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Home Range and Movement Patterns of White-lipped Peccary (*Tayassu pecari*) Herds in the Northern Brazilian Amazon¹

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ABSTRACT

Two white-lipped peccary (*Tayassu pecari*) herds were radio-tracked for 5 and 13 mo, respectively, on Maracá Island Ecological Reserve, Roraima, Brazil. Home range size was 109.6 km² for the larger herd (130 animals) and 21.8 km² for the smaller herd (53 animals). Neither herd migrated or moved nomadically during the study period. The herd with the longer observation period increased its home range size during the flooded season by including new sites not used in the nonflooded season and continuing to use the nonflooded season sites. This pattern of simultaneously using distinct seasonal ranges also occurred between the rainy and dry periods and the herd regularly and predictably returned to favored feeding sites. Population declines and disappearances in this study and others may have been caused by *in situ* mortality rather than by long-distance movements.

Key words: home range size; mammal densities; Maracá Island; migration; population declines; white-lipped peccaries.

WHITE-LIPPED PECCARIES (*Tayassu pecari*) are one of three species of peccaries (Tayassuidae) inhabiting the Neotropics (Eisenberg 1989). They are among the largest ungulates in tropical South and Central America (25–40 kg; Robinson & Redford 1986), smaller than tapirs (*Tapirus* spp.) but about the same size as *Mazama americana* deer (ca 40 kg). They range throughout the wet and dry tropical forest regions from southern Mexico to northern Argentina (Leopold 1959, Sowsls 1984, Mayer & Wetzel 1987, Eisenberg 1989, Redford & Eisenberg 1992). White-lipped peccaries (white-lips) are one of only two species of tropical forest ungulates, the other species being the bearded pig (*Sus barbatus*) of southeast Asia (Caldecott 1988), that form large herds containing at least 200 individuals (Sowsls 1984). There are anecdotal accounts of herds with 1000–2000 individuals (Mayer & Wetzel 1987).

Our knowledge of white-lipped peccary biology derives mainly from two studies. Kiltie (1980, 1981a, b, c; 1982) and Kiltie and Terborgh (1983) examined niche separation between white-lipped and collared peccaries (*Tayassu tajacu*) based on their jaw morphologies and mechanics from museum specimens, describing white-lip behavioral ecology based on signs left by passing herds and

the number of visits to a single site. Bodmer (1989a,b; 1990; 1991a,b; 1993, 1995a,b) analyzed the stomach contents of hunter-killed animals and estimated population densities using these kills and counts along transects. Additionally, Sowsls (1984) provided a description of white-lip behavior from observations of a herd feeding at bait stations in the Atlantic forest of Brazil. Mayer and Wetzel (1987) and March (1993) have reviewed this literature.

Several researchers have suggested that white-lipped peccaries are migratory (e.g., Sowsls 1984; Bodmer 1989a, 1990) or nomadic (e.g., Kiltie 1980, Kiltie & Terborgh 1983), but white-lips had not been radiotracked prior to this study. Therefore no measures of home range size existed and there was no evidence to support or disprove hypotheses of migration or nomadism. I used ground and aerial radiotelemetry as well as visual locations to study the home range, movements, and other behaviors of a wild population of white-lipped peccaries in Amazonian Brazil. Here I describe home range size for two herds and discuss the relationship between herd size, home range size, and population density. I test the null hypothesis that white-lips do not migrate by comparing nonflooded and flooded season home ranges and locations, and dry and rainy season locations; if white-lip herds migrate, the two ranges should be spatially distinct (Baker 1978). I test the hypothesis of irregular movements (nomadism) by looking for predictable foraging patterns and a pattern of consistently repeated visits to sites within a distinct home range. If white-lips

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repeatedly return to distinct spots, they are not nomadic.

METHODS AND STUDY SITE

STUDY AREA AND DATE.—Maracá Island lies at 3°25'N and 61°40'W, on the northern edge of the Amazon River basin in Roraima State, Brazil. Approximately 60 × 25 km at the longest and widest points, this riverine island is formed by the branching of the Uraricoera River, a tributary of the Rio Branco (Amazon drainage). All 110,000 ha of tropical rain forest, wetlands, and isolated savannas on the island are protected by I.B.A.M.A. (Brazilian Institute for the Environment) as the Reserva Ecológica Ilha de Maracá, a site for research and forest protection. The dominant vegetation of the region is primary tropical evergreen lowland rain forest (Moskovits 1985), contiguous with the Amazon rain forest (Milliken & Ratter 1989). In addition to white-lips, Maracá supports populations of collared peccaries (*Tayassu tajacu*), tapirs (*Tapirus terrestris*), pumas (*Felis concolor*), jaguars (*Panthera onca*), and other animals typical of a Neotropical rain forest area undisturbed by Europeans and their descendants (Moskovits 1985, Fragoso 1998). Although small mammals may show disjunct distributions between the "mainland" and the island, large mammals are continuously distributed and their populations appear to overlap both river banks (Fragoso, pers. obs.). White-lipped peccaries, tapirs and large and small cats have been observed crossing the river (Fragoso, pers. obs.; Dr. Jill Thompson, G. de Oliveira pers. comm.), which at some points is as narrow as 10 m. There have been no permanent human settlements on the island within historical time (although an Indian village may have existed on Maracá in the mid 1800s; J. Proctor & R. Miller, pers. comm.), and it has never been logged. Approximately eight isolated families lived at different times along the river banks of the eastern tip until 1977. A low human population density near Maracá results in minimal illegal hunting on the outskirts of the reserve along navigable areas of the river; hunters avoid the area around the research station. The study site is described in detail in Fragoso (1994). The study of white-lipped peccaries extended from December 1990-January 1993. The study area was limited to about 114 km² on the eastern part of the island, the area used by the two study herds.

WHITE-LIP CAPTURES.—To determine the presence

of white-lips or their signs (tracks, rooting and scent) in the study area, 60 km of trail were searched every two days (by two teams operating separately) almost continuously from January 1991-December 1992. More intensive searches were conducted for signs (tracks or rooted soil) along preferred areas such as *Mauritia flexuosa* swamps and creek beds. Herds encountered were stalked and the nearest adult-size animal tranquilized with 2.5 ml of Ketamine and 0.5 ml Azaperone, delivered by a Tele-inject dart gun. Animals that were not completely tranquilized by the first injection were administered an additional 0.5 ml of Ketamine. I was assisted in the tracking and capturing by a Macuxi Amerindian hunter. For each individual captured, standard body measurements were recorded (Fragoso 1994), as well as sex, age (young, juvenile, or adult), reproductive condition, herd size, time, date, and location. All captured animals were marked with an individually numbered ear tag with a color unique to each herd, and six received Telonics radio collars around their necks. The animals were monitored until they recovered sufficiently (1–3 h) from tranquilization to walk beyond sight. To determine if captured white-lips rejoined their herds and to monitor herd movements, radios were placed on at least two individuals/herd, and animals were visually located a few days after their capture. Activity monitors on the radiotransmitters indicated when the animals were active or inactive.

RADIO-TRACKING, HOME RANGE AND MOVEMENTS.—Radio-collared animals were usually located twice a week from a Challenger ultralight airplane equipped with a Telonics H-antenna on each wing, flying at an altitude of between 250–650 m above the forest canopy. Searches were initiated by circling over the last known location for an animal, then flying in parallel lines separated by 2 km from that point until the signal was located. Individual aerial searches were continued until all animals were located. Locations were immediately plotted. Due to hazardous climatic and flying conditions, and the type of airplane used, flying was limited to 0600–0930 h in the morning and 1500–1800 h in the evening. Whenever possible, follow-up visual-ground locations were conducted throughout the day using a three-element Yagi antenna. In some instances, animals were located only from the ground.

The percent convex polygon method of the computer program HOME RANGE (Ackerman *et al.* 1990) was used to compute home range size

based on the placement of locations within a 310×310 m square of land. Home range sizes are presented using both 100 percent of the locations (100% contour line) and 95 percent of locations (95% contour line). Ackerman *et al.* (1990) discuss the advantages and disadvantages of using the different contour lines for estimating home range size. I rely on the 100% contour line because it incorporates the maximum number of locations when calculating home ranges.

Seasonal range use was examined using two separate criteria: (1) comparing range use between flooded and nonflooded seasons, defined as sequential periods when streams and seasonal ponds are with (July–December 1992) and without water (January–June 1992), respectively; and (2) comparing range use between wet (or rainy) and dry seasons, the sequential months when it actually rains (April–September 1992) and the dry period when rains are light and scarce (January–March 1992 and October–December 1992). The two season types did not overlap completely in time, and white-lip movements may have been influenced more by the presence of surface water than by rainfall (Bodmer 1990). I present home range sizes for the flooded and nonflooded seasons, and compare the locations of animals in the flooded and nonflooded, and wet and dry seasons.

ACTIVITY OBSERVATIONS.—To determine the frequency of white-lip visits to sites within their home range, detailed observations were conducted of their activity at one site, a drying pond full of eels and other fish (Savanna Pond). The presence of white-lips was checked visually and by radiotelemetry four times/d (*ca* 0700, 1200, 1800, and 2000 h) from 26 January–29 March 1992. I noted the time herds visited the pond, their length of stay, their departure time and described their activities. Herds in or by the pond were observed visually with 10×40 Zeiss binoculars, from an observation platform located 4 m up a tree and 50 m from Savanna Pond.

POPULATION DENSITIES.—Population densities were determined through repeated counts of animals/herd. The most accurate count (based on unobstructed observation of the entire herd) was divided by the amount of area used by that herd. For areas where herd ranges overlapped, I divided the total number of animals by the area used in common.

RESULTS

WHITE-LIP OBSERVATIONS, CAPTURES, TRACKING PERIODS, AND LOCATIONS.—I first observed a white-

TABLE 1. *White-lipped peccary captures/herd, number of locations, number of months tracked (number of months on which locations were obtained) and the date of the first and last location/individual.*

| Herd | Individual no. | No. months tracked | No. of locations | Date of capture and start of tracking | Last location mo/d/yr |
|------|----------------|--------------------|------------------|---------------------------------------|-----------------------|
| A | 108 | 3 | 33 | 01 30 92* | 03 02 92 |
| A | 146 | 7 | 42 | 02 07 92 | 07 15 92 |
| A | 109 | 13 | 67 | 02 10 92 | 01 08 93 |
| A | 105 | 7 | 34 | 02 10 92 | 07 15 92 |
| A | W6 | 8 | 27 | 02 22 92 | 08 06 92 |
| B | 117 | 5 | 46 | 07 16 92 | 11 16 92 |
| B | 101 | 3 | 31 | 08 06 92 | 10 30 92 |

* Note that tracking began on 26 January 1992, when this herd was first sighted.

lip herd of 30–40 animals on 8 January 1991 near Savanna Pond. A herd with a similar number of individuals (30–50) was encountered on 28 June at Forest Lake, 3 km distant, and again on 5 and 15 July. On 1 December 1991, 46 white-lips were seen near Forest Lake, and 40 individuals were sighted at Savanna Pond on 26 January 1992. On 30 January, I captured the first individual (a female, no. 108) from the above group (henceforth herd A), that was still at Savanna Pond (Table 1). I then captured a male (146) on 7 February, two males on the 10th (109 & 105) and lastly, male W6 on the 22nd. The similarity between the number of white-lips observed in the herd(s) early in the study and herd A suggests that it was the same group. This is supported by the home range analysis which indicates that all of the precapture herd observations occurred within herd A's home range.

With the exception of one observation for a herd of between 100–200 individuals on 6 September 1991, herd A was the only white-lip group encountered on and east of the trail system from the time of the first white-lip capture until 13 July 1992, when a second herd entered the region. On 16 July, I captured a female belonging to the latter herd (herd B), followed shortly by another female capture (Table 1). This herd contained *ca* 130 animals and could have been the same herd observed on 6 September. No herds other than those with radio-collared animals were subsequently encountered in the study area.

I thus captured a total of seven white-lips, five in herd A and two in herd B. Four of the herd A individuals were radio tagged; male W-6 was ear tagged only. All of the captured white-lips suc-

TABLE 2. *The nonflooded (January–June 1992) and flooded (July 1992–January 1993) seasons, and yr home range sizes of white-lipped peccaries from two herds at the 100 and 95 percent contour intervals. Also shown are the number of locations for each animal, the number of locations defining the boundary of the home range, and the mean distance between consecutive locations. N-100% and 95% indicate number of locations for 95 and 100% contours, respectively. Differences in individual home ranges for peccaries in the same herd result from differences in length of tracking times.*

| Herd/season | Individual | Home range size-100% (km ²) | Home range size-95% (km ²) | N-100% | N-95% | Mean km between consecutive locations |
|--------------|------------|---|--|--------|-------|---------------------------------------|
| A | 108 | 11.5 | 11.9 | 33 | 31 | 1.2 |
| A | 146 | 18.6 | 16.7 | 42 | 39 | 1.6 |
| A | 109 | 21.8 | 17.7 | 66 | 62 | 1.5 |
| A | 105 | 13.2 | 13.0 | 33 | 31 | 1.6 |
| B | 117 | 109.6 | 59.3 | 8 | 43 | 2.4 |
| B | 101 | 87.5 | 51.4 | 9 | 29 | 2.6 |
| A Nonflooded | 109 | 12.5 | 11.4 | 29 | 27 | 1.5 |
| A Flooded | 109 | 21.7 | 17.6 | 37 | 35 | 2.4 |

cessfully rejoined their herds, and all but one remained with them until their deaths. The one exception was subadult W6, which dispersed from herd A to B. Individual white-lips were radio-tracked for 3–13 mo, and the number of locations/animal ranged from 27–67 ($x = 39.9$, $SD = 13.2$; Table 1). I obtained location data for herd A for 13 mo from 26 January 1992–8 January 1993 (but the pretracking observation data indicated the herd probably used the area for at least 27 mo) and for herd B for 5 mo (probably 10 mo based on the September 1991 sighting). Forty-four percent of herd A's and 50 percent of B's locations were obtained from the airplane using radiotelemetry; the remaining positions were derived from visual observations of animals during ground telemetry location. Variation in tracking time and number of locations among individuals occurred due to loss of collars or the death of some animals.

WHITE-LIPPED PECCARY HOME RANGES.—Herd A was radiotracked for one year, both in the non-flooded and flooded, and dry and wet seasons, while herd B was followed only for the wet season. The home range of a herd consisted of the locations for the longest surviving herd member (Table 1). Home range size increased with herd size (Table 2); herd A with 39 white-lips (53 individuals at the end of the study) ranged over 21.8 km², while B with 124–134 individuals ranged over 109.6 km². On average, the individuals in the larger herd traveled farther between locations than those in the smaller group (Table 2).

The two white-lip herds had overlapping home

ranges, with A's home range being almost completely encompassed by B's (Fig. 1). Generally, the two white-lip herds remained apart. However, aerial locations just before sunset and a confirming location just after sunrise the following day, indicated that the herds spent the night at the same site on three occasions. White-lips do not usually travel at night, as revealed by 24-h activity monitoring (Fragoso 1994). The nature of these encounters could not be determined from the airplane, but at 0700 h the morning after the first night together (18 July), radio signals indicated that the alpha male from herd A was active while female 117 from herd B was inactive (resting or sleeping). The two herds were again together from 1714 until at least 1745 h on 29 August. At that time all three radio-collared individuals in the two herds were active. The herds were again together from 3–4 November, during which time they slept and foraged near one another. After the first two nights together, the herds separated and moved in *ca* opposite directions. During the third meeting, they foraged and traveled within hearing and smelling distance (*ca* 50–100 m) of one another for at least two days.

After the first herd meeting, the subadult male W6, originally of herd A, was seen traveling and foraging with herd B on two separate occasions when A was 4 km distant. W6 thus seemed to have dispersed from his presumed natal herd to the larger group after the two herds had come into contact.

POPULATION DENSITIES.—With increasing herd size, the number of individuals/km² decreased from 2.4 for herd A ($N = 53$) to 1.2 for B ($N = 134$).

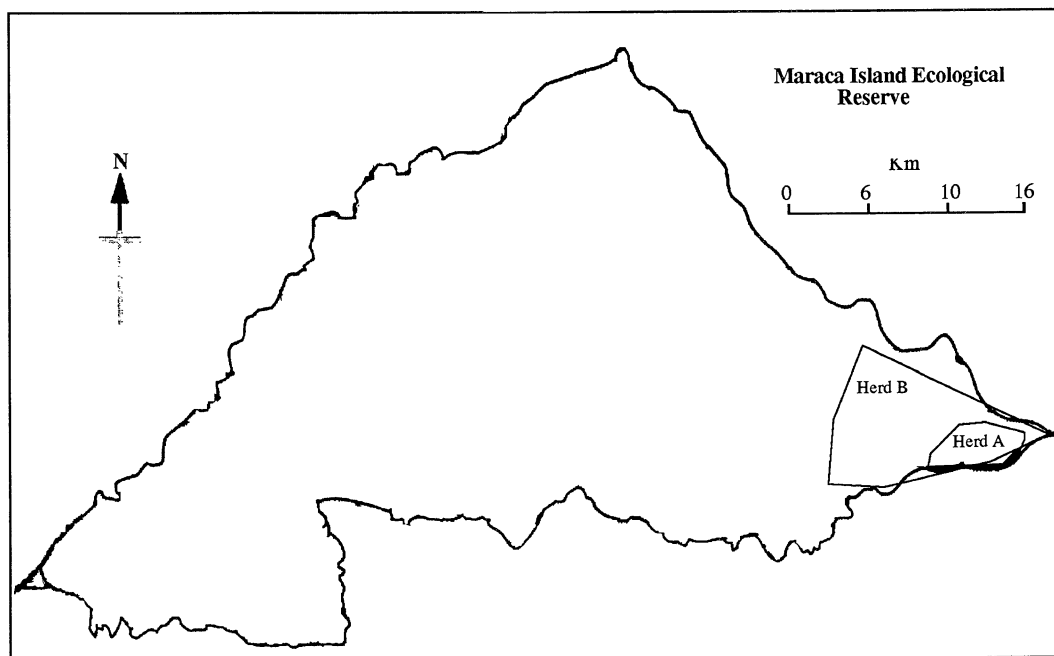


FIGURE 1. The spatial extent and relationship of two white-lipped peccary home ranges on Maracá Island Ecological Reserve.

These figures are not true density estimates because the herds had overlapping home ranges, with A's home range almost being completely encompassed by B's (Fig. 1). Since we know that herd A's home range supported two white-lip herds, we can determine population density for this area by dividing the number of white-lips in the two herds by the area ($177/21.8 \text{ km}^2$). This gives $8.1 \text{ white-lips/km}^2$. Similarly, we can also estimate the density for the remaining 87.9 km^2 of herd B's home range by dividing 124 animals into the 87.9 km^2 . This assumes that no other herds ranged over the area and gives $1.4 \text{ white-lips/km}^2$. Thus, the white-lip population density for eastern Maracá can range from $1.4\text{--}8.1 \text{ white-lips/km}^2$.

WHITE-LIP HERD MOVEMENTS: MIGRATORY, NOMADIC, OR REGULAR?—I tested the hypothesis that white-lips migrate by examining the prediction that herds have distinct seasonal ranges. Home range size varied between the flooded and non-flooded seasons (Table 2; Fig. 2a). This was most evident for herd A, the only group for which there was sufficient data for a seasonal comparison (Fig. 2). For herd A, home range size almost doubled from the nonflooded (January-June 1992) to the flooded season (July 1992-January 1993), from

12.5 to 21.7 km^2 (100% contour intervals and 95% intervals equal 11.3 and 17.6 , respectively). However, this increase resulted from an expansion outward around the entire nonflooded season home range boundary, rather than from a seasonal movement into a new and discrete flooded season range (Fig. 2a). The same pattern occurred in the comparison between the wet and dry season locations (Fig. 2b). The herd continued using their dry season range along with the wet season extension, so that wet season locations were at times identical with dry season locations. In contrast, herd B made one trip of 13 km into a new area to the west of the island on 23 September (Fig. 3), which may have been related to changing rainfall patterns; however, by 30 September they had returned to their previous foraging area. Since this herd did not move into this foraging area until 13 July, it is not surprising to discover their use of a more distant region of their home range. As with herd A, herd B continued to use its old range despite a new wet season location.

Herd A repeatedly returned to a food-rich pond (Savanna Pond) in the savanna from 26 January-29 March 1992 (Fig. 4). These visits ranged in length from a few hours to 6 d, for a total of 23 d (Table 3). Herd A visited Savanna Pond seven

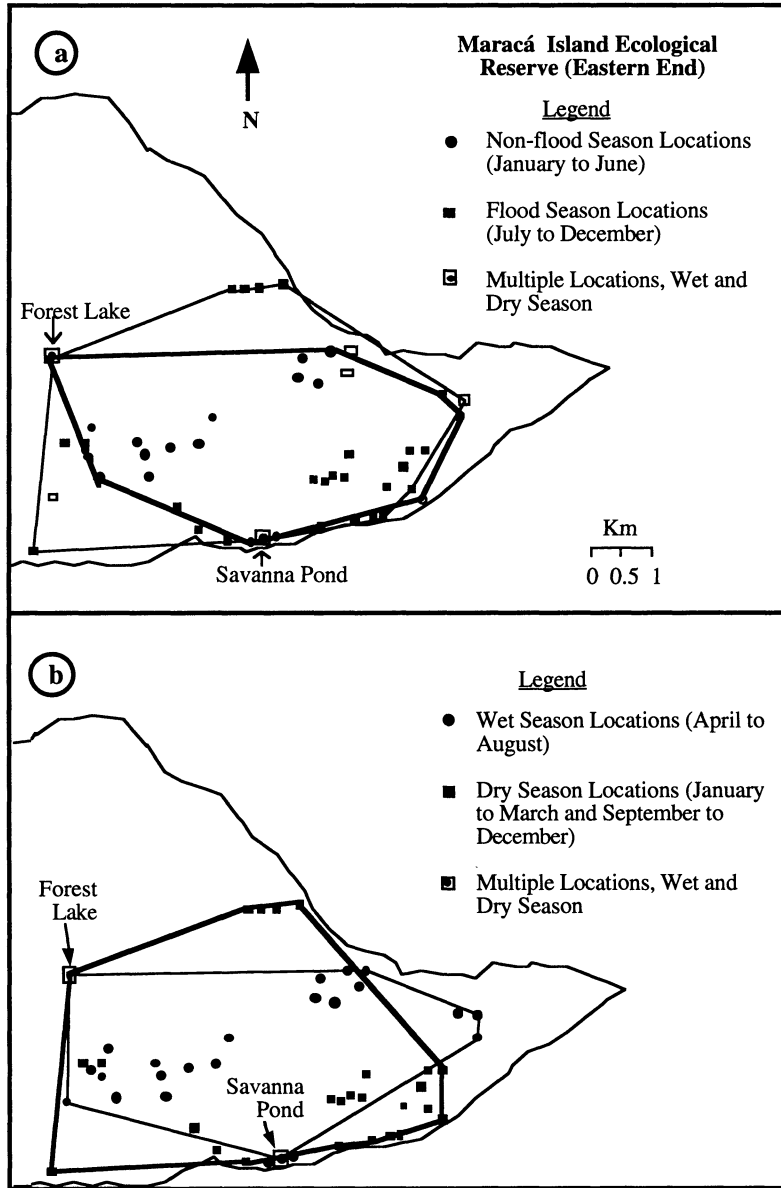


FIGURE 2. Locations and ranges for white-lip herd A for (a) nonflooded and flooded season and (b) rainy and dry seasons. Also shown are the locations of Forest Lake and Savanna Pond.

times from 26 January–29 March (Fig. 4). On the few occasions when the peccaries left Savanna Pond, they visited Forest Lake, a *Mauritia* wetland in terra firme forest, or a creek flowing through the riverine forest. These were brief visits from which they always returned to Savanna Pond. The white-lips visited the pond to eat eels and other fish exposed by the evaporating water. The pattern of visits to the pond decreased in frequency and length

in March, a change correlated with the almost complete drying of the pond and the absence of fresh fish.

The herd last visited the pond during this cycle on 29 March, when it had almost completely dried out. After this they began spending more time in *Mauritia* wetlands (11/44 locations for this period) and terra firme forest (11/44 locations). In early September they began utilizing riverine habitats to

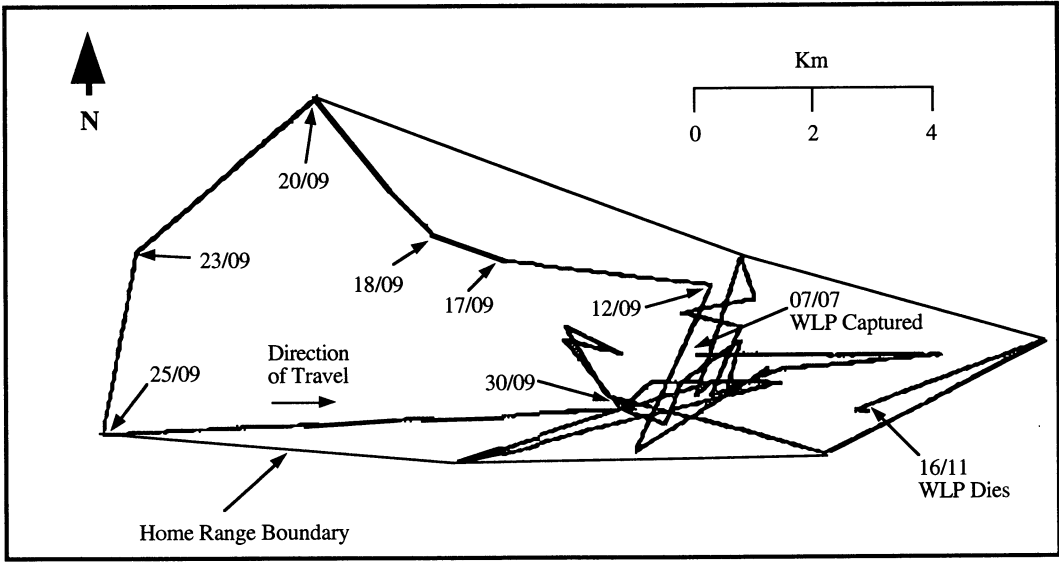


FIGURE 3. The straight-line movements of white-lip herd B as determined from consecutive radio-telemetry locations. Movements occurred from 16 July to 16 November 1992, within the home range depicted in Figure. 1. The dates of key locations (d/mo) are noted. Note that from 12–30 September, the herd travelled 25 km, following a circular route and returning to their point of origin.

a greater degree and continued doing so until November (10/44 locations for this period), when they once again began using Savanna Pond (January 1993) at the time the site was again in the initial stages of drying out.

DISCUSSION

WHITE-LIPPED PECCARY HERD DYNAMICS ON MARACÁ.—Although there were identifiable single sex subgroups within white-lip herds (Fragoso 1994),

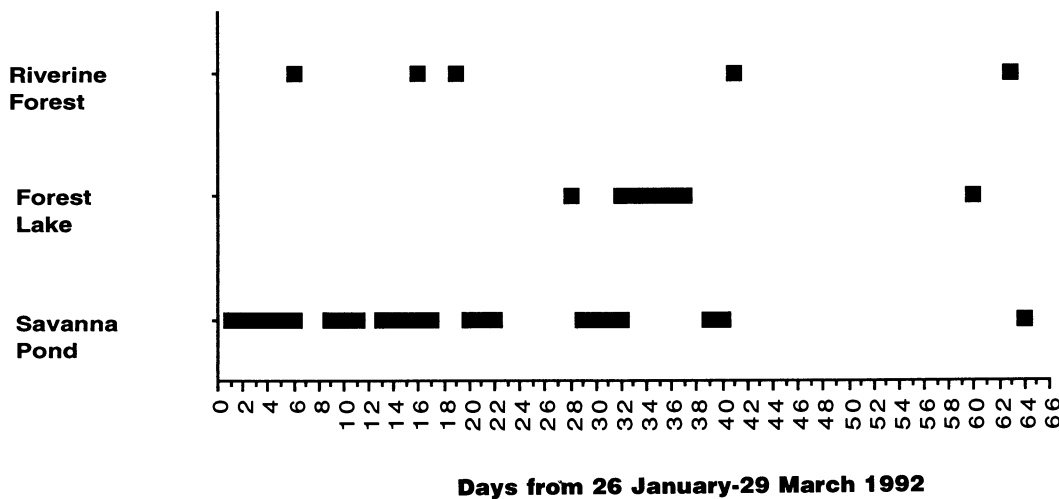


FIGURE 4. The frequency and periodicity of white-lip herd A's foraging visits to two drying ponds (or lakes) and the riverine forest adjacent to Savanna Pond. Unbroken bar indicates that the animals remained continuously at the site.

TABLE 3. *Dates of telemetry and visual monitoring of white-lipped peccary herd A at Savanna Pond. Also presented are the number of hours/observation period, and the days/nights of 24-h monitoring.*

| Date | Observation type | | | |
|--------|----------------------------------|---------------------------|------------------------------|--------------------|
| | Telemetry & visual (h:min) | Visual only (h:min) | Telemetry only (h:min) | Night telemetry |
| 26 Jan | | 2:00 | | |
| 29 Jan | | 3:00 | | |
| 31 Jan | | | 4:00 | |
| 03 Feb | 5:00 | | | |
| 04 Feb | 11:47 | | 4:13 | |
| 05 Feb | 12:05 | | | |
| 07 Feb | 3:39 | | 1:43 | |
| 08 Feb | 11:00 | | 1:28 | |
| 09 Feb | 3:35 | | 7:20 | |
| 10 Feb | | | 9:55 | |
| 11 Feb | 12:00 | | 2:30 | |
| 12 Feb | 12:00 | | 3:00 | |
| 13 Feb | | | 3:00 | |
| 14 Feb | 5:26 | | 5:19 | Yes |
| 15 Feb | 11:30 | | 9:30 | Yes |
| 16 Feb | 2:23 | | | |
| 23 Feb | 5:45 | | 5:30 | |
| 24 Feb | 9:45 | | 4:00 | |
| 25 Feb | 11:27 | | | |
| 19 Mar | | | 3:45 | Yes |
| 20 Mar | | | 17:00 | Yes |
| 28 Mar | | | 9:00 | |
| 29 Mar | 3:30 | | 0:38 | |
| Total | 119:36 | 5:00 | 91:51 | |

the herd remained together throughout the year. White-lip herds were extremely cohesive units; individuals were never alone or beyond the hearing and scent range of the group. Nor did they fission as seasons changed or food availability declined, in contrast to the well-known fusion and fissioning pattern of collared peccary herds (Castellanos 1983, Fragoso 1994, Robinson & Eisenberg 1985, Barreto & Hernandez 1988). Splintering in collared peccaries is related to a seasonal decline in food availability (Castellanos 1983, Robinson & Eisenberg 1985, Barreto & Hernandez 1988). A similar splintering pattern occurs in collared peccaries in the southwestern desert areas of the United States (Sowls 1984). Many groups of tropical primate species also fission when food availability is reduced or becomes more patchy (Terborgh 1983, Symington 1990).

White-lipped peccary herds had overlapping home ranges, indicating that they do not maintain exclusive use of areas. This differs from the situation found by Taber *et al.* (1994) for sympatric

Chacoan (*Catagonus wagneri*) and collared peccaries in the Paraguayan Chaco. The four Chacoan peccary herds and the collared herds Taber *et al.* (1994) followed, showed very little overlap among conspecifics in territory area, although collared peccary home ranges were almost completely encompassed within the larger Chacoan territories. Collared peccary herds on Maracá also had exclusive home ranges (Fragoso 1994).

The only other tropical rain forest ungulate forming herds comparable in size to those of white-lips is the bearded pig (*Sus barbatus*) of southeast Asia (Caldecott 1988, 1992; Caldecott *et al.* 1993). In this species, solitary males and small female-offspring units are the norm with larger herds forming irregularly, apparently in response to spatially and temporally localized high densities of fruits. In contrast, white-lip herd size remained large and fairly constant over time and among seasons. This suggests that white-lips experienced no severe food scarcity over two years, a counterintuitive conclusion given the large biomass of a peccary herd and the evidence for regular lean seasons in some Neotropical areas (Glanz 1982, 1990; Terborgh 1983; Milton 1990; van Schaik *et al.* 1993). However, white-lips doubled their home range size from nonflooded to flooded season which indicated that they found sufficient food by searching for seasonal foods over a larger area. In the flooded varzea forests of Amazonian Peru, the reverse seems to occur. Home range size may increase from the flooded to nonflooded season; this speculation is based on an observation by Bodmer (1990) that white-lip herds move into the varzea forests when they are not flooded.

HOME RANGES AND DENSITIES.—White-lipped peccary home range size appeared to be related to herd size. Herd A with 39 white-lips ranged over 22 km² and B with 130 individuals ranged over 109 km². There are no other home range values in the literature to allow comparisons of home range size for herds of other sizes or in other habitats. Kiltie and Terborgh (1983) estimated herd densities at 1/60–200 km² in Manu National Park-Peru, numbers interpreted by other researchers to be synonymous with the home range size of the 90–138 white-lips observed by Kiltie and Terborgh (*e.g.*, March 1993).

Peccary densities, like those of other large mammals, may fluctuate or oscillate on several scales: the large, multiyear scale of population cycles and the smaller, within year scale as a herd moves tens of km within its home range. For ex-

ample, herd A's home range contained 4.2 animals/km² during the nonflooded season. Density would have decreased to 2.4 individuals/km² for the flooded season if herd A had remained the only group in the area. However, because herd B moved into the region during the flooded season, density actually increased to 8.1 white-lips/km². The usual transect methodology used to measure densities cannot distinguish between these two scales of variation, unless transects are carried out repeatedly over the long-term and used only for within site and among year comparisons. Short term studies used to compare widely separated sites (e.g., Emmons 1984, Gentry 1990) may not be valid.

WHITE-LIP MOVEMENTS: MIGRATORY, NOMADIC, OR IRREGULAR?—White-lips on Maracá exhibited regular and predictable movements within a well-defined home range. Despite changes in food availability over the year (Fragoso 1994), herd A had not moved in a migratory (cf. Baker 1978) or nomadic manner. Herd B may have either migrated seasonally or expanded its range beyond the entire dry or nonflooded season border; tracking time was insufficient to allow for a distinction. The evidence supporting the possible migratory tendency or range expansion along all home range borders of this herd is weak. It is based on an early observation of a similarly sized herd in what was later identified as herd B's home range.

Although herds did not cross the river channels forming the island during this study period, they have done so many times in the past (Dr. Jill Thompson & G. de Oliveira, pers. comms.), indicating that the channels do not block white-lip movements. Even if the river channels somewhat restrict migration to the north and south, the herds could still move westward for up to 40 km out of their regular home range before encountering the river. Migratory mammals generally move among areas with different rainfall regimes and patterns of plant species diversity in their search for food (Baker 1978). In Roraima and on Maracá, rainfall increases from east to west, a change that correlates with a 70 percent turnover in plant species between the two ends of the island (Milliken & Ratter 1989). Thus, a westward migration would have enabled the animals to reach new food sources if these were needed.

White-lips in this study exhibited strong site fidelity, in that they consistently returned to feeding, bedding, and watering sites. Return visits were both short-term (1 d to a few weeks within a season) and long-term (from one year to another).

When the Savanna Pond contained abundant food, herd A visited it repeatedly, often remaining there for several days (Fragoso 1994). This pattern of visits continued for three months in 1992. During this period, when the herd left the site it did so only briefly before returning. However, once the site dried up and no longer held food, the white-lips ignored it until the same time the following year when eels and other fish were once again available. Herd B also showed regularity and patterning in its movements (based on a visual examination of movement patterns; Fig. 3), returning to the same foraging areas even after an extended trip of >20 km. The same return visits characterized white-lip relations with palm patches. The Forest Pond, an almost monospecific *Mauritia flexuosa* palm clump, was visited as regularly as the Savanna Pond. Here the white-lips ate from the thousands of *Maximiliana maripa* seeds defecated by tapirs (*Tapirus terrestris*), as well as the fruit pulp, seeds, and seedlings of *Mauritia* (Fragoso 1994). White-lip herds also foraged repeatedly in clumps of *Maximiliana* palms (Fragoso 1994). When a herd of white-lips entered a clump of *Maximiliana* during the mast period, they often ate the pulp from all the thousands of fruit on the ground and spat out the seeds (Fragoso, pers. obs.).

The only other descriptions of white-lip movements in the literature are those of Kiltie (1980), Kiltie and Terborgh (1983), and Bodmer (1989a, 1990). Kiltie (1980) and Kiltie and Terborgh (1983) compared rates of visits to one site to results from a random model, and reported that "[f]or practical purposes, then, appearances of *T. pecari* herds at the site were random events, occurring with a constant probability from day to day within a season. This result agrees with anthropologists' reports that *T. pecari* is a prey species which aboriginal hunters encounter unpredictably" (p. 250, Kiltie & Terborgh 1983). The scale of observation in that study, however, was too small in relation to the scale of animal movement for the model to reflect reality. Bodmer's (1989a) analysis of sites where hunters killed white-lips led him to conclude that white-lips were migratory, although he based this conclusion on movements of only about 10 km. Bodmer's (1990) local informants reported that white-lips were more likely to be found near "varzea" towns during the dry period than were collared peccaries. Bodmer interpreted this to mean that they remained there during the nonflooded portion of the dry season and left during the rainy

season when the area was inundated by water. Movement patterns may have been different in this varzea-flooded forest area; on Maracá, only seasonal ponds and streams usually flooded, and the pattern of dry ground normally did not change much from season to season.

Baker (1978) discussed the difficulty associated with differentiating migration from regular movements within a home range. However, the range expansion by white-lips on Maracá from the nonflooded to flooded seasons and the seasonally simultaneous use of both ranges cannot be considered a migration, even in the broadest sense as defined by Baker (1978). On Maracá, the two herds stayed within well-defined home ranges during the study period, and they found sufficient food within this limited but heterogeneous home range. If we extrapolate from the Maracá data, a herd of 400 individuals would have a home range of *ca* 380 km². A white-lip herd moving over a home range of this extent when observed from only a few points, could easily give the impression of migrating or wandering when it might only be regularly covering many points in its vast home range. Whether white-lips in other areas have a similar ranging pattern remains to be studied.

Throughout their range, white-lip populations have been noted to occasionally disappear or decline sharply in numbers (*e.g.*, Kiltie & Terborgh 1983 for Peru; Vickers 1991 for Ecuador; Stearman 1992 for Bolivia; Fragoso 1997). This observation has fueled the speculations that animals migrate or move nomadically, possibly while tracking fruit resources (Kiltie 1980, Sowls 1984, Bodmer 1989a). Unless individually recognized white-lip herds are tracked continuously for long periods of time, there is no way of distinguishing between *in situ* population declines (Fragoso 1994) and long-distance nonseasonal movements (those that take animals outside of their usual home range for reasons not associated with seasonal changes) as causes for the large-scale disappearance of white-lips from the areas reported.

The small size of white-lip herd A contrasts with sizes reported in the literature, with the exception of Sowls' (1984) count of 60 animals for a herd in a remnant patch of the Atlantic forest in southern Brazil and the two small "satellite" groups observed by Kiltie and Terborgh (1983). In 1988 (Fragoso 1998), I described white-lip densities in eastern Maracá at 139 (King method) and 542 (Webb method) individuals/km². This is much higher than the estimated density of 8.1 peccaries/km² for 1990–1993. Although the 1988 estimates

were derived using a different method (animals counts and distance/angle measurements along transect lines), I am reasonably sure the difference between the study periods represents a population decline because: (1) the white-lip kill rate of Macuxi Amerindian hunters living by Maracá dropped correspondingly from 3–5 animals/hunter/month in 1988 to 0.01 in 1990–92 (Fragoso 1994, 1997), and (2) in the pristine forest of the Yanomami Indian Reserve, an area about half the size of France (located to the west, north, and south of Maracá), no white-lips have been killed since *ca* 1987–1989, even though it is a preferred game species (Fragoso 1994, 1997). Based on this indirect evidence, I conclude that the white-lip population in the region may have experienced a major decline due to a pandemic disease (Fragoso 1994). If true, this could explain the small size of herd A (and herd B relative to the hundreds of animals estimated for herds before 1989; (J. Alves, Dr. J. Thompson, G. de Oliveira, pers. comm.) and the low population density in 1990–1992 compared to 1988–1989. It also provides an alternative explanation for the population disappearances or declines noted by others.

Could a population decline have affected or eliminated the migratory behavior of white-lip herds on Maracá? This explanation is unlikely based on the similarity of herd sizes in this and other studies. Herds A and B, with 53 and 130 animals, respectively, are within or near the range (60–200 individuals) described by Kiltie (1980) and Kiltie and Terborgh (1983) as moving nomadically. They are also within the range of what is generally considered as a large herd of white-lips (Eisenberg 1989). I expect that home range size will increase as herd size increases during population recovery. The similarity in behavior between the two herds in this study, however, suggests that movement patterns will remain the same, unless extremely high population densities trigger dispersal movements.

White-lip population density estimates for other Neotropical regions include 1.3 individuals/km² (Bodmer *et al.* 1988) for a hunted site in the Peruvian Amazon (estimated from hunter kills), and 4.9/km² for an unidentified Neotropical site (Robinson & Redford 1986). These estimates and those from Maracá in 1992 are extremely low relative to the 1988–1989 estimates on Maracá, suggesting that white-lip peccary populations recently have been reduced in many sites in Amazonia, either by a recently introduced mortality factor or as part of regularly occurring population fluctuations. This

possibility is the focus of a current study of white-lipped peccaries in Roraima.

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