Reports

Game Depletion Hypothesis of Amazonian Adaptation: Data from a Native Community

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The low population densities and impermanent settlements of Amazonian Indians are often interpreted as adaptations to a fauna that offers limited protein resources and is rapidly depleted by hunting. Data spanning the 10-year life cycle of one northwestern Amazonian settlement show that variations in hunt yields result from temporal variations in peccary (*Tayassu pecari* and *T. tajacu*) kills that appear extrinsic to native population size. After 10 years, hunting success remained high and the kill rates for most prey did not suggest depletion. An array of environmental factors accounts for the incipient settlement relocation observed.

H UNTING IS IMPORTANT IN THE adaptation of Amazonian Indians because it and fishing provide most of their dietary proteins. The low population densities of upland (*terra firme*) societies have been interpreted as an adaptation to a neotropical fauna that offers a low biomass of terrestrial mammals and few species of ungulates (1-5). The concept of "game depletion" is also central to this hypothesis. Game availability is posited as an inverse function of human density, especially for large terrestrial mammals (2, 4, 5), and small and impermanent settlements are seen as the societal responses.

This model is plausible but has deficiencies. First, it has never been adequately demonstrated with long-term data. Second, the conceptualization of "depletion" often blurs species-level processes. Third, there is a tendency to view a territory as an area in which prey populations are progressively reduced, thus underestimating the possibilities of population maintenance, growth, or recruitment from adjacent forest (δ).

The data presented here were collected in the Siona-Secoya community of Shushufindi (or "San Pablo") on the Aguarico River in northeastern Ecuador (0°15'S, 76°27'W). The mean elevation is 250 m, with mild relief. The mature vegetation is tropical wet forest. The study began in 1973 as the settlement was established after migration from the Cuyabeno River, 40 km to the northeast. Observations continued in 1974, 1975, 1979, 1980, and 1981-82. By 1980 the settlement was considered "old" and declined as some households relocated. Hence the data span most of the settlement's life and are suited to the evaluation of the depletion prediction.

The traditional weapons of the Siona-Secoya are the blowgun for primates and birds, and the spear for large terrestrial mammals. Since the 1950s, the shotgun has largely replaced both weapons and should accelerate any tendency toward game depletion (7, 8). Hunts were of variable duration, including brief forays near settlements, 1day hunts, and occasional expeditions of greater length. The maximum hunting range covered 2500 km², but only 1150 km² was hunted year-round. A core area of 590 km² received some hunting each day. The total sample is a record of 863 man-days of hunting (9). Of this, 696 man-days (totaling 5286.06 man-hours), or 80.65%, occurred within the core area (10). The analysis here focuses on this subset where hunting was most intensive.

Figure 1 shows the population in the core area from 1973 to 1981-82, and the mean yield per man-hour of hunting per year. The human density ranged from 0.17 persons per square kilometer in 1973 to 0.35 in 1979, or about the mean density of 0.2 persons per square kilometer for aboriginal inhabitants of the lowland forest habitat (11). These data have been analyzed by linear regression with the yield rate as the dependent variable (Y') and population as the independent variable (X), following the formula, Y' = A + BX. The derived equation is $Y' = 9.679 (\pm 2.316) - 0.034$ $(\pm 0.013)X$, n = 6, with $r^2 = 0.638$, SEE (standard error of the estimate) = 1.165, and F = 7.052 (P < 0.10). These results suggest that the observed values for human population and hunting yields may be described by a regression line, but with considerable error (yields for 1974 and 1981-82 are well above predicted values and account for 67.1% of the residual sum of squares error) and questionable significance (the 0.05 confidence level is not met).

Further evaluation is possible through inspection of the yields of various animals. For Fig. 2, hourly yields (live weight) are converted to net yields (butchered weight) per man-day of hunting. Figure 2 also indicates the proportional contributions of ungulates, primates, birds, rodents, and "other" (edentates, reptiles, and carnivores). Most meat came from ungulates (ranging from 90.22% in 1981–82 to 62.78% in 1975; mean = 77.66 \pm 10.88%). The yields of primates, birds, rodents, and other game involve much smaller amounts.

White-lipped peccaries (Tayassu pecari) contributed $37.35 \pm 22.85\%$ of the net ungulate yields by weight, and collared peccaries (T. tajacu) supplied $36.92 \pm 32.26\%$. Tapir (Tapirus terrestris) contributed $22.04 \pm 12.56\%$ and deer (Cervidae) $3.68 \pm 3.28\%$. Unlike peccaries, tapir and deer were taken at low, but stable, rates that never exceeded one kill per 100 man-hours of hunting per year. White-lipped peccary kill rates were highly variable, with a mean of 3.936 ± 3.227 kills per 100 man-hours of hunting per year. This variation reflects the occasional movements of large herds through the core area (12), rather than depletion due to hunting. Fluctuations in collared peccary kill rates were less marked, with mean of 3.451 ± 1.522 . Linear regression analysis of peccary kill rates as a function of native population gives weak or insignificant results. For white-lipped peccary the equation is $Y' = 14.972 (\pm 4.435)$ $-0.063 (\pm 0.025)X, n = 6, SEE = 2.231,$ $r^2 = 0.618, F = 6.465 (P < 0.10).$ Dubious significance is suggested for these results because the dramatic fluctuations in whitelipped kills are better explained by sudden appearances of peripatetic herds than by long-term interations within the core area. The collared peccary is a local resident but variations in its kill rates are unrelated to

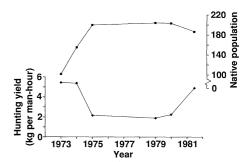


Fig. 1. Native population and hunting yields in the 590 km² core area around Shushufindi. Population is mean annual value for persons present in the core area (adjusted for births, deaths, immigration, emigration, and time outside the area). Yields are mean live weight per man-hour of hunting per year. Analysis indicates that yields are influenced more by temporal variations in peccary kills than by native population levels or game depletion.

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Fig. 2. Net yields in butchered meat per man-day of hunting. Ungulates provide most of the meat in all years (mean = $77.66 \pm 10.88\%$). Two pecmeat in cary species, Tayassu pecari and tajacu, contribute 74.27 $\pm 14.38\%$ of the ungulate yields, and account for most of the variation in both ungulate and total net yields.

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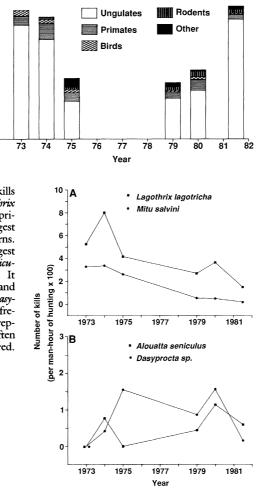
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Net yield in butchered meat (kg per man-day of hunting)

Fig. 3. (A) Two species whose declining kills suggest depletion. The woolly monkey (Lagothrix lagotricha) was the most frequently killed primate. The curassow (Mitu salvini) is the largest game bird. Only three species show such patterns. (B) Two species whose kills do not suggest depletion. The howler monkey (Alouatta senicu-lus) was always taken at low frequencies. It formed smaller social groups than Lagothrix, and probably had a lower density. The agouti (Dasyprocta sp.) was common, but also killed infrequently. Such rodents, as well as edentates, reptiles, and smaller primates and birds were often ignored unless larger game were not encountered.



variations in human population size: $Y' = 3.366 \ (\pm 3.384) + 0.0005 \ (\pm 0.019)X,$ n = 6, SEE = 1.702, $r^2 = 0.0002$, F =0.0007 (P > 0.75)

The kill data for three species suggest their depletion within the core area. These are woolly monkeys (Lagothrix lagotricha), the curassow (Mitu salvini), a large bird of the forest understory, and the trumpeter (Psophia crepitans), a large ground-dwelling bird (Lagothrix and Mitu trends are presented in Fig. 3A). Depletion is not suggested for other prey, including peccaries, tapir, deer, primates other than Lagothrix, birds other than Mitu and Psophia, rodents, edentates, and reptiles. (Alouatta and Dasyprocta trends are presented as examples in Fig. 3B.)

Hunters took many small animals when larger game were not encountered. Hence, in 1975, the year of lowest ungulate returns, the hourly yield rate was still 2.16 kg (live weight) or 10.89 kg (butchered weight) per man-day of hunting. The proportion of hunts with at least one kill was always high (ranging from 91.3% in 1973 to 81.16% in 1979). The mean return for all years of 16.75 kg (butchered weight) per man-day of hunting compares favorably with the 25 kg reported for Bisa large game hunters in

Zambia (13), and is better than the 2.6 kg per day reported for Dobe !Kung hunters of Namibia and Botswana (14). The mean Siona-Secoya success rate of 84.77% is superior to the Bisa range of 9 to 33%, and the !Kung rate of 23%. Hence, although there are fewer species of ungulates and lower biomass of mammals in Amazonia, hunters do well hunting species that are present.

The Shushufindi data do not support the prediction of impoverished yields due to game depletion. An array of factors accounts for the settlement's decline, including the depletion of cedar trees (Cedrela odorata) for canoes and palms for thatch. More importantly, each year it was necessary to travel farther to establish gardens, thus increasing the transportation costs of horticulture. Siona-Secoya also view older villages as decrepit and infested by pests. Migration offers a fresh start with many resources, and game conditions are only one consideration in such decisions (15).

Undoubtedly, dense human populations may deplete or eliminate animal populations by habitat modification or overpredation. But terra firme societies traditionally formed settlements of 250 individuals or less associated with hunting territories in excess of 1000 km². Under such conditions, most prey populations probably were not controlled by their human predators. As the Amazon is developed, there will be increasing stress on flora, fauna, and native people alike. To establish parks and land holdings of sufficient size to satisfy the needs of all three, a better understanding of critical sizes for such areas is needed (16).

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- 9. Methods included direct observation of hunting and post-hunt interviews. These elicited name; date; time of departure and return; location; species and numbers of animals taken, if any; weight of animals (by weighing or by estimation); companions, if any (for follow-up); and hunting conditions. Total hunting for the six observed years is estimated to be 10,933 man-days. The record of 863 man-days is a sample of 8%.
- 10. A "man-day" is the mean duration of recorded hunting days within the core area for a year; the values for 1973, 1974, 1975, 1979, 1980, and 1981-82 are, respectively, 6.66, 6.56, 7.14, 8.36, 8.22, and 7.92 man-hours.
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