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Source: *Journal of Mammalogy*, 92(2):267-274. 2011.

Published By: American Society of Mammalogists

DOI: 10.1644/10-MAMM-A-174.1

URL: <http://www.bioone.org/doi/full/10.1644/10-MAMM-A-174.1>

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Population genetic structure and dispersal in white-lipped peccaries (*Tayassu pecari*) from the Brazilian Pantanal

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In many mammals social organization promotes genetic structuring, which can be influenced by the dispersal pattern of the species. We analyzed the population genetic structure and dispersal of white-lipped peccaries (*Tayassu pecari*) from the Pantanal, Brazil. We genotyped 100 individuals at 7 microsatellite loci from 2 adjacent locations with no obvious geographic barrier between them. We found a significant but low F_{ST} value, and the Bayesian analysis indicated a unique cluster. No significant differences were observed between mean assignment indices of resident males and females from both locations, and the probability of being born at the location sampled of >30% of the individuals analyzed was lower than average. Mean relatedness between resident female, male, and opposite-sex pairs was not statistically different in both locations. These results suggest a low degree of genetic differentiation between the locations analyzed, and dispersal by both sexes (contrary to the predicted male-biased dispersal of most mammalian species).

Key words: Bayesian approach, dispersal, microsatellite markers, Pantanal wetland, *Tayassu pecari*, Tayassuidae

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DOI: 10.1644/10-MAMM-A-174.1

Many mammalian species are subdivided into social groups that constitute reproductive units. This organization provokes the prediction that social species should present genetic structuring and inbreeding, because individuals tend to reproduce with members of their own groups (Storz 1999). However, the degree of genetic differentiation in socially structured populations also can be influenced by the dispersal pattern of the species (Storz 1999); that is, differential dispersion of one of the sexes might provide gene flow, thus decreasing levels of genetic structure. Among mammals and birds, most members of one sex disperse, and individuals of the other sex remain in their natal group (Greenwood 1980). Sex-biased dispersal has been hypothesized to result from local mate competition, resource competition, and inbreeding avoidance (Dobson 1982; Greenwood 1980; Pusey 1987; Wolff 1993). Among mammals, male-biased dispersal is the most common pattern and considered to be a result of male mate competition (Lawson Handley and Perrin 2007).

White-lipped peccaries (*Tayassu pecari*) are social, frugivorous–omnivorous ungulates in the family Tayassuidae and

are distributed in the Americas from southeastern Mexico to northern Argentina and southern Brazil (Sowls 1984). This species occupies a variety of habitats (e.g., forests, savannahs, and wetlands). Studies emphasize the importance of their ecological role particularly in Neotropical forests, because they predate and disperse seeds, and as they root and forage, they cause secondary impacts on forest vegetation via soil disturbance and seedling damage (Keuroghlian and Eaton 2008a, 2009; Kiltie and Terborgh 1983; Silman et al. 2003). As a social species they form large herds that often exceed 100 individuals of both sexes in various age classes. Home range of a single herd can vary in size from 1,500 to 20,000 ha (Altrichter and Almeida 2002; Bodmer 1990; Carrillo et al. 2002; Fragoso 1998; Keuroghlian et al. 2004; Kiltie and Terborgh 1983). Herds can be subdivided into subherds with periodic fusion and fission, with a high frequency of exchange



of individuals among subherds (Keuroghlian et al. 2004). Movements as long as 5 km (Costa Rica—Altrichter et al. 2002) or even 10 km (Peru—Kiltie and Terborgh 1983) can be undertaken by herds. Such movements are generally seasonal and may be triggered by changes in available fruit patches (Altrichter and Almeida 2002; Altrichter et al. 2002; Carrillo et al. 2002; Fragoso 1998; Keuroghlian and Eaton 2008a; Keuroghlian et al. 2009) and water sources (Keuroghlian and Eaton 2008b). Such movements have been hypothesized to facilitate occasional genetic mixing among peccary herds (Altrichter and Almeida 2002).

The Pantanal wetland covers an area of approximately 200,000 km² in South America, mostly within Brazil but also in portions in Bolivia and Paraguay, making it the largest wetland in the world. This ecosystem is highly diverse in plant and animal species. Although considered to be largely intact (Mittermeier et al. 1998), over the last 30 years human activities have been threatening this region, especially because of large-scale agriculture on the encircling plateaus, gold mining, heavy fishing pressure, and environmentally disastrous development schemes for increasing barge traffic on the Paraguay River (Gottgens et al. 2001; Willink et al. 2001). These environmental threats could be affecting habitat use and the population dynamics of white-lipped peccaries (Desbiez et al. 2009) and, consequently, the age distribution and sex ratios of the population (A. Keuroghlian, pers. obs.). In addition, if natural resources are naturally limited during certain seasons (Keuroghlian et al. 2009), environmental degradation might increase starvation, dispersal, or both, thus affecting the survival of different age classes and sexes (Fragoso et al. 2000). Inferences of genetic diversity and population structure are necessary to determine whether dispersal is male biased and the degree to which adjacent populations are connected genetically. These data can be used as an indicator tool for the status of white-lipped peccary populations under various regimes of environmental degradation.

We used microsatellite markers to assess genetic diversity and population structure, and verify the occurrence of sex-biased dispersal, in white-lipped peccaries from 2 adjacent locations of the Brazilian Pantanal. Based on published studies about peccary ecology and behavior, we expected a low degree of genetic differentiation in pristine regions for the following reasons: the high capacity of white-lipped peccaries to travel long distances, the fission–fusion pattern between subherds, and frequent switching of individuals between subherds. These known characteristics should facilitate gene flow between subherds and herds. In addition, following the typical pattern of mammalian dispersal, we hypothesized that gene flow is male-biased.

MATERIALS AND METHODS

Study area and sampling.—We sampled individuals from 2 locations that are approximately 80 km apart in the Nhecolândia and Aquidauana subregions of the southern Pantanal (Mato Grosso do Sul, Brazil; Fig. 1). Fazenda Rio Negro (19°34'S, 56°14'W; hereafter RN), sampled from 2001

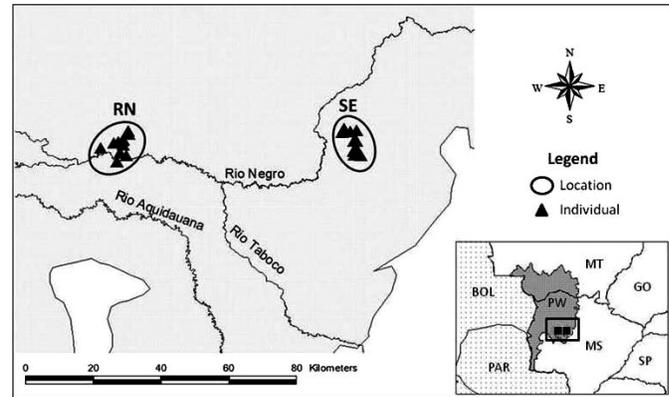


FIG. 1.—Sampling locations for *Tayassu pecari* in the Nhecolândia and Aquidauana subregions of the southern Pantanal (Mato Grosso do Sul, Brazil). The circles indicate the 2 regions studied, Fazenda Rio Negro (RN) and Fazenda Campo Lourdes, Fazenda Santa Maria Pica Pau, and Fazenda Santa Emília (collectively, SE). Individuals sampled are represented by black triangles. The 3 major rivers of the region are shown: Rio Negro, Rio Taboco, and Rio Aquidauana. Inset shows the sampling locations (black squares) in the Brazilian Pantanal (dark gray). PW, Brazilian Pantanal wetland; BOL, Bolivia; PAR, Paraguay; MT, state of Mato Grosso; MS, state of Mato Grosso do Sul; GO, state of Goiás; SP, state of São Paulo.

to 2006, is a 7,647-ha area of the lower–middle Rio Negro of the Brazilian southern Pantanal. Approximately 89% of RN (7,000 ha) is a private reserve designated for research and ecotourism, and the remaining 11% is used for cattle. The region is characterized by forests, some open grasslands associated with flooded grasslands (vazantes), and many lakes (Eaton 2006). The other study region (hereafter SE), sampled from 2005 to 2008, encompassed 3 adjacent ranches along the upper–middle Rio Negro region, with a range of well-preserved to highly disturbed sites: 5,700-ha Fazenda Campo Lourdes (19°32'S, 55°33'W), 4,400-ha Fazenda Santa Maria Pica Pau (19°32'S, 55°38'W), and 2,600-ha Fazenda Santa Emília (19°30'S, 55°36'W). Each location corresponds to a white-lipped peccary herd with its respective subherds.

As part of a long-term ecological study more than 300 peccaries from these 2 locations were immobilized with zolazepam and tiletamine hydrochloride (Zoletil 50; Virbac, São Paulo, Brazil), marked with a radiofrequency identification microchip (Biomark, Boise, Idaho), sexed, weighed, and placed in an approximate age class based on tooth wear (Keuroghlian and Desbiez 2010). We conducted a 2-tailed Z-test (using annual sex ratios from each region as replicates) to determine if mean sex ratios from the 2 locations were different from 1:1. Of these captured animals we sampled 111 individuals by collecting 4 ml of blood in Vacutainer tubes containing ethylenediaminetetraacetic acid (BD, Franklin Lakes, New Jersey). Samples were stored at -20°C until the moment of DNA extraction. Animal trapping and handling were authorized by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (protocol 13601) and followed guidelines of the American Society of Mammalogists (Gannon et al. 2007).

Laboratory procedures.—DNA was extracted from blood samples using standard proteinase K and phenol–chloroform protocol (Sambrook et al. 1989). We amplified by polymerase chain reaction 6 polymorphic microsatellites using primers developed for the domestic pig (*Sus scrofa*; ACTG2, IGF1, SW444, SW857, SW957, and SW240—Rohrer et al. 1994, 1996), some of them already tested in peccaries (Gongora et al. 2002; Lowden et al. 2002; Silva et al. 2010), and 1 previously designed for collared peccaries (*Pecari tajacu*; PT0226F 5' ACACACATAAATACACACACAAG 3' and PT0226R 5' CAGAATAAAAAGCTCCACGAGAG 3'). Forward primers were manufactured with a 5'-M13 tail (5' CACGACGTTGTAACGAC 3'—Boutin-Ganache et al. 2001). Polymerase chain reaction was performed in 12- μ l volumes containing 1.5 μ l of DNA (20–30 ng/ μ l), 1.2 μ l of polymerase chain reaction buffer (10 \times ; Pharmacia, Piscataway, New Jersey), 1 μ l of deoxynucleoside triphosphate mix (2 mM), 0.4 μ l of MgCl₂ (25 mM), 0.3 μ l of reverse primer (10 mM), 0.2 μ l of fluorescent (FAM, HEX, or TET; Applied Biosystems, Foster City, California) M13 sequence primer (10 mM), 0.1 μ l of forward primer (10 mM), 0.1 μ l of *Taq* polymerase (5 U/ml; Pharmacia), and 7.2 μ l of MilliQ water (Millipore Corporation, Billerica, Massachusetts). Cycling conditions were initial denaturation at 95°C for 5 min, 35 cycles of 94°C for 30 s, annealing temperature (ACTG and SW957 at 62°C; IGF1, SW857, and SW444 at 58°C; SW240 at 50°C; and PT0226 at 55°C) for 30 s and 72°C for 30 s, followed by a final step at 72°C for 10 min. Because we used heterologous primers, pig and collared peccary samples were used as positive controls. Polymerase chain reaction products were genotyped on a MegaBACE 1000 (GE Healthcare, Piscataway, New Jersey) automated sequencer and scored using Genetic Profiler 2.2 software (Amersham Biosciences, Piscataway, New Jersey). All samples were amplified and genotyped independently at least twice to check for genotyping errors. In most of the cases these 2 genotypes were identical. When different genotypes were observed, we repeated the genotyping procedure until we obtained a consensus genotype.

Data analysis.—Genetic diversity was analyzed by calculating the number of alleles and observed and expected heterozygosities using GENEPOP 3.4 (Raymond and Rousset 1995) and allelic richness using FSTAT 2.9.3.2 (Goudet 2002) for each locus and location. These measures were compared between locations using the Wilcoxon signed-rank test performed in SPSS 13.0 (SPSS Inc., Chicago, Illinois). Significant departures from Hardy–Weinberg and linkage equilibrium were evaluated using probability tests and log-likelihood ratio *G*-tests, respectively, performed in GENEPOP. In cases of multiple comparisons we applied Bonferroni corrections (Rice 1989). We tested each locus for null alleles and other genotyping errors (scoring errors due to stuttering and large allele dropout) using MICRO-CHECKER 2.2.3 (van Oosterhout et al. 2004).

To infer the degree of genetic differentiation we calculated the fixation index F_{ST} according to Weir and Cockerham (1984) and evaluated its significance using a *G*-test and 1,000 randomizations in FSTAT. In addition, we used the Bayesian

clustering approach as implemented in STRUCTURE 2.2 (Pritchard et al. 2000). This method infers genetic differentiation without previous information about geographical location of sampled individuals. We ran the analyses using the admixture model and correlated allele frequencies option, which has been considered the best in cases of subtle structuring (Falush et al. 2003). We tested number of populations (*K*) from 1 to 6 and performed 20 runs at each *K* using 30,000 for burn-in followed by 1,000,000 iterations. To determine the most probable number of populations we estimated Pr (*K*|*X*) following Pritchard et al. (2000) and the ΔK (Evanno et al. 2005) using log-likelihood values of the posterior probabilities, $L(K)$, averaged across runs. Because ΔK cannot determine the best *K* if *K* = 1 (Evanno et al. 2005), we did not apply this approach to such a circumstance.

To evaluate sex-biased dispersal we used 2 approaches, assignment tests and relatedness estimations. We computed assignment tests using the Bayesian method of Rannala and Mountain (1997) and probabilities using the simulation algorithm in the software GENECLASS 2.0 (Cornuet et al. 1999), which employs the “leave one out” procedure excluding the current individual being assigned from its sampled population. To obtain corrected assignment indices for population effects we used the approach of Favre et al. (1997), which consists of the subtraction of the population means after log-transformation. If sex-biased dispersal occurs, the dispersing sex is predicted to show lower mean corrected indices than the philopatric sex (Favre et al. 1997). Relatedness between resident females, males, and opposite-sex pairs in each location was calculated using the maximum-likelihood (Wagner et al. 2006) and the Queller–Goodnight (Queller and Goodnight 1989) estimators implemented in the programs ML-RELATE (Kalinowski et al. 2006) and GENALEX 6 (Peakall and Smouse 2006), respectively. We expected higher mean relatedness between members of the philopatric sex than the dispersing sex if sex-biased dispersal occurs. We compared male and female assignment indices using a Mann–Whitney *U*-test and relatedness between female, male, and opposite-sex pairs using Kruskal–Wallis (χ^2) analysis of variance computed in SPSS 13.0.

RESULTS

Characterization of genetic diversity.—Of the 227 white-lipped peccaries captured at RN 131 were females and 96 were males (female : male sex ratio = 1.36:1). Of the 170 white-lipped peccaries captured at SE 111 were females and 59 were males (female : male sex ratio = 1.88:1). In both study regions the sex ratios of white-lipped peccary populations were female biased and differed significantly from 1:1 (RN: $Z = 3.71$, $P = 0.0002$; SE: $Z = 3.68$, $P = 0.0002$). From the 111 blood samples collected 100 were successfully genotyped, 53 from RN and 47 from SE. However, to avoid bias in the structuring and dispersal analyses we considered only adults, totaling 41 individuals from RN (13 males and 28 females) and 31 from SE (11 males and 20 females).

TABLE 1.—Number of alleles (NA), allelic richness (AR), expected heterozygosity (H_E), and observed heterozygosity (H_O) for the 7 microsatellite loci of *Tayassu pecari* analyzed for the locations Fazenda Rio Negro (RN) and Fazendas Campo Lourdes, Santa Maria Pica Pau, and Santa Emília (collectively, SE).

| Locus | RN | | | | SE | | | |
|----------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | NA | AR | H_E | H_O | NA | AR | H_E | H_O |
| ACTG2 | 9 | 8.08 | 0.82 | 0.78 | 9 | 8.93 | 0.84 | 0.90 |
| IGFI | 3 | 3.00 | 0.46 | 0.38 | 3 | 3.00 | 0.56 | 0.58 |
| SW444 | 3 | 3.00 | 0.40 | 0.46 | 4 | 4.00 | 0.32 | 0.30 |
| SW857 | 3 | 3.00 | 0.49 | 0.51 | 3 | 2.99 | 0.51 | 0.58 |
| SW957 | 9 | 8.97 | 0.87 | 0.83 | 8 | 8.00 | 0.83 | 0.89 |
| SW240 | 2 | 2.00 | 0.20 | 0.22 | 2 | 2.00 | 0.20 | 0.23 |
| PT0226 | 7 | 6.67 | 0.78 | 0.73 | 6 | 6.00 | 0.82 | 0.87 |
| \bar{X} (SD) | 5.14 (3.08) | 4.96 (2.86) | 0.57 (0.25) | 0.56 (0.23) | 5.00 (2.71) | 4.98 (2.69) | 0.58 (0.26) | 0.62 (0.28) |

We observed 2–9 alleles per locus in both locations (Table 1). We found 3 private alleles (loci ACTG2, PT0226, and SW957) in RN and 2 (loci ACTG2 and SW444) in SE. We observed moderate levels of genetic diversity in both locations based on mean allelic richness (4.96 in RN and 4.98 in SE) and mean expected (0.57 in RN and 0.58 in SE) and observed (0.56 in RN and 0.62 in SE; Table 1) heterozygosities. We did not find significant differences between RN and SE for allelic richness ($Z = -0.14, P = 0.89$) and expected ($Z = -0.51, P = 0.61$) and observed ($Z = -1.35, P = 0.18$) heterozygosities. We observed no significant departures from Hardy–Weinberg ($P > 0.007$, the critical value after Bonferroni correction) and linkage ($P > 0.002$, the critical value after Bonferroni correction) equilibrium. No evidence for null alleles or other genotyping errors was found according to analyses in MICRO-CHECKER (van Oosterhout et al. 2004).

Population genetic structure and dispersal pattern.—The observed F_{ST} was 0.02 and significantly different from 0 ($P < 0.001$), indicating a certain level of genetic differentiation between the 2 locations. However, the Bayesian analysis, according to the Pr (KIX) (Pritchard et al. 2000), supported a unique cluster as most probable ($K = 1$; Table 2).

Corrected assignment indices ranged from -0.64 to 0.38 ($\bar{X} \pm SD = 0.01 \pm 0.27$) for resident males and -2.52 to 0.46 ($\bar{X} \pm SD = -0.01 \pm 0.53$) for resident females. No significant difference existed between locations, so we pooled the data and examined the locations together. Similarly, we found no significant difference between male and female indices ($U = 495.5, n_1 = 24, n_2 = 48, P = 0.34$). We found that 34.0% of females and 41.6% males were in the negative portion of the

TABLE 2.—Mean (SD) of log-likelihood of the posterior probabilities, $L(K)$, and the ad hoc estimation of the probable number of populations, Pr (KIX), for each K (number of populations) of *Tayassu pecari*.

| K | $L(K)$ | Pr (KIX) |
|-----|-------------------|----------|
| 1 | -1,229.84 (0.54) | 0.98 |
| 2 | -1,233.85 (3.76) | 0.02 |
| 3 | -1,245.68 (9.76) | 0.00 |
| 4 | -1,250.80 (13.43) | 0.00 |
| 5 | -1,255.23 (11.95) | 0.00 |
| 6 | -1,255.26 (18.34) | 0.00 |

frequency distribution for the corrected assignment indices (Fig. 2). Because negative values correspond to individuals that have lower probability than average of being born in the location where they were sampled, these results indicated that more than one-third of the individuals were dispersers in both sexes (Fig. 2). In agreement with the results obtained using assignment indices, relatedness between resident female, male, and opposite-sex pairs was not statistically different for both estimators in either RN (maximum likelihood: $\chi^2_2 = 3.89, P = 0.14$; Queller–Goodnight: $\chi^2_2 = 0.35, P = 0.84$) and SE (maximum likelihood: $\chi^2_2 = 0.44, P = 0.80$; Queller–Goodnight: $\chi^2_2 = 0.12, P = 0.94$), which indicates absence of sex-biased dispersal (Table 3).

DISCUSSION

The most important results of this study are that both locations have similarly moderate levels of genetic diversity

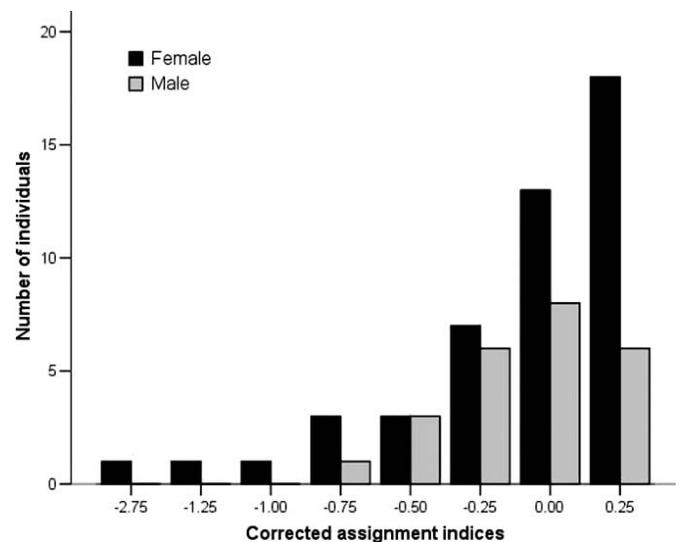


FIG. 2.—Frequency distribution of corrected assignment indices for resident male and female *Tayassu pecari* from Fazenda Rio Negro (RN) and Fazenda Campo Lourdes, Fazenda Santa Maria Pica Pau, and Fazenda Santa Emília (collectively, SE). More than one-third of the individuals of both sexes are in the negative portion of the distribution and have lower probability than average of being born in the location where they were sampled.

TABLE 3.—Mean (*SD*) relatedness between female (FF), male (MM), and opposite-sex (MF) pairs of *Tayassu pecari* from Fazenda Rio Negro (RN) and Fazendas Campo Lourdes, Santa Maria Pica Pau, and Santa Emília (collectively, SE) locations, according to the maximum-likelihood (ML—Wagner et al. 2006) and the Queller–Goodnight (QG—Queller and Goodnight 1989) estimators.

| Location | Estimator | FF | MM | MF |
|----------|-----------|--------------|--------------|--------------|
| RN | ML | 0.09 (0.14) | 0.06 (0.13) | 0.10 (0.15) |
| | QG | −0.04 (0.29) | −0.04 (0.28) | −0.02 (0.29) |
| SE | ML | 0.12 (0.18) | 0.09 (0.14) | 0.10 (0.16) |
| | QG | −0.04 (0.33) | −0.01 (0.30) | −0.01 (0.30) |

and are weakly differentiated, as predicted for a highly mobile species such as the white-lipped peccary; and significant evidence exists for dispersal by both sexes instead of strictly male-biased dispersal predicted for most mammalian species. We found moderate levels of genetic diversity in both locations analyzed. Similar results were found for 3 populations of collared peccaries (*P. tajacu*) from Texas, whose allelic diversity and observed and expected heterozygosities averaged across populations and 11 microsatellite loci were 5.9, 0.61, and 0.65, respectively (Cooper et al. 2010b).

White-lipped peccaries live in large herds that have fission–fusion patterns with switching of individuals among subherds (Keuroghlian et al. 2004) and are highly mobile (Altrichter and Almeida 2002; Altrichter et al. 2002; Kiltie and Terborgh 1983). Therefore, we predicted a low degree of genetic differentiation between the studied locations, which are only 80 km apart and without any obvious physical barrier to dispersal by peccaries. Although we found significant levels of genetic differentiation between locations and private alleles in both of them, the observed value of F_{ST} (0.02) was low, as expected. In addition, population structure was not observed when individuals were not assigned to a population a priori. This result was not completely unexpected because Latch et al. (2006) showed that STRUCTURE might not identify correctly the number of populations when F_{ST} is approximately 0.02 or lower. Low levels of differentiation can be related to scenarios of recent separation or high levels of gene flow between populations. Based on assignment indices calculated for resident individuals from both locations, we found that >30% of males and females were predicted to be dispersers, which can indicate high levels of gene flow. Both locations are along the Rio Negro (Fig. 1), and riparian zones have an important role for white-lipped peccaries as sources of fruits, travel routes, and as corridors for movement in the landscape matrix, thereby promoting gene flow between the 2 locations (Keuroghlian and Eaton 2008b; Lee and Peres 2008).

We predicted male-biased dispersal commonly described in the literature for many mammalian species (Lawson Handley and Perrin 2007). However, we found no significant differences between male and female assignment indices and relatedness, which indicates an absence of sex-biased dispersal. In addition, as discussed above, >30% of males and females were in the negative portion of the frequency distribution of the assignment indices, confirming that both

sexes are dispersing. Although this result contradicts our hypothesis, it was not completely unexpected because we have evidence that in the fission–fusion cycles of peccary herds in the Atlantic Forest (Keuroghlian et al. 2004) and in the Pantanal (A. Keuroghlian, pers. obs.), both males and females can switch between subherds and herds.

Male-biased dispersal in mammals usually is induced by male competition for females to mate (Greenwood 1980). However, game theory models suggest that mate competition induces male-biased dispersal if resource competition is insufficient to promote the dispersal of females (Perrin and Mazalov 2000). Many studies have reported that white-lipped peccaries have a significant female-biased sex ratio (Altrichter et al. 2001; Fragoso 1994; Jácomo 2004; Painter 1998), which also was observed for both of our study sites. This bias could promote female competition over key resources (e.g., fruits) and consequently the dispersal of females. In addition, the higher number of females than males in the population might relax male mate competition, decreasing the tendency of males to disperse. Dispersal by both sexes in white-lipped peccaries could be a consequence of the equilibrium between sexes in the intensity of sex-specific pressures for dispersal, female competition over resources, and male competition over females.

Variation in sex ratio among different populations of white-lipped peccaries that are hunted causes increased female bias (Fragoso et al. 2000). In regions where white-lipped peccaries are vulnerable, males have been observed positioned at the periphery of herds, a behavior that presumably protects females and young (Altrichter et al. 2001; Fragoso 1994; Hernandez et al. 1995). This also increases the exposure of males to hunters, causing a differential loss of males and a female-biased sex ratio. Following our hypothesis, an increase in females in herds of hunted areas could result in higher rates of competition among females over key resources, and consequently, a female-biased dispersal. Our results clearly show a difference in the sex ratio between the 2 study sites; however, examination of our data has not indicated a difference in dispersal patterns between males and females. This needs to be monitored over years to determine if the continued increase in environmental threats such as deforestation and the loss of habitat diversity in the region will result in female-biased dispersal.

In contrast to the absence of sex-biased dispersal in white-lipped peccaries, comparisons on the degree of genetic differentiation between mitochondrial DNA and microsatellites revealed male-biased dispersal in populations of collared peccaries from Texas (Cooper et al. 2010a; Cooper et al. 2010b). This can be explained by differences in the social systems between these species; collared peccaries live in smaller groups with sex ratios closer to 1:1 (Sowls 1984, 1997) and have a well-defined home range (Byers and Bekoff 1981; Keuroghlian et al. 2004); whereas white-lipped peccaries live in larger groups frequently characterized by female-biased sex ratios (Altrichter et al. 2001; Fragoso 1994; Jácomo 2004; Painter 1998), use a larger home range with seasonal movements, move large distances, and comprise subherds with fission–fusion patterns (Carrillo et al. 2002; Fragoso 1998;

Keuroghlian et al. 2004). Social characteristics of collared peccaries are more in agreement with the hypothesized genetic structuring and dispersal patterns of social mammals than is the behavioral ecology of white-lipped peccaries.

Conservation implications.—Because environments are continuously changing, genetic diversity is a requisite for the evolution and adaptation of populations to new situations. Low levels of genetic diversity usually are associated with increased levels of inbreeding, which can reduce the fitness of individuals and make them more susceptible to such environmental challenges as climate changes and diseases (Frankham et al. 2004). Although the Pantanal, as a wilderness area, is largely intact (Mittermeier et al. 1998), in the last 3 decades the region has been vulnerable to economic trends that have driven large-scale deforestation and agricultural development. White-lipped peccaries are distributed widely in the region, but if the Pantanal continues to experience the current rate of environmental degradation and habitat loss, its peccary populations will become isolated due to habitat conversion and fragmentation. This isolation could limit gene flow among populations, possibly resulting in significant genetic structuring. These isolated populations might be small and suffer from the effects of genetic drift and inbreeding, which could reduce their genetic diversity. Consequently, these populations could become more susceptible to environmental changes and diseases. Eventually this type of environmental scenario will lead to local extinctions of white-lipped peccaries throughout the Pantanal.

We observed moderate levels of genetic diversity, a low degree of genetic differentiation, and high rates of dispersal between white-lipped peccaries from 2 adjacent locations. To maintain the levels of gene flow and genetic diversity observed these locations should be conserved and managed as a unique population. Riparian zones can function as corridors, especially in environmentally degraded regions (Keuroghlian and Eaton 2008b; Lee and Peres 2008), enabling white-lipped peccary dispersal. Therefore, maintaining riparian zones and natural links between floodplain forests should be considered an important goal in conservation plans.

RESUMO

Em muitos mamíferos, a organização social promove estruturação genética, que pode ser influenciada pelo padrão de dispersão da espécie. Aqui, nós analisamos a estrutura populacional genética e a dispersão de queixadas (*Tayassu pecari*) do Pantanal, Brasil. Nós genotipamos 100 indivíduos de 2 localidades adjacentes, sem barreira geográfica óbvia entre elas, para 7 locos de microsatélite. Nós encontramos um valor de F_{ST} significativo, porém baixo, e a análise Bayesiana indicou um único agrupamento. Não foram observadas diferenças significativas entre os índices de atribuição médios de machos e fêmeas residentes em ambas as localidades; e a probabilidade de ter nascido no local amostrado de mais de 30% dos indivíduos analisados foi menor que a média. O parentesco médio entre fêmeas, machos e pares de sexo oposto

residentes não foram estatisticamente diferentes em ambas as localidades. Estes resultados sugerem um baixo grau de diferenciação genética entre as localidades analisadas e dispersão de ambos os sexos (ao contrário da dispersão de machos, esperada para a maioria das espécies de mamíferos).

ACKNOWLEDGMENTS

We are grateful for the logistical support provided by Fazenda Campo Lourdes, Fazenda Santa Emília/Pousada Ararauna, and Fazenda Rio Negro. We thank veterinarian T. P. Freitas, our field assistants E. Arruda and C. Vicente, and our laboratory assistant D. A. Rufo. We also thank F. S. Raposo do Amaral and two anonymous reviewers for helpful comments on earlier versions of this manuscript. This project was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo, Universidade para o Desenvolvimento do Estado e da Região do Pantanal, Fundação Manoel de Barros, Instituto de Biologia da Conservação, Earthwatch Institute Volunteers, York High School, Wildlife Conservation Society Brazil, Conservation International, Conselho Nacional de Desenvolvimento Científico e Tecnológico, and Coordenadoria de Aperfeiçoamento de Pessoal de Nível Superior. C. Biondo performed the data analyses at the University of Sydney (Australia), as part of a program of international collaboration between this university and the Universidade de São Paulo (Brazil) funded by the University of Sydney International Program Development Fund.

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Submitted 26 May 2010. Accepted 16 September 2010.

Associate Editor was Harald Beck.