty-three specimens of *P. unifilis* at the Trombetas Biological Reserve. Estivation thus appears to be common but less predictable and probably less documented in areas with short dry seasons (Gibbons, Greene, and Congdon 1990). According to Vaillant and Grandidier (1910) and Tronc and Vuillemin (1973) (cited in Kuchling 1988), most *Erymnochelys* bury themselves in the mud during the dry season, even though the habitats they occupy are not completely dry.

CONSERVATION AND MANAGEMENT

Following the decline of *P. expansa* populations in Peru and Brazil, more pressure was placed on *P. unifilis*, *P. sextuberculata*, and *Peltocephalus dumerilianus* (Fachín-Terán, Chumbe, and Taleixo 1996; Vogt and Soini in press). The progressive substitution of large, valuable species by smaller species was confirmed in the RDSM. Here, *P. unifilis* and *P. sextuberculata* are more frequently consumed, especially the latter species, which is captured in large quantities by professional fishermen at different locations of the reserve and sold in the cities of Tefé and Alvarães. This trend in the exploitation of Amazonian turtles is reminiscent of that observed in the whaling industry, leading Mittermeier (1975) to characterize the aquatic quelonians of Amazonia as suffering from the whaling syndrome.

Factors contributing to the decrease in turtle populations in the reserve include lack of protection of nesting sites; capture of adult females and overharvesting of their eggs; artisanal and commercial fisheries in paranás, ressacas, canos, and lakes by both community dwellers and those commercial fishermen who carry out their activities within the area of the reserve; the commercial demand in urban centers; lack of control of illegal trade in urban centers; and loss of nests due to the repiquete. However, the most predatory hunting method, which causes the greatest harm to the population and which poses the greatest threat to reproductive animals, is the use of drag nets by professional fishermen and some community dwellers who capture large numbers of *P. sextuberculata* in river remansos. Using this method, one community member captured 130 individuals of the species in August of 1996 in the remanso of Praia Machado on the Solimões River. In 1997, in the same area and season, we only captured two males and two females during forty-eight hours of sampling. Similarly, Ojasti (1971) observed fishermen using drag nets to capture *P. expansa* in remansos of the Orinoco River.

To initiate the recuperation of quelonian populations in the reserve, a protection and management program accompanied by an environmental education program must be developed in the short term and with the agreement of the communities. Community leaders have already agreed during assemblies to forbid the use of gill nets, fence or encirclement nets (*redinhas*), and *arrastadeiras* (drag nets used along beaches) near turtle nesting sites. They also identified lakes and nesting sites that should be preserved in different locations of the reserve by prohibiting the capture of turtles, eggs, and hatchlings.

It is a priority to implement these agreements with the full participation of community members, who would thus help to protect the resource and would no longer represent a threat to the survival of these reptiles. According to Rebêlo and Lugli (1996), only the active participation of local inhabitants in the planning and implementation of a quelonian management plan will guarantee the success of the plan, as local peoples are both the problem and the long-term solution for large areas that require permanent inhabitants to protect them. Additionally, the Brazilian Agency for the Environment and Renewable Natural Resources (IBAMA) should invest greater effort in inspecting and monitoring turtle sellers and intermediaries in the trade.

To reduce the intentional capture of turtles, which is illegal in Brazil, it is necessary to apply our knowledge of species ecology (Alho 1985). There is a proven synchronization between the flood regime and nesting behavior. Therefore, in addition to protecting nesting and breeding sites, it is possible and essential to protect the migrating population and the migratory routes themselves as turtles move out of their aquatic habitats. This is the time when the population is most vulnerable to gill nets as they move through narrow river channels. In the river the reproductive population is vulnerable to drag nets because turtles are located in the remansos near the beaches. Hunting in these locations and seasons will negate any benefit derived from turtle protection in water bodies.

Captive breeding has been suggested as a way of minimizing illegal harvest of turtles in Amazonia (Alho 1985). Captive breeding may be a temporary salvation for some species that have reached the point were they are unable to survive in the wild. However, it is not recommend to spend money raising species in captivity when the funds are better spent on measures to prevent their extinction in the wild (Magnusson 1993). In várzea areas, where it is difficult carry out captive breeding for both socioeconomic and ecological reasons, other alternatives such as management in the wild should be implemented in agreement with local communities.

Podocnemis sextuberculata nesting sites in the Japurá and Solimões rivers should be identified and permanently protected, and the capture of the species should be temporarily forbidden. Some beaches should be completely protected, while others are managed by dividing them half and half into a protected section and a section that can be used for egg collection by local inhabitants. The lower beaches where nests are bound to fail should be considered as harvestable beaches. These actions should be coordinated between the personnel of the Mamirauá Project and the local communities. If natural predation and egg loss due to the repiquete and capture of juveniles are controlled, then high survivorships may be obtained.

Unlike *P. sextuberculata*, whose nests are concentrated on sandy beaches, *P. unifilis* nests on dispersed sites and uses a variety of substrates. Therefore it is crucial to identify *P. unifilis* nesting sites within the reserve and to protect them permanently from human interference during the dry season. Nest loss due to the repiquete should be minimized by translocation of eggs to sand beaches on the Japurá and Solimões rivers. Hatchlings should then be released at the site where eggs were collected.

Because of the risk of extinction faced by *P. expansa* in the reserve, all surviving individuals must be protected until the population recovers, a period that may occur in 80 to 120 years. Initially, the recovery of *P. expansa* populations can be aided by total protection of nesting beaches to prevent predation by humans and translocation of nests that are in danger of flooding by the repiquete. It may also be necessary to release into the reserve hatchlings of this species collected on nesting beaches farther upstream in the Solimões and Japurá rivers. The release of five to ten thousand PIT (Passive Integrated Transponder)-tagged hatchlings per year during ten years would serve as an experiment to determine the effectiveness of this technique.

Protective measures should be implemented year round. For now, we lack demographic data to determine whether areas such as the RDSM are sufficient to conserve quelonians in the Amazon basin (Santos 1996). The most basic information about the minimum area required to protect *Podocnemis* turtles is still unknown. In the Trombetas Biological Reserve all *P. expansa* nesting beaches are protected. However, once the reproductive season is over, the turtles move at least 65 km downstream to feeding sites, where they are often captured by fishermen (Moreira and Vogt 1990). In the RDSM the opposite situation exists: feeding areas are protected, but little effort is put into protecting nesting sites. Still, a new factor may soon alter this scenario. The Amanã Sustainable Development Reserve was created in 1997. Together with Jaú National Park and the RDSM, it makes up the Central Amazonian Ecological Corridor, which may enable the maintenance of genetically healthy populations with increasing recruitment rates.

This study shows that commercial sale of turtles is low in the communities. However, there is a substantial trade in *P. sextuberculata* in Tefé. Over 300 animals are sold every eight to ten days during the season of vazante and the start of the enchente. It is interesting to note that most animals sold are male *P. sextuberculata*. Capture for commerce takes place in the ressacas and remansos, primarily with gill nets and drag nets; the latter capture nearly all of the reproductive population. This finding was confirmed by our field observations, when in a remanso of the Piranhas beach, on the Solimões river, we captured 132 males and 19 females in forty-eight hours of sampling.

Individuals of *P. unifilis* from the Tefé, Japurá, and Juruá rivers are sold in Tefé. The few female *P. expansa* that emerge to lay eggs on the beaches of the Solimões and Japurá rivers are also captured for sale. Johns (1987) reported that local inhabitants of Tefé estimated that 300 *P. expansa* are sold annually. This number may be an underestimatation because some turtles are transported directly to Manaus. Santos (1996) recorded 400 *P. sextuberculata* unloaded at the Tefé market on one occasion. Smith (1979) estimated that 8,000 *P. unifilis* were captured annually in a 60-km radius around Itacoatiara; of these, about 6,000 were unloaded in Tefé and half of them were eventually sent to Manaus. Cooked *Podocnemis expansa* were still being served openly in restaurants in Tefé in September 2003 as part of the local noon luncheon buffet, along with other wild game (R. C. Vogt pers. obs.)

To preserve and make rational, sustainable use of this important resource, the following studies are needed in the short term: quantify and describe the *P. sextuberculata* and *P. unifilis* trade in Tefé and Alvarães; map the nesting beaches and their level of exploitation on the Japurá and Solimões rivers; and evaluate and monitor *P. unifilis* and *P. sextuberculata* populations in all of the RDSM. According to Calouro (1995), the effects of hunting on animal populations are not easily quantified because one must estimate both the hunting pressure to which the populations are exposed and their basic population parameters. In parts of the RDSM where turtles are captured by riverine communities and where commercial fisheries still take place, a long-term study is required to compare the population structure and densities in hunted and unhunted areas. This will allow us to determine whether populations decline because of exploitation and whether current hunting patterns are efficient. This information will serve as a base from which we can design strategies for the recovery and management of turtles in the RDSM, so that they may continue to provide a source of food for its inhabitants.

ACKNOWLEDGMENTS

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23

Fisheries, Fishing Effort, and Fish Consumption in the Pacaya-Samiria National Reserve and its Area of Influence

SALVADOR TELLO

Fisheries in the Peruvian Amazon constitute an important source of animal protein and of income for *ribereño* people (local inhabitants who live alongside rivers in várzea ecosystems). Fish is the principal component of family diets, and the overall fisheries yield is approximately 80,000 tons per year (Bayley et al. 1992), representing an contribution of about US$ 80 million per year to the regional economy. In the Peruvian Amazon the largest volumes of fish originate in the lower reaches of the Ucayali and Marañon rivers, where the Reserva Nacional Pacaya-Samiria (RNPS) is located. Named for the two rivers that run through its territory, the RNPS has a surface area of 2,156,770 ha and covers portions of the provinces of Loreto and Requena in the Loreto region.

Despite the importance of fish in the region, to date we lack detailed information that will allow us to answer key questions about the factors that affect the fisheries. The current study contributes information necessary to improve planning and orientation of sustainable use of fish resources. It does not attempt to present all information pertinent to the fisheries linked to the reserve because that would require data on captures, effort, and consumption for communities located in the interior of the reserve and in the buffer zone. Although this study obtained data on overall fish consumption in several ribereño communities, more information is needed on fish consumption patterns and preferences.

METHODS

CATCH AND CATCH PER UNIT EFFORT

Information was obtained by means of direct interviews carried out between April 1994 and February 1995. Four experienced field assistants were hired and trained as data collectors in the cities of Iquitos, Requena, and Nauta. Additionally, the volume of fish exported from the RNPS and its buffer zone to Iquitos, Pucallpa, and Yurimaguas were estimated on the basis of information provided by the Ministry of Fisheries, whose technicians collect daily information on the provenance of fish landings at these cities.

To obtain information on amount of fish caught, fish landed at the ports were recorded daily according to their method of preservation, species, and source area. Weights of fresh salted and dry salted fish were converted to fresh weight using the factors 1.8 and 2.5, respectively. The number of trips, number of fishermen in the trip, number of days spent fishing, and number of casts (line or net) were recorded to estimate fishing effort for the commercial fishery fleet in Iquitos, Nauta y Requena. Data were collected daily by the field assistants as each vessel arrived in port when fishermen opened their coolers to sell their catch. This procedure enabled identification of the catch to species.

Information was also collected on a daily basis on cargo and passenger vessels that cover the routes to Iquitos, Pucallpa, Yurimaguas, Requena, and Nauta. These vessels mainly transport salted fish, and they carry a detailed registry of the amounts transported.

INTERVIEWS ON FISH CONSUMPTION

In addition to the sampling in the ports, in the cities of Nauta and Requena we carried out household interviews to determine the amount of fish consumed. In Nauta (8,548 inhabitants) interviews were carried out daily during the study period because of the population size, while in Requena (14,690 inhabitants) interviews were carried out ten days per month, with the days selected using a random numbers table. Data on fish consumption in Iquitos were already available from government sources.

Data collection was designed using street maps at scales of 1:500 and 1:2,500 for Nauta and Requena, respectively. Each household was numbered on the maps. Since each map was composed of three sheets that divided the cities into three zones, we considered these divisions as blocks for statistical analyses. These blocks correspond to zones located at differing distances from the river; in each zone households are also characterized by different socioeconomic indicators. In each block we randomly selected houses, allowing for replacement houses in case we were unable to complete interviews at the selected houses.

LOCATION OF FISHING AREAS

The origin of each catch was noted on the data sheets, allowing us to locate precisely fishing areas using a 1:4,000,000-scale map. We measured distances from the fishing areas to Iquitos on the Fotocarta Nacional (scale of 1:100,000) prepared by the Instituto Geográfico Nacional (National Geographic Institute). To classify fishing areas as within the reserve, within the buffer zone, or outside the buffer zone, we used as a reference the RNPS Master Plan (Plan Maestro de la RNPS; COREPASA 1986), which defines the buffer zone as a 5-km wide strip around the protected area. Data on capture and fishing effort where analyzed with FoxPro 2.6 (Microsoft Corporation 1989-1994), while data on fish consumption were analyzed with StatPac (Statistical Analysis Package, version 5.2; Walconick 1985).

RESULTS

CHARACTERISTICS OF THE FISHERY

Three classes of fishery can be distinguished in the study area, differentiated by the final destination of the catch. Subsistence fishing is carried out by ribereños as a daily activity for self-sustenance. They use canoes or small boats, along with nets, primarily gill nets, of various mesh sizes and lengths. During seasons when fish are plentiful, the uneaten excess catch is salted, dried, and sold to an intermediary, who accumulates fish to supply markets in larger cities such as Iquitos, Pucallpa, and Yurimaguas. Dry salted fish is carried by both cargo and passenger vessels that cover these routes.

Local commercial fishing is carried out daily by fishermen from medium-sized cities, such as Requena and Nauta, in order to supply these urban centers with fresh fish. Fishermen have moderate-sized boats powered by 9 to 16 HP engines known as *peque-peque*; these are stationary motors adapted with a long extension for navigation in shallow areas. They use *honderas*—medium sized nets with a stretched mesh size of two inches—and frequently depart on fishing trips in the afternoon, returning at sunrise on the following day.

Regional commercial fishing supplies fresh fish to large cities such as Iquitos, Pucallpa, and Yurimaguas. The fishing fleet is comprised of vessels of varying size and design which frequently fish at large distances from the port of origin and cross regional boundaries. Vessels use very large hondera nets of two-inch stretched mesh size and are equipped with iceboxes, allowing them to remain out of port for an average of 30 days.

STATISTICS ON FISH LANDED

A total of fifty species of fish were sold in the markets of Iquitos, Pucallpa, Yurimaguas, Requena, and Nauta (table 23.1). The number of species is actually larger because often a single name is used for more than one species of fish. Five species essentially sustain the fisheries, making up 80% of the catch. The *boquichico* (*Prochilodus nigricans*) alone makes up 40% of the catch (table 23.2).

In the Peruvian Amazon the *paiche* (*Arapaima gigas*) can be legally sold from April to September, while its sale is prohibited from October to March. Despite this restriction, fishermen find ways to land their catch in places of difficult access

TABLE 23.1 List of Fish Captured by the Commercial and Subsistence Fleets in the Study Area

COMMON NAME	LATIN NAME	FAMILY	ORDER
Arahuana	*Osteoglossum bicirrhosum*	Osteoglossidae	Osteoglossiformes
Paiche	*Arapaima gigas*	Arapaimidae	Osteoglossiformes
Pez torre	*Acestrorhynchus* sp.	Characidae	Characiformes
Sábalo cola roja	*Brycon erythropterum*	Characidae	Characiformes
Sábalo cola negra	*Brycon melanopterus*	Characidae	Characiformes
Palometa	*Mylossoma* sp.	Characidae	Characiformes
Gamitana	*Colossoma macropomum*	Characidae	Characiformes
Paco	*Piaractus brachypomus*	Characidae	Characiformes
Paña	*Serrasalmus* sp.	Characidae	Characiformes
Sardina	*Triportheus* sp.	Characidae	Characiformes
Huapeta	*Hydrolicus scomberoides*	Cynodontidae	Characiformes
Chambira	*Raphiodon vulpinus*	Hemiodontidae	Characiformes
Yulilla	*Hemiodus* sp.	Hemiodontidae	Characiformes
Shuyo	*Erythrinus* sp.	Erythrinidae	Characiformes
Fasaco	*Hoplias malabaricus*	Erythrinidae	Characiformes
Boquichico	*Prochilodus nigricans*	Prochilodontidae	Characiformes
Yaraquí	*Semaprochilodus* sp.	Prochilodontidae	Characiformes
Ractacara	*Curimata* sp.	Curimatidae	Characiformes
Chío chío	*Psectrogaster* sp.	Curimatidae	Characiformes
Llambina	*Potamorhina altamazonia*	Curimatidae	Characiformes
Yahuarachi	*Potamorhina latior*	Curimatidae	Characiformes
Lisa común	*Schizodon fasciatus*	Anostomidae	Characiformes
Lisa	*Leporinus* sp.	Anostomidae	Characiformes
Turushuqui	*Oxydoras niger*	Doradidae	Characiformes
Bocón	*Ageneiosus* sp.	Ageneiosidae	Siluriformes
Saltón	*Brachyplatystoma filamentosum*	Pimelodidae	Siluriformes
Dorado	*Brachyplatystoma flavicans*	Pimelodidae	Siluriformes
Manitoa	*Brachyplatystoma vaillanti*	Pimelodidae	Siluriformes
Zúngaro alianza	*Brachyplatystoma juruense*	Pimelodidae	Siluriformes
Mota	*Gallophysus macropterus*	Pimelodidae	Siluriformes
Achara	*Leiarus marmoratus*	Pimelodidae	Siluriformes
Cunchi	*Pimelodella* sp.	Pimelodidae	Siluriformes
Doncella	*Pseudoplatystoma fasciatum*	Pimelodidae	Siluriformes
Tigre zúngaro	*Pseudoplatystoma tigrinus*	Pimelodidae	Siluriformes
Zúngaro mama	*Paulicea lutkeni*	Pimelodidae	Siluriformes
Shiripira	*Sorubim lima*	Pimelodidae	Siluriformes
Tabla barba	*Goslynea platynema*	Pimelodidae	Siluriformes
Maparate	*Hypophthalmus* sp.	Hypophthalmidae	Siluriformes
Shirui	*Hoplosternum* sp.	Callichthydae	Siluriformes
Carachama	*Pterygoplichthys multiradistus*	Loricariidae	Siluriformes
Shitari	*Loricariichthys* sp.	Loricariidae	Siluriformes

TABLE 23.1 Continued

COMMON NAME	LATIN NAME	FAMILY	ORDER
Corvina	*Plagioscion* sp.	Sciaenidae	Perciformes
Bujurqui	*Satanoperca jurupari*	Cichlidae	Perciformes
Tucunaré	*Cichla monoculus*	Cichlidae	Perciformes
Acarahuazú	*Astronotus ocellatus*	Cichlidae	Perciformes
Añashúa	*Crenicichla* sp.	Cichlidae	Perciformes

TABLE 23.2 Fresh Fish Captured by the Commercial Fishery and Landed in the Study Area in 1994

SPECIES	TONS	% OF TOTAL
Boquichico	1,036	43.7
Llambina	284	12.0
Palometa	278	11.7
Chio-Chio	166	7.0
Lisa	124	5.2
Other	480	20.4
Total	2,368	100.0

where there is no legal control. On the basis of our daily samples, we calculated that sixteen tons of paiche were landed in Requena alone in 1994. Of this amount, 62% was caught in the reserve and 38% in the buffer zone.

We estimated the total catch landed by the commercial fishery in 1994 in Iquitos, Yurimagua, Requena, and Nauta at approximately 19,000 tons of fresh fish (table 23.3). Of this tonnage about 27% came from the interior of the reserve, 13% from the buffer zone, and 60% from sites outside the protected area. These results allow us to state unequivocally that the RNPS is an important area for the regional fisheries.

FISHING AREAS

The Iquitos commercial fleet fishes in different rivers, depending on the abundance of fish. During this study vessels operated in the Amazonas, Ucayali, Marañon, Napo, and Nanay rivers. Close to 57% of fish landed in Iquitos came from the lower Amazonas, making it the most important source of fish that year.

TABLE 23.3 Fish Catch Landed in 1994

LOCATION UNLOADED	SOURCE AREA RNPS Reserve	 Buffer Zone	 Outside Reserve	TOTAL
Iquitos	1,388	252	2,231	3,871
Requena	485	367	87	939
Nauta	284	58	91	434
Pucallpa	1,633	712	3,841	6,216
Yurimaguas	1,201	1,052	5,024*	7,277
Total	5,021	2,441	11,274	18,737

Note: Catch is in tons and is categorized by source area and location of sale. Fresh salted and dry salted fish are converted to fresh weight using the factors 1.8 and 2.5, respectively.
*Includes fish transported from Iquitos.

TABLE 23.4 Most Important Fishing Zones in the Study Area, Frequented by the Commercial Fleets of Iquitos, Requena, and Nauta

FISHING AREA	APPROXIMATE DISTRIBUTION (KM)	CATCH IN TONS	% OF TOTAL
Ucayali river	**1,390**	**80.4**	
Requena	262	400	23.8
Tipishca	262	198	11.5
Curahuaytillo	260	83	4.8
Pucate	280	70	4.1
Carocurahuayte	316	69	4.0
Yuracocha	172	64	3.7
Contamanillo	256	62	3.6
Huarmi Isla	300	60	3.5
Montebello	580	60	3.5
Machín Tipishca	580	52	3.0
Marañon river		**335**	**19.4**
Sarapanga	152	131	7.6
Nauta	136	62	3.6
Shiriyacu	160	24	1.4
San Pablo Tipishca	212	10	0.6

The commercial fishing fleets of Requena and Nauta fish with more frequency in the Ucayali and Marañon rivers, with the most important sites located in the RNPS and its buffer zone (table 23.4; fig. 23.1). The largest catches came from the main river channels, where fishermen take advantage of fish migrations.

The Ucayali is the most important river basin with respect to fish production,

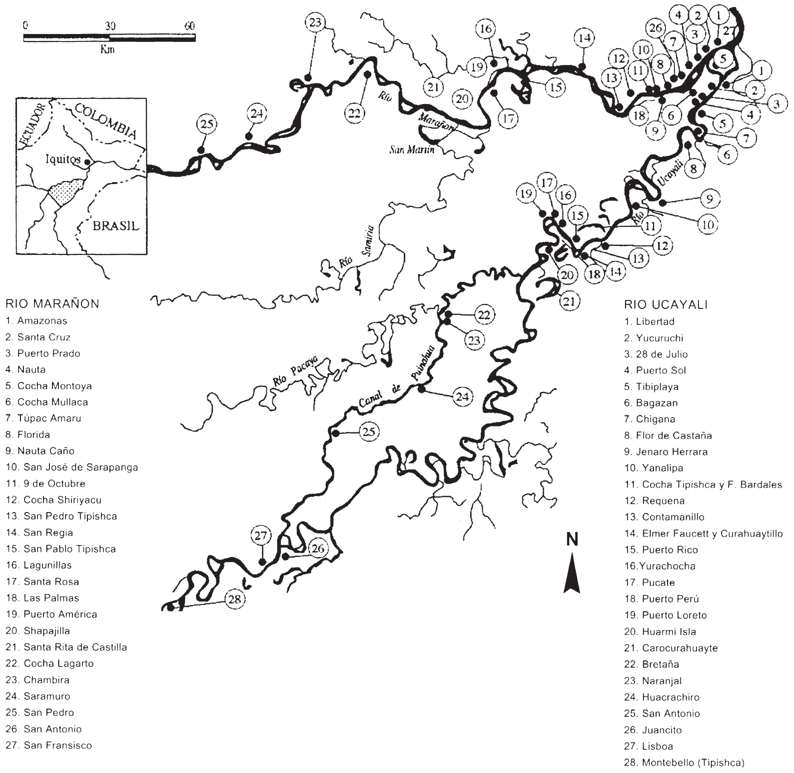

FIGURE 23.1 Fishing zones on the Ucayali and Marañon Rivers in the RNPS (Reserva Nacional Pacaya-Samiria) study area.

providing 80% of captures recorded for the entire study area. At least 70% of the dry salted fish that were landed in Pucallpa originated in the Puinahua channel, a tributary of the Ucayali, which itself is the main route for the stocking and transporting of fish extracted from the reserve.

ESTIMATING CATCH PER UNIT EFFORT

Because there is a lot of variation in vessel type and fishing methods among and within the different fisheries, we calculated the coefficient of variation to select the most representative measure of effort among all the measures recorded (number of net casts, days spent fishing, number of crew members, total catch, etc.). For Iquitos number of fishermen was the best measure of effort because the index of kg/fisherman had the lowest coefficient of variation of all possible indices. Number of casts (number of times a net is set or thrown) was not considered as a reliable measure of effort because fishermen do not remember with any precision the numbers of times they used a net. Unfortunately, there is no system by which this information is registered during daily fishing tasks. The number of trips carried out also does not represent an adequate measure of effort because of the huge variability in the storage capacity of the different vessels that make up the Iquitos fleet.

For Requena and Nauta the choice of an index was more easily made because the boats, fishing methods, number of fishermen, and days spent fishing show little variation within the fleet. For this reason we chose number of trips as the unit of measure and kg/trip as the index of catch per unit effort.

On the basis of the selected indices of catch per unit effort, the greatest fish abundance for the Iquitos fleet occurred in May and June, and the most important fishing sites were in the lower Amazonas river (table 23.5). For Nauta and Requena the largest catches occurred in August and September, coinciding with the highest indices of catch per unit effort (table 23.5). The largest catches occurred during the migrations when fish move out of the flooded area with the receding water levels and become concentrated in the main river channels.

FISH CONSUMPTION AND FISHERIES YIELD

Using as a reference data on fish consumption provided by the Instituto Nacional de Estadísticas (National Institute of Statistics; INEI 1972, 1993), we estimated the supply and demand of fish inIquitos. The INEI gives a per capita consumption of 20.4 kg of fish per year, which multiplied by the population of that time (225,000 inhabitants), gives a demand of 4,590 tons of fresh fish per year. According to our study, an average of 354 tons of fish are landed each month in Iquitos, representing a total of 4,250 tons per year. Commercial fishing thus satisfies 92% of the fish demand, with the remaining 8% supplied by subsistence fishing carried out near Iquitos, an activity not measured in this study.

To analyze supply and demand in the RNPS and its buffer zone, we estimated the per capita consumption of fish in Requena and Nauta based on our interview

TABLE 23.5 Mean Catch Per Unit Effort (CPUE) Per Boat During 1994 for Commercial Fisheries

	MONTHS									
SITE	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan
Iquitos[a]	540.0	556.0	578.0	536.0	524.0	537.0	639.0	542.0	504.0	522.5
Requena[b]	86.5	114.2	179.0	205.6	138.9	236.0	116.5	72.8	91.7	56.7
Nauta[b]	161.2	117.6	183.0	218.0	281.0	165.6	118.3	141.0	98.4	76.5

[a] CPUE = Kg/fisherman.

[b] CPUE = Kg/trip.

TABLE 23.6 Per Capita Fish Consumption in Requena and Nauta

	INDICE	
SITE	Gr/person/day	Kg/person/year
Requena	215	78.6
Nauta	327	119.5

data (table 23.6). For rural areas we used the value of 55.8 kg/person per year estimated by Tello (1993) and based on data collected by IIAP (Instituto de Investigaciones de la Amazonía Peruana) in nearly fifty communities in the RNPS. The estimated fish consumption in Requena and Nauta was 1,152 and 1,029 tons, respectively, while for the rural areas it was 2,905 tons, for a total of 5,000 tons.

Thus the total amount of fish landed by the commercial and subsistence fishery fleets at Iquitos, Pucallpa, Yurimaguas, Requena, and Nauta, together with the dry salted fish carried in passenger and freight vessels to the different cities, is nearly 7,800 tons, of which 66% originates in the RNPS and 34% in its buffer zone. If we add to this figure the amount consumed by local populations, we arrive at a total annual catch of more than 12,800 tons. On the basis of the above proportions, approximately 8,500 and 4,300 tons of fish per year are extracted from the RNPS and the buffer zone, respectively. To summarize, 12,800 tons of fish are caught in the RNPS and its zone of influence per year, 5,000 tons are consumed locally, and 7,800 tons are exported.

Using the percentages and amounts estimated by this study and combining them with fish consumption by local communities, we can estimate the total commercial catch for the area, including catches derived from areas outside of the RNPS and its influence zone, such as the Amazonas, Juanache, Tapiche, and other rivers. Figure 23.2 illustrates the dynamics of the fisheries and fish trade for the entire study area, including the amount of fish consumed in each community and the final destination of exported catches.

In his estimate of the yield of fisheries in the 520,000 km^2 of the Peruvian Amazon that lie under 270-m altitude above sea level, Hanek (1982) determined that 75% of the volume of the total catch is captured by subsistence fisheries and 25% by commercial fisheries. Using these proportions, if the approximately 19,000 tons of commercial catch estimated by the present study (fig. 23.2) represent 25% of the total catch, then subsistence fisheries contribute an additional 57,000 tons (75%), for a total of 76,000 tons caught in the study area. The fish yield calculated in this study (76,000 tons) is very similar to that of the 80,000 tons calculated by Bayley et al. (1992), who used as a reference for his calculations Hanek's 1982 value of 277 grams/day per capita consumption and a 3.1% growth rate of the population.

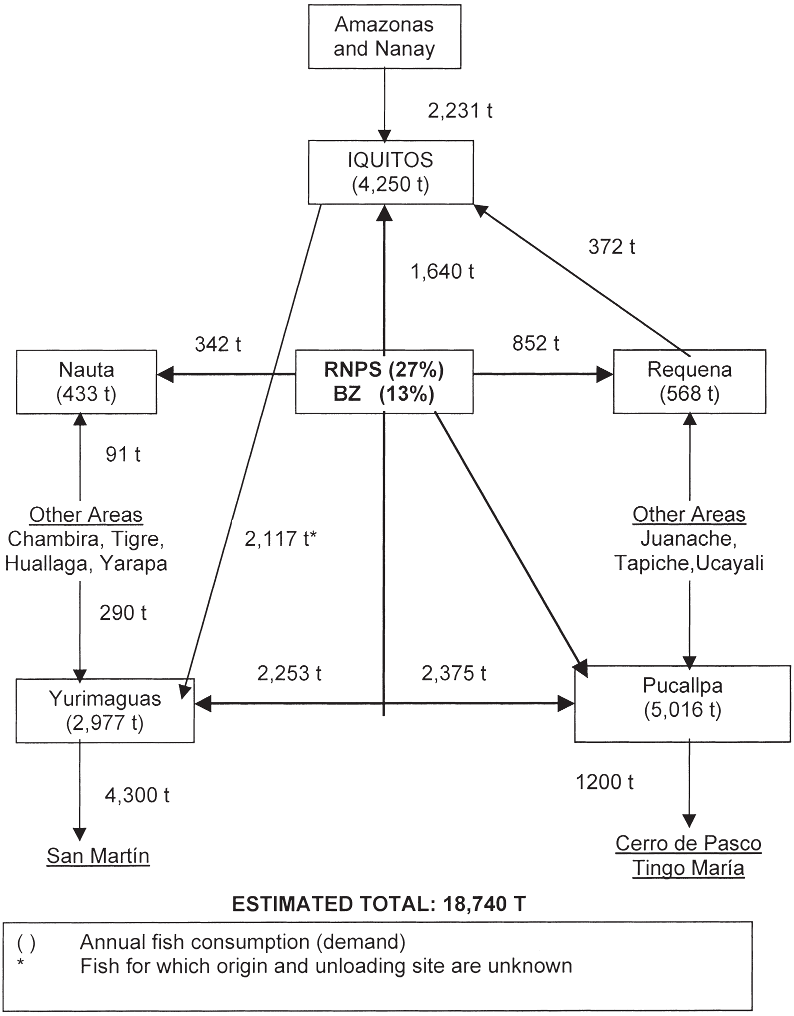

FIGURE 23.2 Diagram showing flux of catch landings. BZ = Buffer Zone of the Reserve.

DISCUSSION, CONCLUSIONS, AND RECOMMENDATIONS

In flooding river systems fish productivity, migrations, and populations dynamics are profoundly influenced by interactions between physical, chemical, and biological characteristics, including flooding regimes, extent of flooded area, water temperature, and pH. These factors are in turn influenced primarily by environmental and geographical issues, which themselves vary among sites and seasons. Therefore it is not an easy task to develop fisheries evaluation and management programs. Studies carried out in the last two decades indicate that the simplest approach is to obtain capture and effort data (Petrere 1978a,b; Welcomme 1985; Bayley and Petrere 1989; Montreuil and Tello 1990; Montreuil et al. 1997). These two parameters are used to calculate an index of catch per unit effort, which when recorded for a determined length of time, allows an evaluation of the abundance of the resource (Ricker 1975). One of the great limitations in the Peruvian Amazon is the lack of adequate data on catch per unit effort, making it difficult to compare our effort and production values with those of previous years. Also, it will be difficult to carry out future comparisons if this work is not continued.

In the catches landed in the study area, large species are being replaced with smaller species of high yield and low price because of increases in fishing intensity and changes in fishing methods. This selective process results from the preference by fishermen and consumers for large species in combination with the susceptibility of large species to high mortality levels from fishing (Welcomme 1985). When fishing efforts intensify, larger species are overexploited and progressively replaced in biomass by smaller, shorter-lived species that are better able to withstand intensive extraction due to their high production/biomass indices (Regier and Henderson 1973; Turner 1985; Lowe McConnell 1987).

Changes in species composition have occurred in many flooded river systems. Novoa (1989) noted a reduction in the mean size of catfish and in the proportion of captures made up of large catfish in the Orinoco. Similarly, Bayley and Petrere (1989) found evidence of the disappearance of such large species as *Colossoma macroponum* and *Arapaima gigas* in catches of the Manaus fishing fleet, in Brazil.

Despite these changes in catch composition and the size reduction noted for some species, I agree with Bayley (1992) in the assessment that, as long as there are no drastic changes in environmental conditions (caused by the construction of dams, for example), fish resources in the Peruvian Amazon will not fail, and the human population will continue to benefit from them. The continued decrease in fishing stocks is caused more by indirect human activities than by fishing activities. For example, deforestation leads to significant changes in aquatic systems, including increases in daily temperature fluctuations; higher turbidity because of sediment outflow from the clear-cut area; decrease in areas available for dispersal, shelter, and reproduction; and abnormal changes in the water levels. All of these conditions negatively affect the development of fish populations.

Significant catches result when fishermen take advantage of fish migrations. Local fishermen indicate that the migrations that sustain the local commercial fisheries in Nauta and Requena frequently originate inside the RNPS. This finding again highlighting the ecological importance of this area. There are few studies of migrations in the Peruvian Amazon. We know that there are two main types: one for reproduction and one for trophic purposes. Reproductive migrations take place in relatively short periods, and their importance for fish catches is minimal. On the other hand, migration in search of feeding areas can be lengthy—Goulding (1979) calculates that some species cover 450 kilometers—and are more important for fish supplies in the study area. Water level is the most important of several key environmental factors influencing the migratory behavior of tropical species. Fishermen believe that rainfall and lunar cycles also affect the timing of characin migrations (Goulding 1979). Information on these migrations, along with records of the hydrological regime and monthly precipitation at strategic sites on the Ucayali, Marañon, Pacaya, and Samiria rivers, would be of great value for the sustainable management of the fisheries in the study area.

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Implications of the Spatial Structure of Game Populations for the Sustainability of Hunting in the Neotropics

ANDRÉS J. NOVARO

Harvest theory has been built almost entirely on assumptions of uniformly distributed populations (Beddington and May 1977; Walters 1986; Caughley and Sinclair 1994). Most natural populations, however, are spatially structured, and this structure has profound effects on the dynamics of the populations and, consequently, on their responses to hunting (Kareiva 1990; Hanski and Gilpin 1997). Harvest theory therefore must be revised to incorporate spatial structure, and the resulting models need to account for the spatial heterogeneity of populations and their environments.

The spatial heterogeneity of hunted game populations in the Neotropics has begun to be analyzed explicitly only in recent years (Hill and Padwe 2000; Novaro, Redford, and Bodmer 2000). This lack of previous analyses may be because of the lack of comprehensive demographic data on game populations and in particular on the spatial variation of hunting in this region. The importance of spatial heterogeneity of hunting also has been recognized for wildlife populations in other regions where spatial data are scarce: African forests (Fimbel, Curran, and Usongo 2000; Hart 2000) and savannas (Owen-Smith 1988). Spatial heterogeneity has long been suggested, although not incorporated into harvest models, as a relevant factor in the dynamics of game in regions where data are more abundant (Pyrah 1984; Bergerud 1988; Knick 1990; Slough and Mowat 1996).

In this paper I first review the processes that can structure populations in ways that are relevant to the sustainability of game hunting. Then I discuss the approaches that are being used to account for the spatial structure of game when evaluating hunting sustainability and consider some of the limitations of these approaches. Finally, I suggest some topics for research, discuss difficulties of identifying game spatial structure, and present a model to incorporate the effects of one type of spatial structure on the population dynamics of game when demographic data are scarce.

SPATIALLY STRUCTURED POPULATIONS

Game populations can be spatially structured naturally or as a result of human activities. Nonhuman factors that structure populations range from naturally fragmented habitats to spatial heterogeneity in habitat quality that produces local differences in reproduction and/or mortality rates. These local differences in turn may be due to interspecific interactions (including availability of food, competitors, predators, and pathogens) and availability of refuge or breeding sites (Pulliam 1996; Tilman and Kareiva 1997). Human activities that can structure populations, on the other hand, include habitat transformation, degradation, and fragmentation (Hanski and Simberloff 1997) and hunting itself when it is spatially heterogeneous (Novaro, Redford, and Bodmer 2000).

Whether caused by natural or human-related processes, a wide range of patterns of spatial structure in populations has been described (Kareiva 1990; Hanski and Gilpin 1997; Tilman and Kareiva 1997). There is a continuum of probable patterns of spatial structure between totally structured and continuous populations. Spatial structure can involve discrete, more-or-less isolated subpopulations separated by an unsuitable matrix and connected by dispersal, or continuous populations without discontinuities in distribution but with spatially specific demographies (Hanski and Simberloff 1997). In the former case a series of subpopulations may function as a metapopulation of different types(e.g., classical or mainland-island) if dispersal allows for recolonization of habitat patches where subpopulations have gone extinct. If the rate of dispersal is high, the subpopulations are likely to function as a population with a patchy distribution (Harrison 1991). If dispersal is low and does not allow for recolonization, the structure is termed a nonequilibrium metapopulation, and the fate of each subpopulation is independent of the others.

Continuous populations can also be heterogeneous and have spatial structure if there are habitat-specific differences in mortality or reproduction. Both in the case of discrete and continuous populations, differences in mortality and reproduction between habitats or patches can determine that rates of local population increase (r; in the absence of immigration) may be larger or smaller than zero. Local populations with r's larger and smaller than zero have been termed sources and sinks, respectively (Pulliam 1988; Hanski and Simberloff 1997). In the absence of migration from nearby sources, sink populations will go extinct. Local populations that have low productivity and densities that will decline in the absence of migration but that do not necessarily go extinct are called pseudosinks (Watkinson and Sutherland 1995). Finally, as one of the many possible combinations, the type of spatial structure in which discrete metapopulation patches act as sources or sinks (depending on their quality) has been termed a source-sink metapopulation (Hanski and Simberloff 1997).

Hunting of a population that has any of the types of spatial structure mentioned above (or any combination of different types) has implications for its dynamics and its probability of persistence. In the rest of the paper I will refer mostly to metapopulations and source-sink populations because they are two models that have been considered in more detail. It is important to bear in mind, however, that most real game populations are likely to have spatial structures that are combinations of these or other types of structures.

EVALUATIONS OF THE SUSTAINABILITY OF HUNTING AND SPATIAL STRUCTURE

Different studies have used diverse methods to evaluate the sustainability of game hunting or to propose ways to increase the likelihood of sustainability. Some have assumed homogeneous populations, particularly in areas such as the Neotropics where demographic and spatial data are scarce, whereas others have begun to consider the spatial structure of these populations. In this section I will describe the sustainability analyses that have been done to date, assuming different types of spatial structure, including no structure, and considering some of the limitations.

Until the early 1990s the sustainability of hunting was evaluated mostly using sustainability indices. These indices (reviewed by Robinson and Redford 1994) included population trends of hunted species and comparisons of age structures and hunting yields across time and space. They allowed only a measure of relative levels of sustainability (Bodmer and Robinson this volume). By including comparisons among sites, however, it became evident that there were marked differences in the intensity of hunting across space and that these differences could have implications for the regional dynamics of game populations.

During the 1990s several evaluations of hunting sustainability were published using sustainability models. These models are used to estimate population production at a site with data on densities and reproductive rates (Bodmer 1994) or to estimate maximum population growth with data on reproduction (Robinson and Redford 1991) and on survival (Slade, Gomulkiewicz, and Alexander 1998). Estimations of population production or growth are then compared to harvest rates that are estimated at a specific site in order to determine if harvest is sustainable. These models have been applied for the most part assuming that all of the recruitment into game populations came from reproduction within the harvested area. The models have been useful in many cases and have been applied widely (Robinson and Bennett 2000c; earlier studies reviewed by Robinson and Bodmer 1999). These authors and others, however, have found inconsistencies between model predictions and actual population trends or harvest rates, and many of them have attributed these inconsistencies to potential dispersal of game from nearby sources into harvested areas (Alvard et al. 1997; Robinson and Bodmer 1999; Hill and Padwe 2000).

Another approach to estimating hunting sustainability has been to apply the models mentioned above while attempting to incorporate the potential effect of dispersal from adjacent and presumed sources of game. This approach estimates the current harvest for a combined area that includes the harvested area plus adjacent, potential sources that may be producing immigrants to repopulate the harvested area. The current harvest for the combined area is then compared to the maximum population growth (calculated with Robinson and Redford's method) in order to evaluate hunting sustainability. This approach was used by Townsend (1995a) and by Hill and Padwe (2000) to evaluate hunting by the Sirionó in Bolivia and the Aché in Paraguay, respectively. The approach uses the models developed for homogeneous populations but assumes that hunting creates a system of sources and sinks. It then tries to account for this heterogeneity by extrapolating the harvest pressure to the entire source-sink area

One of the limitations of this approach is that if dispersal of game between the sources and the hunted areas can not compensate intense hunting levels, local extinction can occur. Other limitations are that the nature and location of source areas are assumed, but not known, and that source areas may be different among game species, depending on the species's different dispersal abilities.

During the last decade Joshi and Gadgil (1991) and McCullough (1996) began to consider more explicitly the effect of spatial structure of populations on the sustainability of hunting. Joshi and Gadgil described a system of protected and hunted areas created by indigenous people in India through trial and error. The researchers conducted simulations to evaluate the population implications of the presence of unhunted sources of game. McCullough, on the other hand, proposed the implementation of a similar trial-and-error system to designate a mosaic of refuge areas within a continuous population (spatial control). By monitoring the total harvest and by changing the number of hunted and refuge areas, it is possible to maximize the harvest without risking overexploitation.

More recently, Novaro, Redford, and Bodmer (2000) suggested that many of the hunted systems that have been studied in the Neotropics may be source-sink systems because hunted areas often are adjacent to large lightly hunted or unhunted areas. These authors proposed combining the methods of Joshi and Gadgil and McCullough, modified an equation given by Joshi and Gadgil to account for stochasticity, and showed its use to estimate the proportion of sink area that could be harvested at an unregulated rate without risking an overall population decline.

These methods do not require much field data or enforcement of quotas, and they are more conservative than quota systems because they maintain refugia that are free of hunting. One of the limitations of the modified method proposed by Novaro, Redford, and Bodmer is that it only allows estimation of the maximum size of sink area that can be completely overharvested. This area is very small for most species, so it is perhaps too conservative to be practical.

McCullough (1996) also evaluated the potential effects of harvest on metapopulations. He concluded that the likelihood for sustainability of hunting of metapopulations is low because hunting reduces the dispersal between subpopulations, increasing their likelihood of extinction. This conclusion is crucial because many game populations in the Neotropics and in other regions occur in increasingly fragmented habitats (Cullen et al. this volume). Game species that evolved in relatively continuous habitats may have been able to tolerate high harvest rates in continuous or naturally fragmented habitats in the past. These same species, however, may now experience rapid local extinction of subpopulations and eventual regional collapse in anthropogenically fragmented habitats in which the distances between patches and the nature of the matrix between patches drastically reduce or preclude dispersal. Unfortunately, it may not be enough to state that sustainability of hunting of game metapopulations is unlikely. Harvest of these game metapopulations will continue because enforcement in regions with poor social and economic conditions is weak or nonexistent and because social and economic pressures are not likely to decline. In the next section I offer some general recommendations to begin to evaluate the ecological implications of harvest in metapopulations.

Finally, in a simulation study of the effect of harvest in spatially structured populations, Lundberg and Jonzén (1999) analyzed the optimal harvesting strategies for a source-sink population, evaluating equilibrium densities, yield, and stability under different harvest options. Lundberg and Jonzén considered subpopulations that had intrinsic differences in their dynamics (population growth surplus in the source and dependence on immigration in the sink) regardless of the level of hunting. Conversely, in the studies mentioned previously (Hill and Padwe, 2000; review of earlier studies in Novaro, Redford, and Bodmer 2000), the sinks may be created by the heterogeneous distribution of hunting. Lundberg and Jonzén's main conclusion, as expected, was that the decision as to whether or not to harvest the source and/or the sink would greatly influence density, yield, and stability of the entire population, three factors that are crucial for sustainable harvest and conservation. The authors concluded that harvesting the sink always produces the highest yields and that harvesting is destabilizing (measured by the range of parameters that produces stable populations) under all conditions. Populations with intermediate growth rates that are harvested only in the sinks, however, are more resilient (measured by the time needed to return to initial conditions) than those in which the source is harvested and are even more resilient than unharvested populations.

Lundberg and Jonzén provide an equation with which to estimate optimal harvest rate in sinks. This equation, however, requires knowledge of dispersal rates between sources and sinks, among other variables, which are difficult to estimate (Novaro, Redford, and Bodmer 2000). Another limitation of Lunberg and Jonzén's analysis, which the authors point out, is the difficulty of identifying source and sink subpopulations that are caused by natural heterogeneity. I discuss this difficulty in more detail in the next and the last section.

EVALUATING THE EFFECT OF SPATIAL STRUCTURE

HARVEST OF METAPOPULATIONS

As indicated above, McCullough concluded that the likelihood of sustainable hunting in metapopulations is low, but increasing fragmentation of habitats in underdeveloped regions may determine that more and more game populations will occur as metapopulations. In areas where hunting of these populations is likely to continue, it is crucial whenever possible to carry out research that can produce information useful in predicting its effects and that can increase its chances of sustainability. The effects of harvest on naturally occurring metapopulations, on the other hand, also are unknown and equally important to understand. Naturally occurring metapopulations may have evolved in naturally fragmented habitats but are not necessarily more likely to withstand harvest because of their population characteristics (i.e., dependence on dispersal for recolonization) and probable alteration of the matrix between patches by anthropogenic changes. Important aspects that need to be researched are

1. the combined effects of fragmentation and hunting on game dispersal, which are likely to be synergistic;
2. the effects of harvest on the extinction probability at the patch and landscape levels;
3. the effects on connectivity (ease of game movement) of different degrees of development of the matrix between habitat fragments;
4. the community- and ecosystem-level effects of game harvest in metapopulations; that is, removal from or reduced dispersal of key species among habitat patches may have negative effects at the patch and landscape level;
5. the potential benefits of harvesting subpopulations of species that are likely to have detrimental effects on their habitat in certain patches (McCullough 1996).

Novaro, Redford, and Bodmer (2000) reviewed some of the empirical methods available for the study of game dispersal. Because of the difficulties of field studies on dispersal of medium-sized and large vertebrates, a combination of empirical data and simulations may be most useful, particularly for population-level processes. This combination may allow predictions and management recommendations more rapidly than from field studies alone and would permit avoiding experimental evaluations that are impractical. Long-term monitoring of harvest of metapopulations would enable scientists and managers to review and update structured population models and to correct management recommendations.

IDENTIFICATION OF GAME SOURCES IN SOURCE-SINK SYSTEMS

Harvest of source-sink populations is more likely to be sustainable than harvest of metapopulations. As for metapopulations, unfortunately, lack of field data and knowledge of processes and mechanisms involved in the harvest of source-sink populations also limit the ability to predict and make management recommendations for these populations.

One important limitation for research and management of source-sink populations that are hunted is the difficulty of identifying sources and sinks. Identification is fairly simple when there is relative homogeneity of habitat, and sources and sinks are produced by the spatial distribution of hunting. In this case, if hunting is intense, hunted areas are likely to be sinks. If sources and sinks occur naturally as a result of local differences in habitat quality, the identification of each type of subpopulation is not trivial. Furthermore, the small size of some source areas can complicate their identification. Even in regionally stable populations, theoretical (Howe, Davis, and Mosca 1991) and empirical studies (reviewed by Pulliam 1996) have shown that sources can be relatively small in area as compared to sinks.

Population density is one of the variables most commonly studied for game populations. Density is often used as an indicator of the sustainability of hunting at a site and sometimes as an indicator of habitat quality. However, there are important limitations in the use of density as an indicator. In areas where hunting is spatially heterogeneous, for example, low density at a site may not necessarily mean that hunting is unsustainable and that the regional population is being overharvested. This lack of correlation was shown by Hill and Padwe (2000) in the Mbaracayú reserve of eastern Paraguay where the Aché hunt. Game densities are low in the vicinity of the Aché village where most hunting takes place, but harvest levels of most species have not declined through time, probably because of immigration from a large, lightly hunted portion of the reserve.

The problem with the use of density levels to identify the location of game sources is perhaps more disturbing. The density level at a site is a poor indicator of habitat quality and thus of the potential source or sink condition of the site, as has been shown empirically and theoretically (van Horne 1981; Watkinson and Sutherland 1995; Pulliam 1996; Lundberg and Jonzén 1999). Population densities in natural sink habitats can often be high because they receive large numbers of dispersers that are forced to leave source areas as a result, for example, of territoriality by source residents. Source populations, conversely, can be very productive and may be able to supply a constant surplus of individuals to sinks, but they may still have low density levels. In other words, low game density in an unhunted area does not mean that this area cannot act as a game source.

Considering the limitations of density as an indicator, it could be misleading to suggest to managers that game sources that need protection should be expected to have high densities (Bennett and Robinson 2000b; Robinson and Bennett 2000c). If only areas of high density are protected, managers may end up protecting sinks and losing small and more sparsely populated sources. The establishment of game reserves in sinks may be advantageous in terms of optimizing the harvest, particularly when dispersal from the sink to the source is low (Lundberg and Jonzén 1999), but it is unlikely to be the safest strategy from a conservation stand point. It is perhaps safer to suggest that source areas that need protection should be the most productive areas for the game species of interest.

Estimating game productivity or habitat quality for game at different sites is often more difficult than estimating game density. Nevertheless, by considering a small set of additional measurements, it may be possible to obtain preliminary indicators of productivity or habitat quality that can aid in the identification of game sources and thus complement estimates of population density. These measurements may be the ratio of adults to offspring or the availability of key food resources or breeding sites. Furthermore, it is important to keep in mind that the source or sink condition of a site can change through time because of natural or anthropogenic disturbances (Pulliam 1996). For this reason a field-monitoring system needs to be implemented in order to evaluate potential changes in the source or sink condition that is estimated initially.

A MODEL TO STUDY AND TO MONITOR HUNTED SOURCE-SINK POPULATIONS

It is necessary to develop new models to begin in order to understand the effects of hunting in source-sink systems and in order to make predictions that can be useful for management. In a recent study I evaluated the effect of changes in the proportion of source and sink habitat on the sustainability of harvest of culpeo foxes (*Pseudalopex culpaeus*) in Argentine Patagonia (Novaro 1997). Sources and sinks are distributed in a mosaic, with sources occurring in cattle ranches where there is no hunting and with sinks in sheep ranches where hunting is intense because culpeos prey on sheep. Periodically, some ranches switch from sheep to cattle ranching and vice versa so that the proportion and area of sources and sinks changes through time.

I used field data to develop a culpeo population model and simulated their dynamics in order to study the relationship between the rate of increase of the regional population and the proportion of the landscape in sources and sinks. Field data that were used included demographic data for source and sink populations (abundance, reproduction, and mortality), dispersal rates between sources and sinks, and the proportion of area in sources and sinks. In the case of the culpeos, a sensitivity analysis showed that their dynamics were strongly affected by adult mortality in the sources, suggesting that occasional killing in cattle ranches should be controlled to prevent a regional decline. The level of culpeo hunting in sinks was predicted to be sustainable for the current proportion of source area in the landscape (ca. 37%), but hunting would not be sustainable if this proportion fell below ca. 30%. The prediction about sustainability of current hunting was confirmed by field monitoring that showed a positive rate of increase of the regional population.

The conceptual model developed for culpeos may be useful for studying the relationship between the dynamics of other game populations and their spatial structure when it is possible to identify potential source and sink subpopulations. This relationship may be studied without estimating all the demographic variables mentioned above. Figure 24.1 shows the relationship between the observed rate of increase (r) of the regional population and the proportion of habitat in sources and sinks (sn). This relationship could be used to predict changes in the sustainability of hunting when there are changes in the proportion of area in sources or sinks. These changes could result from altered land use practices in sources and sinks, as

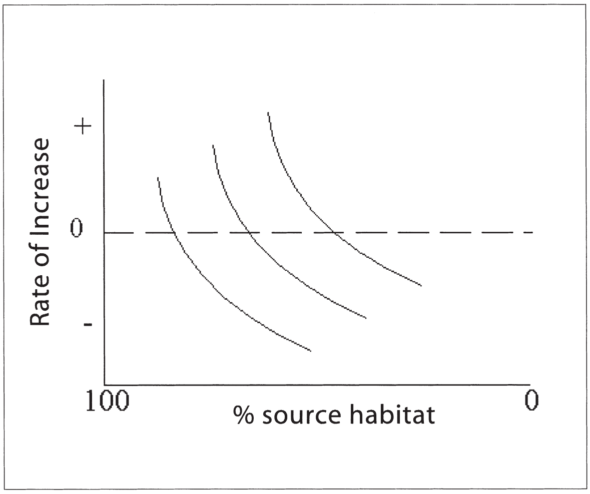

FIGURE 24.1 Relationship between the regional rate of increase and the proportion of source habitat in a source-sink population. Different lines correspond to different levels (increasing toward the right) of adult mortality in the sources.

was the case for culpeos, or from human encroachment into previously unhunted areas or abandonment of hunted areas.

The relationship between *r* and *sn* for the game populations of interest can be studied by obtaining a series of estimates of the rate of increase of the populations and the corresponding proportions of area in sources and sinks. Rates of increase can be estimated from population trend data that must involve estimates of absolute abundance (Eberhardt and Simmons 1992; Caughley and Sinclair 1994). Rates of increase of source and sink subpopulations should be averaged in order to estimate the regional rate of increase (for the entire mosaic of sources and sinks) for the game population, which is the most relevant demographic variable for sustainability. The estimation of game population trends over a number of years and under changing hunting patterns requires a large and long-term monitoring effort. It can, however, be conducted by local people (see Hill and Padwe 2000) and does not require detailed ecological studies that tend to be expensive and of short duration.

If a plot of the *r-sn* relationship is obtained, it can be used to predict whether hunting would be sustainable or not for a given proportion of source and sink area and a given direction of change between the source and sink condition. At least three conditions are necessary for the relationship between *r* and *sn* to remain relatively constant: source areas must remain free from hunting, habitat quality in sources must remain high, and the spatial arrangement of source and sink areas must remain relatively constant. First, as indicated, the *r-sn* relationship for culpeos, and probably for most game species, is relatively robust to changes in most demographic parameters except adult mortality in the source. Thus, even if low levels of hunting in the source occurred, the *r-sn* curve would shift markedly to the right (fig. 24.1), making hunting unsustainable even if the actual *sn* proportion remained constant. This marked shift is probably due to a density-dependent effect on dispersal from source areas. Second, a relatively constant habitat quality in sources means that their high productivity remains unchanged. Finally, dramatic changes in the spatial configuration of source and sink areas as a result, for instance, of large-scale habitat conversion or fragmentation would also affect the *r-sn* relationship, invalidating its application under the new conditions.

The model presented here provides a first approximation to an approach to explicitly evaluating the interaction between hunting, population dynamics and the spatial heterogeneity of some game populations. Other possible approaches were reviewed in the previous section (Joshi and Gadgil 1991; McCullough 1996; Lundberg and Jonzén 1999; Hill and Padwe 2000; Novaro, Redford, and Bodmer 2000). The application of one or the other approaches to hunting studies would depend on the amount of data available and, most importantly, on the spatial-structure model assumed to best represent the real game populations of interest. It is important to keep in mind that unexpected results will be encountered when studying the dynamics of or managing game populations because of stochastic events, failure of enforcement measures, and inconsistencies between model assumptions and real game populations. Long-term monitoring systems of game populations and their habitats are an essential tool needed to periodically adjust our assumptions and to improve our management recommendations.

25

Hunting and Wildlife Management in French Guiana

CURRENT ASPECTS AND FUTURE PROSPECTS

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French Guiana is a French overseas department, located between Brazil and Suriname. Human density is very low, averaging less than two people/km^2. However, the population is not evenly distributed, and most people are concentrated in the coastal area. Ninety-five percent of the territory is covered by evergreen tropical moist forest, representing over eight million hectares of almost intact and nonfragmented forest. Many different ethnic groups share the country: creoles, Bushinengue, Hmong, Chinese, people from metropolitan France, and six different Amerindian groups (Wayãpi, Wayana, Teko, Kali'na, Palikur, and Arawak). For most of the people—except perhaps the Chinese, whose economic focus is on restaurants and food shops—hunting is both a strong local tradition and a current practice. Subsistence hunters are frequent in remote isolated areas. In small rural villages and for people with low income, despite government aid, hunting for meat and selling the surplus represents a nonnegligible economic contribution. More-or-less organized commercial hunting also exists, as well as sport hunting near the main cities.

Starting approximately ten years ago, the Ministry of Environment took a new interest in French Guianan conservation problems. Following the recommendations of the Rio conference, a national park project was initiated, and in 1993 the National Game and Wildlife Service (Office National de la Chasse et de la Faune Sauvage, or ONCFS) began to work for the first time in the country. In France, as well as overseas, ONCFS is responsible for studying and monitoring wildlife and its habitats and for monitoring and regulating hunting. The environmental police fall under ONCFS's jurisdiction, and the agency is also charged with conducting applied studies of wildlife management.

In 1999 national funds were proposed for research projects aimed at studying human impact on the environment in tropical areas. The scientific group Silvolab, which comprises ten scientific and management organizations working on tropical forest issues, engaged in a two-year program called Hunting in French Guiana: Toward Sustainable Management. The main objective of this multidisciplinary program is to establish the necessary scientific, ecological, and sociological bases for the development of a sustainable use of wildlife in French Guiana. Although initial results are not yet published, new and complementary studies have been designed and are currently underway. This paper summarizes the status of wildlife management in the year 2002 in French Guiana, which is not well known in neighboring Neotropical countries, and then describes the current status and orientation of research in wildlife management.

PRESENT HUNTING LAWS IN FRENCH GUIANA

Although French Guiana is a French department, French hunting law does not apply here. French hunting law specifies that its decrees apply throughout the French territory, (including the French West Indies, for example) with the notable exception of French Guiana. No specific reason is given for this omission, but one can imagine that the department was so distant, complex, and different from the national reality that, at the time the law was written, the problem was simply avoided.

As a consequence, in French Guiana there is currently no hunting season nor requirement for a hunting license—anyone can hunt anytime and anywhere, except in protected areas. Additionally, there are very few restrictions to hunting. A general review of the hunting regulations in the various Amazonian countries (Richard-Hansen 1998) has shown that French Guiana has one of the mildest restrictions on hunting practices.

The first regulation on hunting in French Guiana was set in 1975, but as a local decree it has relatively weak enforcement power. Later, in 1986, ministerial decrees enacted basic rules for wildlife protection; those for marine turtles, cetaceans, and sirenians were completed in 1991 and 1995. Also in 1995 another decree gave a more precise statement about the local trade.

At the present time, there are in French Guiana three main legal categories of wildlife: (a) fully protected species (table 25.1), for which any use is forbidden; (b) species for which hunting is allowed but trade in is forbidden; and (c) species for which both hunting and local trade in are allowed. Eight species of mammals can be traded locally: the two species of peccaries (*Tayassu tajacu* and *Tayassu pecari*); the tapir *Tapirus terrestris*; three species of rodents, paca (*Agouti paca*), red-rumped agouti (*Dasyprocta agouti*), and capybara (*Hydrochaeris hydrochaeris*); and two armadillos (*Dasypus novemcinctus* and *Dasypus kappleri*). Anyone concerned with conservation and sustainable use will certainly notice that trading tapir meat can hardly be justified from a biological point of view. Most likely such trade is permitted because of its importance to local people; political reasons might have weighed heavily in these decisions.

The same problem occurs for birds. The black curassow (*Crax alector*), trum-

TABLE 25.1 Fully Protected Animals in French Guiana

MAMMALS	BIRDS	REPTILES
Chironectes minimus	*Anhinga anhinga*	*Melanosuchus niger*
Cyclopes didactylus	*Phalacrocorax olivaceus*	*Chelus fimbriatus*
Tamandua tetradactyla	*Pelecanus occidentalis*	*Platemys platycephala*
Myrmecophaga tridactyla	*Fregata magnificens*	*Podocnemis cayanensis*
Priodontes maximus	*Phoenicopterus ruber*	*Corallus caninus*
Lutra enudris	*Cairina moschata*	*Dermochelys coriacea*
Pteronura brasiliensis	Ciconiformes: all spp.	*Caretta caretta*
Eira barbara	*Mesembrinis cayanensis*	*Lepidochelys olivacea*
Galictis vittata	*Eudocimus ruber*	*Lepidochelys kempii*
Speothos venaticus	*Ajaia ajaja*	*Eretmochelys imbricata*
Cerdocyon thous	Ardeidae: all spp.	*Chelonia mydas*
Procyon cancrivorus	Falconiformes: all spp.	
Herpailurus yagouaroundi	Strigiformes: all spp.	
Trichechus manatus	Lariformes: all spp.	
Ateles paniscus	*Opisthocomus hoazin*	
Chiropotes satanas	*Aburira pipile*	
Pithecia pithecia	*Ara ararauna*	
Aotus trivirgatus	*Ara macao*	
Odocoileus virginianus	*Ara chloroptère*	
Leopardus pardalis	*Rupicola rupicola*	
Leopardus tigrinus		
Leopardus wieidii		
Marine mammals: all spp.		

peter (*Psophia crepitans*), and guan (*Penelope marail*) may be among the most vulnerable to hunting pressure, yet owing to a strong hunting tradition, they are the three species that can be traded locally. Among the reptiles, the green iguana (*Iguana iguana*) is the only species authorized for commerce.

Concerning international trade, France is a party to CITES. Twenty-one species occurring in French Guiana are listed in Appendix I of CITES, and 170 in Appendix II. Moreover, it is illegal to export most species of the French Guianan fauna, even to metropolitan France.

BUSH MEAT TRADE

The local branch of the French government's Veterinary Services has monitored the bush meat trade for several years at the Cayenne Market, a central place for the local food trade. Estimates of tons of meat and individual small animals sold between 1986 and 1997 (figs. 25.1 and 25.2; adapted from Tyburn 1994) show that tapir

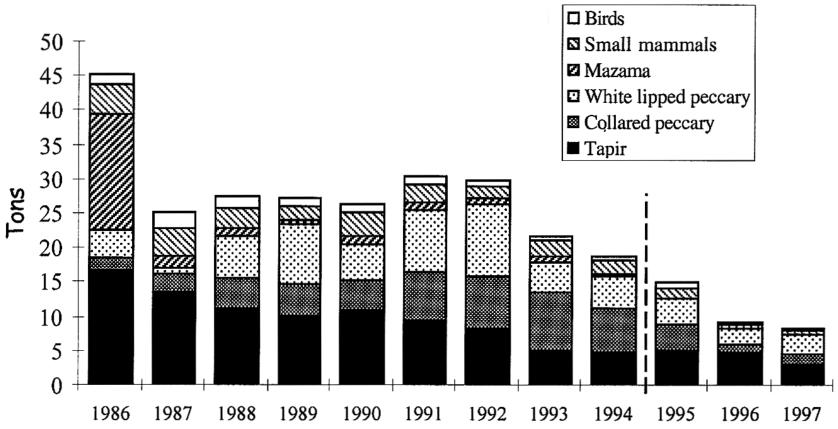

FIGURE 25.1 Tons of bush meat sold in the Cayenne market between 1986 and 1997. The dotted line indicates that data have been collected less systematically after this date. (Data from Tyburn 1994 and Veterinary Services)

and peccary represent the major part of the traded biomass. In 1986 the effect of the new regulation that declared brocket deer (*Mazama sp.*) illegal to trade is clearly seen (fig. 25.1).

The general tendency is for a decrease in the global amount of meat sold at the Cayenne market. However, after 1995 monitoring became less systematic (indicated by the dashed line on the graphs), and the data therefore less reliable. In reality, the presence of bush meat dealers in the market place has become less and less frequent and regular, and controls on the trade are more difficult. In fact, although we assume that a decrease in total amount of bush meat traded has occurred, the decline in meat sales is also related to the emergence of new commercial channels (Magnat 2000; C. Richard-Hansen pers. obs.). Hunters and dealers are more often selling their meat directly to restaurant owners or even to individual people and less often at the market. This situation makes control (site visits followed by application of sanctions if illegal meat is detected) by various police services much more difficult. Restaurant owners are required to declare their bush meat purchases on a specific registry, but this requirement is not very well respected and is also difficult to control.

IMPLEMENTATION

Legal control and police surveillance were very rare before 1993 because no specialized service was present. Beginning in 1993, French Game and Wildlife rangers have been present in French Guiana, but they are still in very small numbers. To deal with this situation, their main means of action is to enhance collaborations

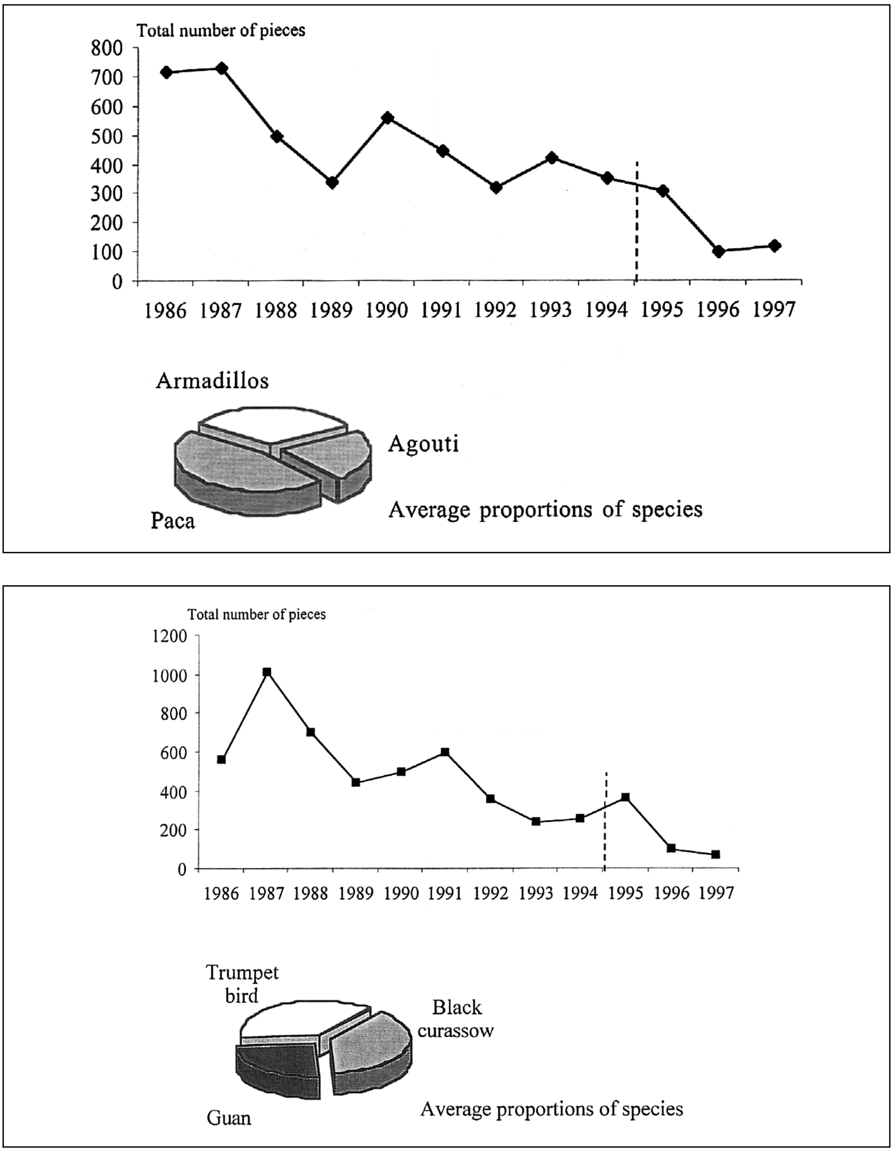

FIGURE 25.2 Number of pieces and mean proportions of total pieces made up by three species of small mammals and birds sold at the Cayenne Market between 1986 and 1997. The dotted line indicates that data have been collected less systematically after this date. (Data from Tyburn 1994 and Veterinary Services)

with other police services, which have the ability to control but previously were not interested nor informed enough about wildlife to take action. Rangers of the French Game and Wildlife service regularly train customs and various policemen in particular aspects of wildlife conservation. Controls are then usually carried out in cooperation with one another.

Specific action has been undertaken for the control of restaurants, based on the assumption that the sales of bush meat to these establishments in the main cities may be the most important cause of wildlife harvest and may bring the greatest risk of overexploitation. Moreover, it is easier and more efficient to control the restaurant trade than to patrol wide forest areas. According to the 1995 decree, restaurants that wish to sell bush meat must request authorization, are required to respect trade and hunting bans (table 25.1), and must fill in a registry indicating all traded pieces. A massive information campaign was carried out, followed by regular restaurant inspections. Monitoring quantities is difficult because the registries are not always very well filled out, but flash inspections allow the detection of illegal species in restaurant freezers. In the main cities of Cayenne and Kourou, the situation has greatly changed (pers. obs.). It is now harder to find illegal species like caiman or brocket deer on the menu, although such listings were very frequent a few years ago when almost all wildlife species could be eaten in restaurants.

Hunting is also regulated in protected areas, but their isolated situation and the small number of agents makes control difficult. Therefore, coastal areas and sensitive species, such as marine turtles nesting on beaches, were given priority. As a further step in protection, the first national reserve was created in 1992. At present time, five national reserves exist: a marine reserve for nesting seabirds, such as terns and frigate birds; two in the interior, nonfragmented forested zone; and two in coastal areas, designed to protect marshes, aquatic habitats, and sea turtles. In the forest reserves, which are uninhabited, hunting is strictly forbidden, but the Kaw marshes and Amana coastal reserves have several different zones, in which hunting or fishing may be forbidden, restricted, or permitted for resident and nonresident people. Those areas are regularly patrolled by local workers and occasionally by national rangers.

In the rest of the country hunting controls involve only checking for protected species or illegal trade. As the country is large and very few means of communication exist, most inspections are made along the roads and rivers. Therefore the situation remains almost uncontrolled in small and remote villages.

PUBLIC INFORMATION

As enforcement actions are relatively recent, it was necessary to inform local people, tourists, and residents of the existing regulations because many bad habits had been acquired. The law texts were translated and explained, and brochures, booklets, posters, and a book (Hansen and Richard-Hansen 2000) were produced to describe the threats to wildlife and to detail which species are protected and which can be legally traded. Environmental education is difficult because of the low literacy rate, and follow-up studies to evaluate the success of the campaign have yet to be carried out. However, it does appear that more and more people in the cities, and especially in restaurants, are aware of the regulations.

SCIENTIFIC STUDIES

CONTEXT AND OBJECTIVES

Applied studies on wildlife management are a very recent concern in French Guiana, and research programs on hunting have been in place for a few years only. Still, detailed studies have previously been conducted on hunting practices of the Wayãpi, an Amerindian group living in southern French Guiana (Grenand 1996; Ouhoud-Renoux 1998).

As a first step in the Silvolab program, we carried out a global review of studies on hunting practices and impacts, ecological knowledge of main game species, sustainable use models, and hunting legislation in Amazonian countries (Richard-Hansen 1998; Richard-Hansen and Hansen 1998). The aim was to assess existing knowledge in order to orient the studies in French Guiana by taking into account and adapting previous experiments in neighboring countries.

Since 2000 study programs on hunting management have been in place. The coordination unit Silvolab was in charge of the first stage, which involved six scientific institutions, ONF (Office national des Forêts), IRD (Institut de la Recherche pour le Dévelopment), CIRAD (Centre de cooperation internationale en recherché agronomique pour le development), CNRS (Centre National de la Recherche Scientifique), ENS (Ecole Normale Supériore), and ENGREF (Ecole Nationale du Génie Rural des Eaux et Forêts), as well as ONCFS and the park project commission (Mission pour la création du Parc). The latter two institutions are now in charge of follow-up and complementary studies.

The context in which these studies are undertaken is a consideration of both the importance of local hunting traditions and the modern changes in human demography and hunting habits. Both traditions and new changes have a growing impact on wildlife populations, particularly in the densely inhabited coastal area. In fact, although local hunters are frightened by the possibility of new hunting regulations, more of them are coming to agree with the need to control the excesses because they feel that it has become difficult to hunt in proximate areas. However, they ask for locally adapted regulations, which take into account the social and faunal particularities of the country. The program is thus based on a bifocal approach combining biological and socioethnological studies.

In the long term the ecological part of the program primarily aims at, first, enhancing basic biological and ecological knowledge on the main hunted species: population structure and dynamics, reproductive rates and periods, relative species abundance in hunted and nonhunted areas, diet, and habitat use. Second, it aspires to develop and perfect simple ecological and hunting indices that allow monitoring of the status of populations and hunting impacts: kilometric index of abundance, fecundity and productivity indices for females, harvest yields, etc.

At the same time, a socioethnological study was conducted on hunting practices. The first stage of the study consisted of (a) characterizing hunting practices quantitatively and qualitatively, quantifying harvests, analyzing the social and ethnic context of hunting, and understanding the traditional representation and value of natural environment for the various ethnic groups, and (b) mapping hunting areas

METHODS

The above studies have been or are being established at selected focal study sites (fig. 25.3) in which both the social and ecological aspects of hunting are examined simultaneously. Additional nonhunted sites have been selected as reference areas for estimating animal densities (fig. 25.3). At focal study sites, a survey is made with hunters who have agreed to collaborate with the study. Local investigators daily visit the hunters and record the place, locality, type of weapon used, mode of transportation, number of hunters, and quantity of harvest for each hunting event.

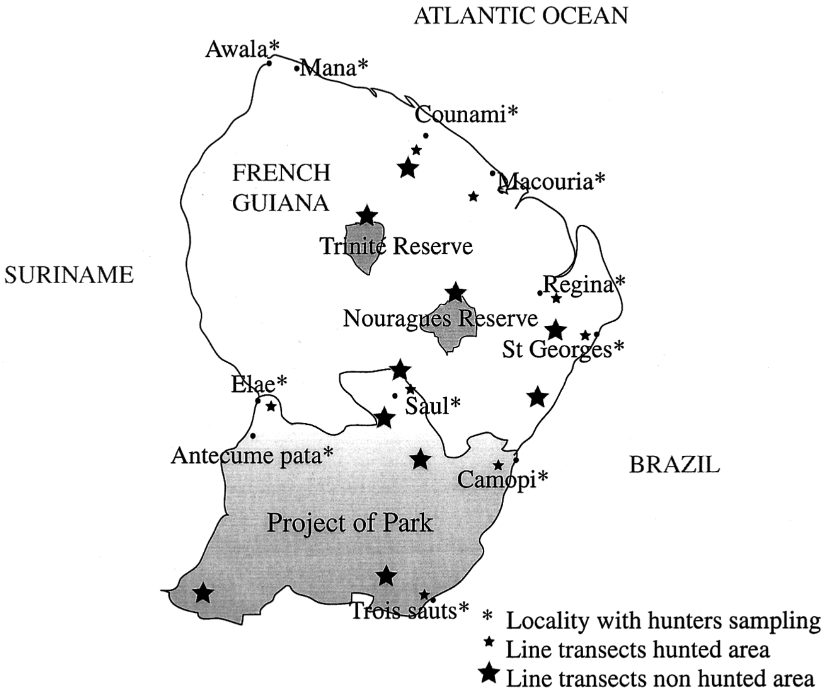

FIGURE 25.3 Main study sites for hunting and game species abundances in French Guiana.

Game harvest data obtained by hunter interviews provide the basic information needed about the overall number of animals harvested, their specific distribution, and the age-sex structure of the harvested population, as well as reproductive parameters of the main species and estimations of the hunting territory for people at each study site. Collecting jaws from hunted animals is undertaken at some study sites for more detailed analysis of age structure and survival.

Game densities and abundances are estimated in the hunted areas previously determined by the survey by using standardized line-transect and distance sampling methods. The same method is also conducted on the nonhunted sites,which are used as reference sites for the analyses of sustainability of hunting. Comparing animal densities in the different nonhunted areas also allows us to document and understand the ecological influences in addition to the human on animal densities. Although there are no strong ecological differences in French Guiana equivalent to those between várzea and terra firme forests in other parts of the Amazon, the carrying capacity may vary according to different animal species and forest types. Hunting impact cannot be clearly assessed if the basic ecological influence on animal densities is not known. For that reason habitat composition is to be described at each site at which animal counts are made.

The study is currently running in most of the coastal area sites. In the southern area establishment of a park has been proposed that would cover a large area occupied by a few indigenous populations (fig. 25.3). Five study sites have been selected in this area, which will allow a comparison of different sociocultural situations, integrating true situations of subsistence hunting. In contrast to the coast, the small size and isolated location of some villages will allow us to make a preliminary diagnosis of the sustainability of practices, applying models elaborated at other sites in Amazonia (Robinson and Redford 1991; Bodmer et al. 1997b; Bodmer and Penn 1997).

Sustainability of the current hunting practices will be estimated through the analysis of both the harvest quantities and the estimated production of various species in the hunted area (i.e., number of animals killed and number of births per square kilometer). The production will as much as possible be estimated locally, according to the reproductive parameters deducted from animals killed in the area. Then the Robinson and Redford 1991 model will be used to set a maximum sustainable harvest level, according to the lifespan of the species (20%, 40%, or 60% of the production as maximum sustainable use, for long-, short-, or very short-lived species, respectively).

The genetic structure of populationsˇ20is also being studied by CNRS through the collection of tissue samples from hunted animals in order to analyze the genetic variability at local and regional scales. Concepts of metapopulation and source-sink systems may be underlying hypothesis with strong conservation implications for wildlife management. Finally, specific studies on the ecoethology of the main game species will then be initiated in order to conduct true management on the basis of ecological local knowledge.

PRACTICAL MANAGEMENT OBJECTIVES

In the park project ecological and hunting analyses will be the basis for a proposal for community management of wildlife resources. In the coastal area the situation is much more complex because several communities and hunter categories share all sites and resources. This sharing makes it very difficult to give people a sense of responsibility for management because there is no appropriation of the resource and its future.

However, we hope that the results of the study will help to integrate local needs, constraints, and realities in future management rules. French Guiana has the opportunity to convert its backwardness in the area of wildlife management in a favorable way. It can do so by integrating as a practical outcome, and at a very large scale, the results of the discussions and models that R. Bodmer, J. G. Robinson, and the five International Conferences on Wildlife Management and Conservation in Latin America and the Amazon have presented. It must do so without the constraints or advantages of an existing rigid legal or protected-area system.

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