

Fragoso J.M.V. 2004. A long-term study of white-lipped peccary (*Tayassu pecari*) population fluctuations in northern Amazonia—anthropogenic versus “natural” causes. *In* K.M. Silvius, R.E. Bodmer and J.M.V. Fragoso (eds.). People in Nature: Wildlife Conservation in South and Central America. Columbia University Press, New York, USA.

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A Long-Term Study of White-Lipped Peccary (*Tayassu pecari*) Population Fluctuations in Northern Amazonia

ANTHROPOGENIC VS. "NATURAL" CAUSES

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White-lipped peccaries (white-lips—*Tayassu pecari*) are among the largest of Neotropical forest mammals, reaching weights of about 50 kg (Sowls 1984; Fragoso 1998a). They can form groups with more than 100 animals, and anecdotal reports exist of groups with 1,000 and even 2,000 individuals (Mayer and Brandt 1982; Mayer and Wetzel 1987; Fragoso 1994). Occasionally, herds and even entire populations have disappeared from areas where they were usually found, leading some researchers to hypothesize that white-lips are migratory, probably in response to variations in food supply (e.g., Kiltie 1980; Kiltie and Terborgh 1983; Sowls 1984; Bodmer 1990; Vickers 1991). This hypothesis has been supported by the stories of several Amerindian groups, who tell that local disappearances of white-lipped peccaries are normal and that the herds return after a given time (e.g., Vickers 1991).

Further support for the migratory hypothesis was provided by Kiltie (1980) and Kiltie and Terborgh (1983), who using a mathematical model based on step length and number of animals, demonstrated that a herd could cover an area of more than 200 km². On the basis of this model, they hypothesized that herds may be nomadic and lack fixed home ranges. Some researchers have interpreted the results of this model as support for the hypothesis of white-lipped peccary migrations (e.g., Vickers 1991), which has come to be considered a fact by many biologists working with white-lips (e.g., Mayer and Brandt 1982; Sowls 1984; Bodmer 1990; March 1993). During fifteen years (1988–2003) of studying white lips in the northern Amazon region of Brazil, however, I have not found support for this hypothesis (Fragoso 1994, 1998a, 1998b, 1999, unpublished data), and have proposed that local disappearances are in fact in situ population declines caused by mortality and/or reproductive failure.

This article describes the disappearance of white-lipped peccaries from the northern portion of Roraima state, Brazil, an area of primary rainforest unimpacted

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by peoples of western descent, including colonists. The area is part of continuous rainforest that extends for about 1,500 km to the west, perhaps the same amount to the south, and hundreds of kilometers to the north of the study region (see below). To the east it borders the naturally occurring cerrado and savanna biome of the Guiana shield region. The Yanomami peoples, one of the least Westernized of native South American groups, inhabit much of the study area (Ricardo 1996). I consider three alternative hypotheses to explain the disappearance of white-lips in this area: (a) out-migration; (b) overhunting by humans; and (c) local in situ population decline resulting from an epidemic caused by an introduced pathogen.

METHODS AND STUDY AREA

Maracá Island Ecological Reserve is located at 3°25' N latitude and 61°40' W longitude, on the northern margin of the Amazon basin in the state of Roraima, Brazil. The riverine island was created by the bifurcation of the Uraricoera River, a tributary of the Rio Branco in the Amazon watershed. The 110,000 ha of rainforest, isolated savannas, and wetlands that make up the reserve are protected by IBAMA (Brazilian Institute of the Environment and Natural Resources) as a site for research and forest conservation. The river provides an incomplete barrier between Maracá and the surrounding forests. In the dry season it is bridged by stepping-stone islands, and white-lips and other animals are frequently sighted swimming the river at all times of year (J. Hemming pers. comm.; J. Thompson pers. com.).

The Yanomami Indigenous Reserve starts almost at the margin of Maracá and extends westward for more than 300 km. It covers 9,400,000 ha of rainforest, montane forest, transitional forest, and some savannas and woodlands. Elevations range from 100 m above sea level in the Amazonian lowlands to 2,000 m in the Parima and Pacaraima mountains that divide the Amazon and Orinoco watersheds. To date the flora and fauna of these two study sites have not been affected by Western peoples, with the exception of the recent invasion by artisanal gold miners (*garimpeiros*) of some parts of the Yanomami reserve (MacMillan 1995; Milliken and Ratter 1998).

POPULATION CENSUSES AND COUNTS ON THE EASTERN END OF MARACÁ ISLAND

Data on abundance and density of white-lipped peccaries on the eastern end of the island were collected during three separate periods. From June 1 to June 28, 1988, density transects were walked on a permanent trail system covering approximately 60 km (Fragoso 1998b). For each encounter the distance and angle of the herd to the transect line were noted along with the number of animals in the herd, and the information was used to calculate density using the King and Webb method (Schemitz 1980). Between June 1988 and June 1989, all individuals and herds en-

countered on the entire trail system during 227 days of walks were counted. All transect walks began between 7:00 and 8:30 A.M. and continued until 5:00 or 6:00 P.M., with a break between 11:00 or 11:30 A.M. to 1:00 or 2:00 P.M. On some days transect walks occurred only in the morning or afternoon. From January 1991 to December 1992, these transects were repeated in the same manner in the same area on 220 days.

RIVER SEARCHES

To assess the status of white-lipped peccaries in the central and western portions of the island, I traveled along 200 km of the north channel (Santa Rosa Channel) of the Uraricoera River and its tributary the Uraricaá during ten days in September 1991. During the trip I interviewed gold miners and Xiriana-Yanomami and opened four 5-km-long trails oriented toward the center of the island along which I searched for white-lips and their sign (tracks, rooted areas, feces, and hair). The transect start points were spaced to maximize coverage of the island: two near the center of the island (separated by approximately 5 km) and another two also separated by about 5 km near the westernmost point of the island. All interviews were informal and included the following questions: (a) when was the last time you or someone you know saw white-lipped peccaries or their sign, (b) when was the last time you or someone you know killed a white-lipped peccary, and (c) how many individuals were killed during hunts?

RADIO TELEMETRY

From January 1992 through January 1993, I radio-tracked seven white-lipped peccaries belonging to the only two herds using the eastern portion of Maracá island (region around the research station) and described their seasonal movement patterns and home range use (Fragoso 1994, 1998a, 1999). From June 1995 to May 1997, I again radio-tracked the two herds, which were still the only ones occupying this region of Maracá (Fragoso unpublished data).

INTERVIEWS IN THE MACUXI INDIGENOUS AREA NEAR MARACÁ ISLAND

To the southeast and northeast of Maracá, the Macuxi indigenous people live in widely spread communities. To assess the status of white-lipped peccary populations immediately east of the island, I interviewed four Macuxi Amerindian hunters from a community (Boqueirão) located approximately 20 km southeast of the Maracá study area. Between 1991 and 1992 I repeated the interviews with fifty hunters from Boqueirão and Mangueira, a neighboring Macuxi community located approximately 15 km to the southwest of Maracá. These were the nearest villages in these directions from Maracá.

INTERVIEWS AND SEARCHES IN THE YANOMAMI AREA

To assess the status of white-lipped peccaries in the Brazilian Yanomami area, I spent twenty-one days hunting with Yanomami hunters in April 1993, using the Paapiu area approximately 180 km southwest of Maracá as a base. I also interviewed representatives of thirty-eight Yanomami communities located throughout the reserve, including Yanomami people, indigenous health workers, Western teachers living in indigenous communities, and FUNAI (National Indian Foundation) personnel. These interviews were repeated with representatives of between thirty-five to fifty communities during the Yanomami Peoples Assemblies (which brings together Yanomami representatives from almost all villages) in 1996, 1997, and 1998. I collected information from at least one individual from each community represented at the assemblies. When one village was represented by more than one person, community members conferred before responding to my questions and then provided one community answer.

All interviews were informal and included the following questions: (a) when was the last time you or someone you know saw white-lipped peccaries or their sign and (b) when was the last time you or someone you know killed a white-lipped peccary? Because most Yanomami do not count beyond the number two (the exceptions are a few individuals with Western educations), I approximated the date of the last hunt by estimating the age of a child in the community who was said to have been born in the same year as the hunt.

DOMESTIC LIVESTOCK AND DISEASE

To assess the health of domestic livestock in Roraima state, I reviewed files kept by the Roraima Department of Agriculture in 1996. Complete yearly records were available dating to the early 1970s. In Roraima almost all domestic livestock, including cattle, sheep, goats, pigs, horses, chickens, turkeys, guinea fowl, and ducks are free ranging.

RESULTS

EASTERN END OF MARACÁ ISLAND

Transect data showed that white-lipped peccaries were extremely abundant at Maracá in June of 1988, reaching densities of 139 to 542 individuals per km² (Fragoso 1998b). Herds were encountered 478 times during the 227 search days between June 1988 and June 1989; however, within this time period no peccaries were sighted after March 1989.

During the January 1991 to December 1992 study period, herds were encountered only thirteen times despite a search intensity similar to that in the 1988–1989

study period (220 search days: 103 days in 1991 and 117 in 1992). Thus abundance and density fell sharply between the first and the second study periods; herd encounter rates indicate that the decrease occurred in or shortly before March 1989. Radio telemetry data collected from 1991 to 1992 indicated that the study area supported between 1.4 and 8.3 individuals per km².

RIVER SEARCHERS AND RADIO TELEMETRY

No white-lipped peccaries or their sign were found on the four 5-km-long transects cut in the central and western part of the island. Neither were animals or their sign found in the forest along the northern river channel toward the Yanomami Reserve. Fifteen gold miners interviewed during the river trip stated that they had not seen or killed white-lipped peccaries since 1989.

Radio telemetry data indicated that white-lipped peccaries have fixed home ranges, regularly use the same feeding sites (that is, they return to the same sites in subsequent years), and do not change their home range from season to season (Fragoso 1994, 1998a, 1999). The continuation of the radio telemetry study in 1995–1997 indicated that two herds continued using the same areas (Fragoso unpublished data). Herds were smaller in 1991–1992 (39 and 130 individuals per herd) than in 1995–1997 (70 and 200 individuals). Home-range size for the small and large herds increased from 21 and 109 km², respectively, during the 1991–1992 study to approximately 200 km² in 1997 for the herd with 200 individuals. The increase in home-range size over time as herd size increased and the fact that the large herd always had a larger home range than the smaller herd indicate that home-range size is related to herd size. Radio-collared individuals belonging to these herds were sighted up until November 2002 (J. M.V. Fragoso pers. obs.; G. de Oliveira pers. comm.).

The important point here is that from 1991 to 2002 the area continued supporting only the same two herds. During both tracking periods home ranges were spatially stable (no seasonal or yearly disjunctions in use of areas) within and among years. In other words, herds showed no sign of migratory behavior. They did not maintain two spatially distinct home ranges between seasons or years or between El Niño and non-El Niño years (the El Niño years of 1992 and 1997 caused marked declines in rainfall in the area, according to the climate records of the meteorological office of the Boa Vista, Roraima International Airport).

MACUXI INDIGENOUS AREA NEAR MARACÁ

If the white-lipped peccary population on Maracá and its surroundings had declined, then there should also have been a reduction in the number of peccaries killed by humans. In 1988 the four Macuxi hunters interviewed near Maracá each killed between three and five peccaries per month (Fragoso 1998b). In the year be-

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tween December 1990 and December 1991, however, the fifty hunters interviewed in the same region jointly killed only seven white-lips.

YANOMAMI AREA

No data are available on white-lipped peccary harvests in the Yanomami area prior to 1990. Still, all the Yanomami interviewed, as well as persons associated with the Yanomami, reported that white-lipped peccaries were common prior to 1989. The anthropologist Bruce Albert who worked extensively in this region supported this report. He stated that during his Ph.D. fieldwork white-lips contributed up to 70% of the meat consumed by some Yanomami communities.

In 1993, during twenty-one days of hunting with Yanomami from five communities in the Paapiu area, no white-lips or their sign were encountered. Interviews with persons representing thirty-eight communities scattered throughout the Yanomami Reserve in 1996 and 1997 indicated that most of them had not seen white-lipped peccaries since 1989 or 1990 and some of them not since 1987.

At the 1998 Yanomami Assembly Davi Yanomami reported the return of one herd of white-lips to Ballalawu, a community located on the Parima mountain range that divides Venezuela (Orinoco drainage) from Brazil (Amazon drainage). In 2000 Marcos Wesley da Silva, the education coordinator for the nongovernmental organization Commission for the Creation of the Yanomami Reserve reported that from 1999 to 2000 hunters from Ballalawu had killed white-lips on two separate hunts spaced apart by approximately three months. Indigenous hunters from the communities of Auaris located in the Pacaraima mountains, (approximately 250 km to the northwest of Ballalawu) also noted the reappearance of white-lips in 2000 and reported killing multiple animals. In the Ballalawu case the interviewees reported that, when following the sign left by white-lips, they concluded that the herd(s) had come up over the mountains from the Orinoco drainage (Venezuela) and was (were) moving into the valleys and lowlands of the Amazon drainage. The Auaris informants did not provide information on the directional movement of herds; however, Auaris sits near the top of Pacaraima mountain range, which forms the northern barrier separating the Orinoco and Amazon drainages.

In 2001 white-lips were again killed at all the aforementioned indigenous communities and at Demeni (far southern region of the Yanomami reserve) and close to the communities of Catrimani (near the southeastern extreme of the Yanomami reserve). Essentially, these communities form an outer ring along the western and southeastern boundaries of the Yanomami reserve. In these regions the reserve borders (and forms part of) the greatest extent of contiguous forest of the Amazon basin. This forest extends for about 1,500 km up and over the Pacaraima and Parima mountain ranges to the Andes Mountains. To the south it extends over mountains of 1,000 to 1,500 m above sea level for about 800 km until encountering the main channel of the Amazon River.

DISCUSSION

At Maracá Island Ecological Reserve and in the surrounding Macuxi and Yanomami indigenous areas, white-lipped peccary populations either disappeared or decreased drastically to the point that even expert indigenous hunters could not find them. On Maracá the disappearance or decrease occurred approximately in March 1989. The sudden lack of white-lip sightings on the island and the reduction in white-lip harvests by indigenous peoples suggest that the phenomenon occurred throughout the contiguous forest and adjacent cerrado-savanna biome (with islands of forest) of the northern region of Amazonas and Roraima states in Brazil.

Here I consider three hypotheses that could explain the disappearance of white-lipped peccaries. The first hypothesis is that the white-lips migrated out of the study area. Most of the data collected do not support this hypothesis. The area over which disappearances took place is too extensive, and the vegetation, topography, and rainfall patterns too varied for the entire region to have become uninhabitable by white-lip herds searching for food. Rainfall ranges from 1,500 mm of rain per year in the east to over 2,000 mm in the west of the disappearance range (Barbosa 1997). This variation results in a diversity of biomes and plant associations, ranging from evergreen lowland rainforest to shrub-dominated areas, cerrado, savannas, and montane forest. Tree species identity also changes markedly from east to west: on Maracá alone, for example, 70% of the species that occur on the eastern end of the island are absent on the western end (Milliken and Ratter 1989).

If white-lipped peccary herds migrated seasonally or nonseasonally in search of food, they should have stopped once they encountered new plant communities or biomes with their potential for new and perhaps abundant food resources. At Maracá fruit availability does not seem to have varied greatly between the 1988–1989 and 1991–1992 sample periods (Moskovits 1985; Nunes 1992; Fragoso 1994). Even if fruit availability declined in some habitats due to changes in rainfall patterns (such as those caused by the El Niño Southern Oscillation, ENSO), many white-lip foods become superabundant in ponds and streams as they dry (many of these dry out only during El Niño years) (Fragoso 1999, pers. obs.).

Thus the hypothesis that the white-lips migrated is not supported because (a) fruit and seed availability did not vary between two critical time periods, (b) the white-lips should have appeared in some portion of the study area (110,000 ha on Maracá, 9 million ha in the Yanomami area), and (c) after a season or two, migrating animals should have returned to their original territory as seasons changed. Furthermore, if migrations were linked to major changes in rainfall patterns rather than seasonal changes, the white-lips should have returned when rainfall patterns normalized. Note, however, that white-lips did not return to the Yanomami area after the El Niño event of 1991–1992, and on Maracá they appeared to be unaffected by that El Niño event and those of 1997–1998 and 2002–2003 (Fragoso unpublished data). The herd with thirty-nine individuals in 1991 now contained ninety-seven animals in January 2003, and in March 2003 it split into two herds, one with twenty-

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seven and the other with seventy individuals (J. M. V. Fragoso and K. M. Silvius pers. obs.).

The radio-tracking data provides additional evidence against the migration hypothesis: during the years that two herds were tracked visually and by radio, they used their large home ranges in a regular fashion and gave no sign of migratory behavior (Fragoso 1994, 1998a, 1998b, 1999, unpublished data). They did not leave the area even when food availability was low in some portions of their home range. Their home ranges provided herds with a sufficient food in the appropriate spatiotemporal pattern (Fragoso 1999) to support population increases from 1991 to 1997 and possibly until 2002.

The only other published study that used radio telemetry to evaluate white-lip herd movements tracked thirty-six individuals in Corcavado, Costa Rica, from 1996 to 1998 and also found that herds did not migrate (Carrillo, Saenz, and Fuller 2002). White-lips did not exhibit migratory behavior at Corcavado even when rainfall decreased dramatically from one year to next because of an El Niño event. The decreased rainfall correlated with a drop in fruit production in the area; however, as in Fragoso's 1999 study the Corcavado white-lips responded by expanding home-range areas to include more habitats rather than by migrating (Carrillo, Saenz, and Fuller 2002).

The second hypothesis, that white-lipped peccary populations were reduced by overhunting, is also difficult to support. White-lips disappeared in 1989 from many areas, whereas the influx of gold hunters into the Yanomami area began in 1983 and reached its peak in 1987 (MacMillan 1995). One would expect overhunting to impact the populations much more rapidly, given that approximately 40,000 gold miners were living and hunting in the area. Furthermore, ten of the Yanomami communities that reported losing white-lips in their hunting areas (Yanomami hunting areas are somewhat larger than the home range of a white-lipped peccary herd; Good 1989) were not invaded by gold miners. If hunting by invaders had caused the loss of white-lips, these noninvaded areas should not have been affected. Additionally, while some illegal hunting by gold miners may have occurred along the northern margin of Maracá, white-lips disappeared from the eastern portion of the island at the same time as in the Yanomami Reserve. This part of Maracá was heavily patrolled by over 100 biological workers of the Maracá Research Project of the Royal Geographical Society and the National Institute for Research in the Amazon (INPA) from the beginning of 1987 to 1989 (Milliken and Ratter 1998).

The third and final hypothesis is that mortality from an epidemic caused a decline in white-lipped peccary populations at the regional level. The following observations support this hypothesis:

1. White-lip populations in noninvaded areas of the Yanomami reserve disappeared.
2. The factor that affected the white-lip populations must have been something that can affect individuals dispersed over an enormous area. Such a widespread agent

- is a characteristic of epidemics in other mammal populations (Crosby 1986; Young 1994).
3. A researcher working with primates on Maracá at the time of the disappearance found the bodies of five white-lipped peccaries at one site (A. Nunes pers. comm.), and her description of the carcasses indicates that they were not killed by humans or other predators.
 4. In 1989 there was an epidemic in free-ranging domestic pigs on ranches adjacent to Maracá and the Yanomami reserve. The disease, undocumented and unidentified by veterinarians, killed over 50% of newborn piglets and caused a higher than normal mortality in adult pigs (J. Alves, local rancher, pers. comm.).
 5. In 1989 there was a documented outbreak of foot and mouth disease in cattle on these same ranches (J. Alves pers. comm.). Further, the largest outbreak of foot and mouth disease documented for Roraima state occurred in 1989 (records maintained by the Roraima Department of Agriculture).
 6. Both the pig and cattle disease outbreaks occurred at the same time that white-lips disappeared on Maracá and in the Yanomami area.
 7. When gold miners entered the Yanomami area, they brought with them domestic pigs as a source of food (Fragoso pers. obs.).
 8. White-lipped peccaries live in herds of more than 100 individuals, the number of animals necessary to maintain an epidemic in a reinfection cycle (A. Dobson pers. comm.).
 9. Where they cooccur, free-ranging or feral domestic pigs and white-lips share use of wetland areas.
 10. Because white-lipped peccaries are not territorial, they do not maintain exclusive use home ranges, and herds occasionally come together (Fragoso 1998a). This socioecology would allow the rapid dissemination of a disease among herds and across the entire population.

Disappearance patterns similar to those described here have been reported for white-lipped peccaries in other areas. For example, white-lips disappeared from Manu National Park, Peru, from 1981 to 1992 (L. Emmons and J. Terborgh pers. comm.), from the Siono-Secoya area of Ecuador from 1975 to 1985 (Vickers 1991), and from the Yuqui area in Bolivia in 1985 (Stearman 1990). In all these cases researchers working in the areas interpreted the disappearances as migrations. It should be noted that in all cases white-lips remained absent from the areas for approximately ten years. Such long periodicity is not normal in migratory ungulates, but it is typical of mammal populations that exhibit boom and bust cycles (Krebs and Myers 1974). Note the reappearance of white-lips in the Yanomami area from 1997 to 2000 after having been absent for about eight to eleven years.

I suggest that what has been described as white-lipped peccary migrations may in most cases have been in situ population declines. Such population cycles are probably a normal characteristic of this species' life history. I propose, however, that the characteristics that make white-lips susceptible to endemic diseases also make

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them susceptible to exotic diseases to which they have no resistance and which can cause more marked population declines with a longer recovery time than that of cycles caused by endemic diseases. The relationship between white-lips and domestic livestock may thus be similar to that between native Amerindian populations and the humans that migrated, together with their diseases, from the Old World.

Most of this report was first presented at the wildlife meeting in Iquitos, Peru, in 1995 and included data collected up until December 1992. As described above, I continued working at Maracá and in the Yanomami area from 1994 to the present (2003), tracking the same herds on the eastern end of Maracá in 1995–1997 and visiting Maracá and/or the Yanomami region in 1998, 1999, 2000, 2001, and 2002 for at least one month each year. Two herds are still using what appear to be the same home ranges in 2002 (Fragoso pers. obs.). This constancy means that the same herds have remained in the same general area for at least eleven years. During this time period herd size has increased, and the largest herd has expanded its home range to the north and west, but both herds still use the same areas they used in 1990–1992 and have not been absent from the study site during the entire period. In addition, the increase and splitting of the smaller herd in 2003 suggests that on Maracá populations are at or nearly at their high points and may once again enter a decline. If true, herds splintering off from the main groups should begin dispersal movements out of their natal home ranges, as discussed below.

On the basis of my extended observations, especially the increase in herd size and the apparent movement of white-lipped peccaries from the Orinoco basin into the Amazon basin, I propose the following scenario for the large scale spatiotemporal ecological dynamics of white-lip populations:

1. White-lip herd disappearances are the result of epidemic outbreaks of disease (either endemic or exotic) that kill off most individuals.
2. In areas where there is hunting by humans, this activity may extirpate white-lips that survive the epidemic.
3. Where there is/was no hunting, populations decline, but enough individuals survive to allow the slow repopulation of an area. At Maracá this has been a thirteen-year period from 1989 to the present, but abundance/density levels have yet to attain the levels observed in 1988–1989.
4. Where hunting may have extirpated populations, initial reappearance is slower (eight to twelve years in the Yanomami area), and this reappearance occurs through a process of recolonization by herds dispersing from very distant areas (hundreds of kilometers) that travel across major geographical barriers (e.g., mountain ranges).

White-lip abundances in the Yanomami reserve are only now approximating the levels observed on Maracá in 1990–1992. Of interest is how long it will take for white-lip populations in the Yanomami area to return to pre-1989 levels, when they formed up to 70% of the meat consumed by many Yanomami communities.

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If the above scenario is correct, then white-lip populations fluctuate synchronously across very large spatial and temporal scales (perhaps decadal time scales). I predict that white-lip populations in both the Yanomami reserve and Maracá will continue increasing and should eventually attain the very high densities observed prior to 1989. At high densities herds will fission and subherds disperse away from the very large resident parent herds. Subherd dispersal will move individuals away from their natal home range toward areas unoccupied by other herds. This type of movement is best described as a population-level dispersal event and not as a migration. Note that this process may already have started at Maracá. There is evidence that herds have begun dispersing across the rivers, as they did prior to 1990. From December 2002 to March 2003, a herd was observed on numerous occasions on Nova Olinda island (G. de Oliveira pers. comm.), an approximately 1000-ha island that lies between Maracá and the mainland. White-lips did not use this island from 1991 to 1997.

Dispersal of this type is probably responsible for the recolonization of the Yanomami reserve by white-lips. This type of dispersal may also explain the cross-river movement of white-lips observed from Maracá in 1987–1988 during the period of peak population densities (J. Hemming, J. Thompson, and G. de Oliveira pers. comm.) and records of white-lips crossing the savannas of northern Roraima (J. Alves and G. de Oliveira pers. comm.). These dispersal events may also be what indigenous peoples refer to when they say that the “white-lips eventually return.” There are many valid definitions of migrations (see Baker 1978), but all necessitate returning to the start point. Dispersion means movement away from a source, most likely without return. At the metapopulation level white-lip populations appear to be linked across scales of thousands of square kilometers. Maintaining white-lip metapopulation dynamics at this scale will continue to be a major challenge as the Western colonization zone penetrates deeper into the Amazon forest.