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What Ecological and Anthropogenic Factors Affect Group Size in White-lipped Peccaries (*Tayassu pecari*)?

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ABSTRACT

Group living among ungulates has evolved mainly in species living in open habitats, such as grasslands and savannas, whereas in the forest, few ungulate species form groups and these tend to be small. Therefore, the white-lipped peccary (*Tayassu pecari*), a Neotropical ungulate listed as Vulnerable by the IUCN, represents an almost unique social occurrence as it lives in large and cohesive groups, yet it inhabits dense tropical forests. Large variations in group sizes have been observed throughout the species range, with reports of herds with less than 10 to around 300 individuals. We examined factors that might cause variation in group size in white-lipped peccary, including ecological and anthropogenic variables. We conducted an extensive literature review and used our original data to compile information on white-lipped peccary's group size across its range. We built models to quantitate generalizations for group sizes distinguishing data from areas with high human influence, and areas that have not been significantly disturbed by humans for at least the last 20 years. We found that white-lipped peccary's group size for all sites was most strongly predicted by a combination of the distances to the nearest human settlement and rainfall and its seasonality. Results from the undisturbed sites indicated that group size is positively influenced by rainfall. Our results contribute to understand why group size varies in different environments that are subjected to different ecological and human conditions. Information on these relationships is a key to advance our understanding of the socio-ecological strategies of animal species living in groups.

Abstract in Spanish is available with online material.

Key words: anthropogenic effects; climate change; ecological variations; herd size; Tayassuidae.

Group formation has evolved in many species and benefits of group living have been broadly classified into three main categories: predator avoidance, optimization of resource use, and avoidance of conspecific threats (Wilson 1975, Smuts & Smuts 1993, Treves & Chapman 1996, Kie 1999, Krause & Ruxton 2002). However, living in groups also presents disadvantages due to increased competition over food resources and access to mates (Kie 1999). Feeding competition has been proposed as one of the main constraints on group size (Wrangham *et al.* 1993, Kie 1999, Chapman & Chapman 2000).

Group living among ungulates has evolved mainly in species living in open habitats, such as grasslands and savannas (Jarman 1974, Kie 1999), whereas in the forest few ungulate species form groups, and these tend to be small (Kingdon 1997). Therefore, the white-lipped peccary (*Tayassu pecari*), a Neotropical ungulate, represents an almost unique social occurrence as it lives in large and highly cohesive groups, yet it inhabits dense humid tropical forests. The only other ungulate that forms such aggregations is the bearded pig (*Sus barbatus*) of Borneo with groups of more than 300 individuals; however, these aggregations are only tempo-

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rary and occur during mast fruiting events of dipterocarps (Kawanishi *et al.* 2008).

White-lipped peccaries form groups that in some areas divide into subgroups and individuals frequently switch between them (Pantanal, Brazil, Keuroghlian & Eaton 2008a, Biondo *et al.* 2011, Atlantic Forest, Brazil, Keuroghlian *et al.* 2004, Corcovado Park, Costa Rica, Carrillo *et al.* 2002, Cerrado, Brazil, Almeida-Jácomo 2004), but there is evidence that in other areas there may be infrequent dispersal of individuals between groups and groups remain together through the year (Calakmul region, Mexico; Reyna-Hurtado *et al.* 2009, Maraca Island, Brazil, Fragoso 1998). A large variation in group size has been observed throughout the species range, with reports of herds with less than 10 to around 300 individuals (Leopold 1959, Kiltie & Terborgh 1983, Emmons & Feer 1990, March 1993, Sowls 1997, Fragoso 1997, 2004, Carrillo *et al.* 2002, Keuroghlian *et al.* 2004, Reyna-Hurtado *et al.* 2009) and anecdotal reports of up to 1000 individuals (Mayer & Wetzel 1987).

Hunting and forest fragmentation cause declines in white-lipped peccary abundance across its geographic range (Peres 1996, 2000, Reyna-Hurtado *et al.* 2010, Altrichter *et al.* 2012). The current range of white-lipped peccary has been reduced by 20.5 percent from its historic distribution, which includes extirpations from entire countries (*i.e.*, El Salvador and Uruguay; Altrichter *et al.* 2012). The species faces multiple threats across its range such as wide-scale habitat destruction and degradation, commercial harvesting, unsustainable levels of subsistence hunting, and zoonotic diseases likely spread from domestic livestock (Fragoso 1997, 2004, Altrichter & Boaglio 2004, Herrera *et al.* 2008, Freitas *et al.* 2010, Altrichter *et al.* 2012). In fragmented forests, the white-lipped peccary is highly vulnerable to extinction because it requires high habitat diversity, including rare habitats with key resources (Keuroghlian & Eaton 2008b), specific sources of water always available (Beck *et al.* 2010, Reyna-Hurtado *et al.* 2012) and relatively large home ranges (Fragoso 1998, Almeida-Jácomo 2004, Reyna-Hurtado *et al.* 2009). In addition, the white-lipped peccary social behavior of protecting in groups when in danger makes it easy for hunters to spot and kill several individuals of the same group (Altrichter & Almeida 2002, R. Reyna-Hurtado, pers. obs.). The vulnerability of the species to human disturbance is especially problematic given the expanding industrial agriculture frontier and elongating road networks across the Neotropics that causes forest loss and fragmentation as well as allow hunters to access remote areas (Rivera 2014). Currently, the species is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and classified as Vulnerable on the IUCN Red List (www.iucnredlist.org; Keuroghlian *et al.* 2013). The species is currently considered as endangered, or critically endangered, for some areas of Brazil and for all Mexico by the environmental institutions of these countries (Brazil: Keuroghlian *et al.* 2012, Mexico: Secretaria de Medio Ambiente y Recursos Naturales-SEMARNAT, NOM-059, 2010).

In this study, we examine ecological and anthropogenic factors that might cause variation in group size of white-lipped peccary using available data from throughout the species geographic range (Mexico to Argentina). We expect groups to be larger in areas with less human perturbation than highly perturbed sites, and for groups that do not experience significant human impacts we expect larger groups in more humid areas than in dry areas. We built general linear models to quantitate generalizations for two sets of group sizes counts. The first set included all data points across the species' range, incorporating those with and without significant human influence (*i.e.*, hunting), while the second subset only included locations that have not been perturbed by humans for at least the last 20 years. Our results provide unique insights into the ecology of white-lipped peccary and opportunities to construct informed management and conservation plans for the species.

METHODS

Group size counts.—We conducted an extensive literature review and also used our original data to compile information on group size of white-lipped peccary across its geographic range (Table 1). We carefully selected only those observations in which, we were confident that the observer had seen the whole group and obtained an accurate count. In large part, these counts come from observers following radio tracked animals for several months enabling them to obtain an accurate count of the groups, or from studies that involve walking transects. In the latter case, we include instances in which the observers have seen the whole group, for example at the wallowing points or when crossing paths. When several different group sizes were reported for a specific location we used the mean value.

Climatic variables.—We obtained rainfall and temperature data for each site from a climatic model built by Willmot & Matsuura (2012) (V3.01, http://climate.geog.udel.edu/~climate/; 2010). This dataset provided a global measure of monthly and annual temperature and rainfall in grids of 0.5° latitude by longitude, obtained from a monthly and annual average that in some cases included data ranging from 1900 to 2010. These data were used to build the following three indexes of seasonality as a way to determine the patterns of rainfall, quantitating the amount of rainfall per month, as well as its variability. First, to evaluate rain availability throughout the year, we used the monthly average rainfall for each site and then calculated the number of months in which precipitation was lower than 100 mm for a given site ('Monthly seasonality index'). Second, we calculated another index based on the variability in rainfall throughout the year ('Seasonality Index'), following Korstjens *et al.* (2006) and using the following equation: Seasonality Index = maximum monthly precipitation—minimum monthly precipitation divided by the annual average of precipitation. Finally, we calculated a third index, named 'Le Houérou index', which relates rainfall with temperature and is calculated as the number of months in which precipitation (in mm) is twice the temperature (Le Houerou 1984). This latter index was developed as a measure of the growing season in tropical African habitats, and also yields a very strong correlation with primary productivity (Le Houerou 1984).

In addition, we obtained an index of habitat productivity EVI (enhanced vegetation index) based on satellite imagery data

TABLE 1. *Data source of 158 observations obtained both from the literature and authors' and others original data (highlighted with*) on white-lipped peccary group sizes across 16 different Neotropical sites.* N *is the number of counts. When available, we have provided standard deviation in parenthesis beside the mean group size.*

Site	Country	*N*	Protection Status	Mean Annual Temperature (C)	Mean Annual Rainfall (mm)	Mean Group size	Source
Communal Forests Southern Mexico	Mexico	12	Perturbed	24.2	1076	19.9 (7.8)	Reyna-Hurtado (2007) (Radiotelemetry and transects data)
Calakmul Biosphere Reserve	Mexico	15	Non-perturbed	25.7	1076	23.3 (8.1)	Reyna-Hurtado (2007) (Radiotelemetry and transects data)
Montes Azules Biosphere Reserve	Mexico	13	Perturbed	23	3000	21.7 (12.9)	Naranjo (2002) (Radiotelemetry and transects data)
Maya Biosphere Reserve	Guatemala	12	Non-perturbed	25.3	1323	31.9 (13.1)	Moreira *et al.* (2015), (Observations and transects data)
Corcovado National Park	Costa Rica	16	Perturbed	28.2	3400	36.2 (13.6)	Altrichter & Almeida (2002), Carrillo *et al.* (2002), Estrada (2005) (all of them Radiotelemetry and transects data)
Hato Piñero Ranch	Venezuela	7	Perturbed	27.5	1469	41.7 (23.2)	Hernandez *et al.* (1995) (Observations and transect data)
Yasuni National Park	Ecuador	1	Non-perturbed	25.1	2750	90.0	R. Reyna-Hurtado* (Observation)
Los Amigos Biological Station	Peru	1	Non-perturbed	26.1	2750	100.0	S. Carrillo & M. Tobler * (Observations)
Manu National Park	Peru	8	Non-perturbed	28.2	2424	88.0 (19.7)	H. Beck unpublished data*; Kiltie & Terborgh (1983), (Transect data)
Maraca Island Reserve	Brazil	3	Non-perturbed	27.3	2300	125.3 (77.1)	Fragoso (1998, 2004) (Radiotelemetry data)
Das Emas National Park	Brazil	16	Perturbed	23.1	1600	70.0 (34.0)	Almeida-Jácomo (2004) (Radiotelemetry and transect data)
Caetetus Reserve, Atlantic Forest	Brazil	10	Perturbed	20.7	1400	41.7	Keuroghlian *et al.* (2004) (RadioTelemetry data), Cullen *et al.* 2000 (Transect data)
Central Pantanal (Nhumirim Ranch)	Brazil	21	Perturbed	25.8	1226	34.2	A. Desbiez* (Transect data)
Pantanal (Nossa Sehora do Carmo Ranch)	Brazil	4	Perturbed	25.7	1172	88.0	A. Desbiez* (Transect data)
El Chaco Impenetrable Forest	Argentina	18	Perturbed	22.2	550	22.5 (14.2)	Altrichter (2005) (Transect data)
El Chaco Humedo	Argentina	14	Perturbed	22.2	825	23.2	Altrichter & Boaglio (2004) (Transect data)

Note: Non-perturbed sites are these larger than 1000 km^2, without recent hunting pressure or with very low hunting pressure.

(MODIS: Huete *et al.* 2002). Average EVI values within each site were calculated for 12-monthly images taken in 2001, and a yearly average was calculated. The monthly images were collected from the year 2001 as it was the average year in which group size data was collected. To mitigate the effects of scale on average EVI estimates (as sites varied in extent) a consistent area within each site was considered, examining EVI values within a circular window of 12 km within each site, placed at the center of the studied area as provided by the researchers. We make the assumption here that EVI values within this window are representative of the site. We believe this assumption is adequate as we are interested in comparing between vastly different regions (dry vs. wet forest sites), and that the variation within sites will be much less than the variation between sites. This index was used as surrogate of habitat productivity and was contrasted against group size.

HUMAN RELATED VARIABLES.—Information on human disturbances was also collected from literature and our own data. We primarily focused on hunting pressure, forest remnant size, distance to nearest human settlement, and protection status.

To assess whether a given study site should be categorized as a fragmented or a continuous forest, we estimated the total forest area for each site according to the original description of the study site. Where this information was not available in print we contacted the author of the study. Considering that some estimates of home range for white-lipped peccary surpasses 100 km^2 for a single group (Fragoso 1998, Almeida-Jácomo 2004, Reyna-Hurtado *et al.* 2009), and that some of the lowest estimates of density published report 0.43 animal/km^2 (Reyna-Hurtado *et al.* 2010), we decided on a 1000 km^2 area as the minimum area to sustain at least a population of 10 groups (based on home ranges) or at least 400 individuals (based on density estimates). Thus, for this species, we

TABLE 2. *Correlation among continuous (Pearson's r) and ordinal (Spearman's rho) independent variables used in the analyses.*

	Rainfall	Temperature	Seasonality index	Months of rainfall < 100 mm	Le Houérou index	Forest size	Fragmentation	Hunting pressure	Distance to human settlements	EVI index
Rainfall	1									
Temperature	0.46	1								
Seasonality index	−0.54	−0.14	1							
Months of rainfall <100 mm	−0.79	−0.35	0.80	1						
Le Houérou index	0.81	0.32	−0.79	−0.97	1					
Forest size	−0.13	0.09	−0.33	−0.13	0.06	1				
Fragmentation	−0.12	−0.10	0.26	0.25	−0.21	−0.62	1			
Hunting pressure	−0.40	−0.65	0.24	0.32	−0.37	−0.36	0.45	1		
Distance to human settlements	0.10	0.56	−0.09	−0.12	0.18	0.14	−0.55	−0.71	1	
EVI Index	0.54	0.40	−0.55	−0.69	0.59	0.48	−0.38	−0.32	0.15	1

classified areas smaller than 1000 km^2 as fragmented and areas larger than 1000 km^2 as continuous. However, we did not consider potential connectivity among these areas or with other areas nearby, as the data on white-lipped peccary dispersal is limited or nonexistent. It is possible that some dispersal exists among populations, but we consider here the populations as closed ones as we lack reliable data on connectivity among sites.

Distance to nearest human settlement was calculated as the Euclidean distance from the geographic center of the observations of groups of white-lipped peccaries to the nearest village or human settlement using Google Earth (Google, Inc. Mountain View, CA), or when available we used information obtained from the authors of each study. To quantitate the impact of hunting we classified areas into three categories; (1) high hunting pressure: areas subjected to subsistence or sport hunting with or without any management plan or regulation (*e.g.*, *ejidos*-communal forest around Calakmul Reserve in Mexico); (2) low hunting pressure: areas that are protected but there is evidence of occasional hunting (*e.g.,* Lacandon forest, Mexico, Caetetus Reserve, Brazil, Parque Das Emas, Brazil); and (3) areas without hunting: protected areas without human communities and where there is no evidence of hunting in the last 20–30 yr (*e.g.*, Calakmul protected area, Mexico; Manu National Park, Peru; Maraca Island, Brazil).

SITE CLASSIFICATION.—To analyze the effect of the combined human and climatic variables on group size of white-lipped peccary, we classified the sites as being with or without recent significant human influence. After a careful review of all the sites' characteristics in terms of human influence measured as hunting pressure, distance to the nearest settlement, and fragmentation status we selected six sites that have none or very low levels of human-induced perturbation and are larger than 1000 km^2 (Table 1). These sites were labeled as non-perturbed sites, and the rest were labeled as perturbed sites.

STATISTICAL ANALYSES.—First, we constructed a correlation matrix for each pair of variables (Table 2). We constructed General Linear Models (GLM) using averaged observed group size as the dependent variable and amount of rainfall, temperature, the three seasonality indices, the habitat productivity index (EVI), distance to the nearest human settlement, hunting pressure, and forest size as the explanatory variables. Complete models, combining all environmental and human disturbance variables were examined for all 16 sites. Subsequently, we examined only the environmental variables in a subset of six sites that were classified as presenting low to no human disturbance (labeled as non-perturbed sites, Table 1), and examined group size responses to: amount of rainfall, temperature, seasonality index, and EVI. Model selection was done using an exhaustive search of all parameter combinations using the glmulti package from R (Calcagno & Mazancourt 2010). We used AICc values for small sample sizes (Akaike 1974), adjusted R-squares, standardized B, and *P*-values of each model. *P*-values lower than 0.05 were considered significant. AICc values of >2 were used to distinguish the fit of each model. Due to the highly correlated nature of our predictor variables, we chose a cut off of $r > 0.7$ (Dormann *et al.* 2013), and make use of the variation inflation factor (VIF score >5) to identify models with potential collinearity problems. Models which show collinearity above these thresholds are reported but are not considered in further analyses. Analyses were performed in the statistical software of R v. 3.01 (R Development Core Team 2011).

RESULTS

Our data set includes 158 observations from 16 sites across eight countries, with the majority of the observations coming from published studies, although several of them were unpublished observations from the authors (Table 1). The complete analyses using all predictors and sites, identified five best models within two AICc of each other (Table 3): (1) distance to human settlements; (2) distance to human settlements and amount of rainfall; (3) distance to human settlements, amount of rainfall, and the Le Houérou index; (4) distance to human settlements, amount of rainfall, and the seasonality index; and (5) distance to

TABLE 3. *General linear models with AICc values for small sample sizes, adjusted* R-*squares, standardized B, and* P-*values of several combinations of independent variables predicting group size of white-lipped peccary for 16 Neotropical sites (complete models) and for a subset of six sites classified as non-perturbed (environmental model).* P-*values lower than 0.05 were considered significant. Models with within two AICc units of the lowest AICc score were considered equally best.*

Model	Variables	Standardized B (SE)	Adjusted *R*-Squared	*P*-value	AICc
Complete models					
1	Distance to human settlements	0.56 (0.21)	0.27	0.02	159.43
2	Distance to human settlements+	0.52 (0.21)	0.37	0.02	159.52
	Rainfall	0.37 (0.21)			
3	Distance to human settlements+	0.57 (0.20)	0.43	0.02	160.86
	Rainfall+	0.79 (0.33)			
	Le Houérou index	-0.53 (0.34)			
4	Distances to human settlements +	0.54 (0.20)	0.43	0.02	160.89
	Rainfall+	0.57 (0.23)			
	Seasonality index	0.36 (0.23)			
5	Distance to human settlements+	0.54 (0.20)	0.42	0.02	161.25
	Rainfall+	0.74 (0.32)			
	Months < 100 mm	0.47 (0.32)			
Environmental model					
1	Rainfall	0.87 (0.25)	0.37	0.02	69.87

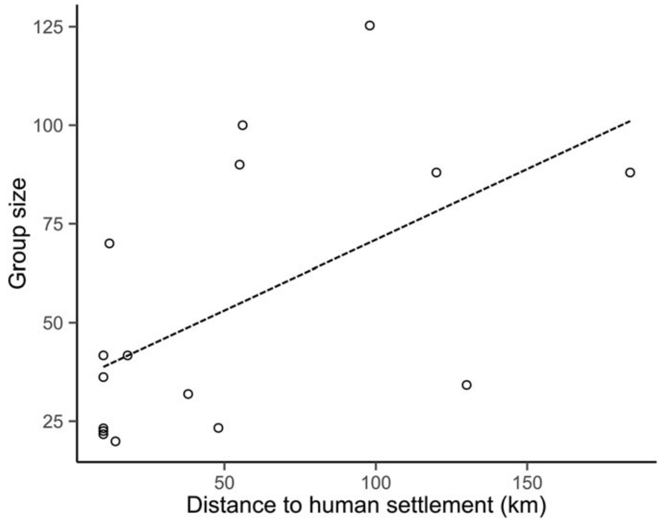

FIGURE 1. Relationship between group size of white-lipped peccary and distances (km) to the nearest human settlement for 16 sites ($F_{(1,14)}$ = 6.457, P = 0.02, Adjusted R^2 = 0.32).

human settlements, amount of rainfall, and the number of months with less than 100 mm of rain. Models 3, and 5, contain parameter pairs that exceeded our chosen threshold of a pairwise correlation of 0.7, although they did not exceed our chosen maximum VIF score of 5. We retain these models in the Table 3 to facilitate comparison, but do not include these models in further analysis. However, when examining the standardized regression coefficients distance to human settlements and amount of rainfall (except for model 1) consistently showed the largest effects on group size across all models (Table 3; Fig. 1).

Focusing on environmental predictors, and considering only the non-perturbed sites, we found that a model including the amount of rainfall at a given site was the best model ($F_{(1,4)}$ = 12.18, P-value = 0.03, r^2 = 0.69, AICc = 69.87; Table 3; Fig. 2), with no other model within 2 AICc.

The limited number of sites (N = 16) presents some difficulty and suggests caution when interpreting models, however, it also provides an opportunity to examine the residuals in greater detail to identify the magnitude to which group sizes are either underestimated or overestimated according to each model predictions (Figs. 3 and 4). We find that for non-perturbed sites the expected group size for Maraca Island is largely underestimated, considering the amount of rainfall at that site (Fig. 3). When considering group size expected given the distance from human settlements we find that Los amigos, Das Emas, Maraca and Yasuni are a cluster of underestimated sites (*i.e.*, they have larger groups then would be expected), whereas Pantanal (central) is overestimated (*i.e.*, lower than expected) (Fig. 4A). When we consider rainfall and distance to human settlements, Das Emas remains underestimated and Lacandon forest now stands out as being overestimated (Fig. 4B).

DISCUSSION

To our knowledge, this is the first study that examined several climatic, ecological, and anthropogenic factors that were predicted to affect white-lipped peccary's group size across its geographic distribution. Our study suggests that group sizes in white-lipped peccary vary across the species range with larger groups in areas with higher precipitation and further away from human settlements.

We found that white-lipped peccary's group size is strongly predicted by the distances to the nearest human settlement. However, this variable might not be causal but may represent a combination of various human disturbances that cannot be isolated as either hunting pressure, diseases transmission from domestic animals, pollution, forest fragmentation, or forest loss. Since 1950s, Leopold (1959) observed in parts of Mexico that white-lipped peccary were among the first species that disappeared when humans colonized undisturbed areas. This could be a consequence of white-lipped peccary suffering high hunting pressure close to human settlements as has been demonstrated in several

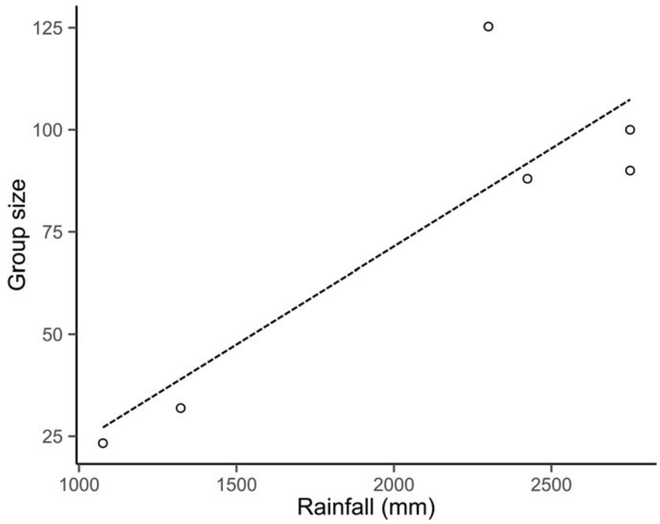

FIGURE 2. Relationship between group size of white-lipped peccary and annual rainfall (mm) of six protected sites where no recent human perturbation exists ($F_{(1,4)}$ = 12.18, P = 0.03, Adjusted R^2 = 0.69).

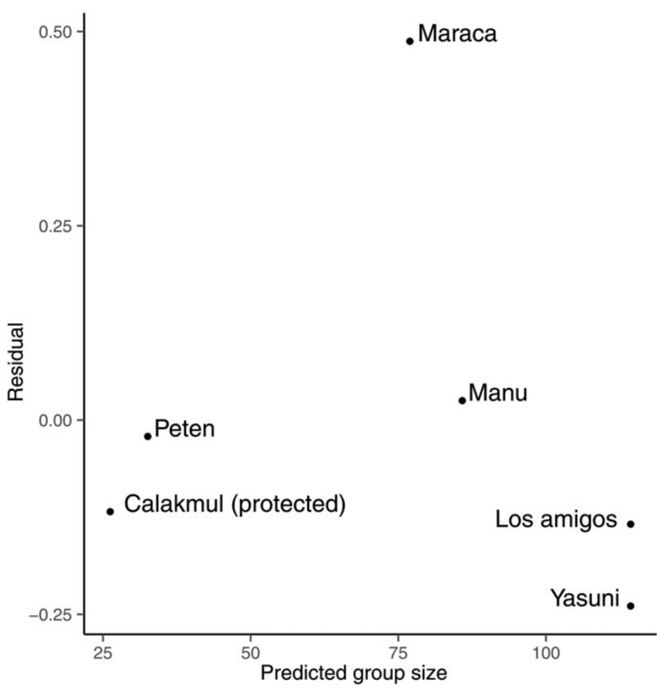

FIGURE 3. Plot of the residual vs predicted values using annual rainfall for group size of white-lipped peccary in six Neotropical sites that were classified as non-perturbed sites.

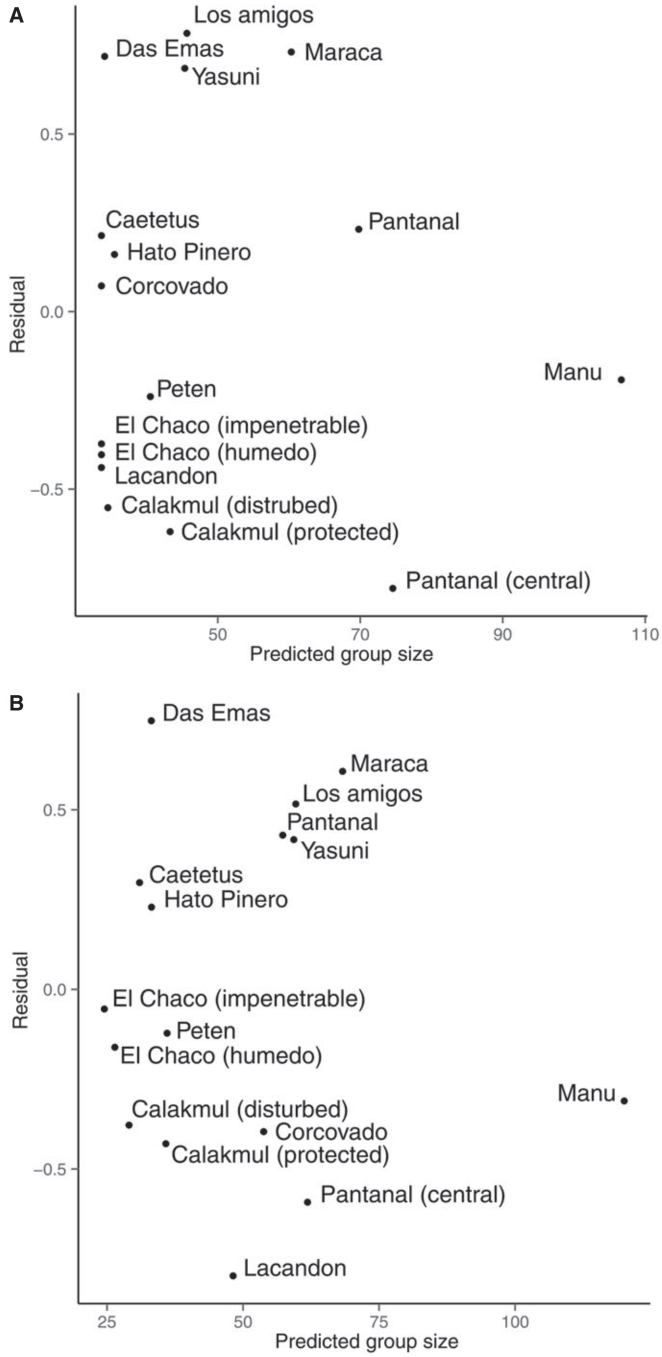

FIGURE 4. Plot of the residual vs predicted values for group size of white-lipped peccary in 16 Neotropical sites using only distance to nearest human settlement (A), and distance to nearest human settlement plus annual rainfall (B).

parts of its geographic range (Peres 1996, 2000, Altrichter & Almeida 2002, Altrichter & Boaglio 2004, Keuroghlian *et al.* 2004, Reyna-Hurtado & Tanner 2007, Reyna-Hurtado *et al.* 2009). However, in addition to hunting pressure, white-lipped peccaries are also sensitive to forest degradation, livestock-induced diseases, and decreases in food availability that can be produced by non-timber resources harvesting (Fragoso 1997, 1998, 2004, Cullen *et al.* 2000, Reyna-Hurtado *et al.* 2009, 2010, Altrichter *et al.* 2012). For example, it is possible that as distance to human settlements increases the contact with domestic animals is reduced, which could greatly reduce the risk of diseases transmission. This possibility was not tested here, but disease has been implicated as a major cause of white-lipped peccary populations decline in some areas of the Brazilian Amazon forest (Fragoso 1997, 2004). In our study case, we found that hunting pressure was highly correlated with distances to nearest settlement, suggesting a synergistic effect between these variables on group size (Spearman's rho = 0.71). Synergy between hunting and deforestation has been found by previous studies to negatively impact populations of white-lipped peccary and other Amazonian mammals (Peres 1996).

Results from the non-perturbed sites indicate that group size is positively influenced by the amount of rainfall, which means that larger groups occurred in areas with higher precipitation. In general, there is a positive relationship between rainfall and primary productivity in tropical forests (Murphy & Lugo 1986). Primary productivity, in turn, can affect fruit availability, which directly influences white-lipped peccary behavior (Altrichter *et al.* 2000, Keuroghlian & Eaton 2008b). The annual net primary productivity for dry forest averages 50–75 percent that of the wet forest (Hartshorn 1983, Murphy & Lugo 1986), and the total plant biomass in dry forests ranges between 78 and 320 tons/ha, whereas in wet forest it ranges between 269 and 1186 tons/ha (Murphy & Lugo 1986). Considering that white-lipped peccary consumes fruits in large quantities, ranging from 43 percent in the dry forest of Venezuela (Barreto *et al.* 1997) to 81 percent in tropical wet forests (Altrichter *et al.* 2000, 2001, Beck 2005, 2006, Pérez-Cortéz & Reyna-Hurtado 2008), we suggest that the positive relationship between rainfall and group size could be attributed to higher food and water availability in wetter forests.

A relationship between group size and food production has been observed in the bearded pig (*Sus barbatus*) from Southeast Asia. This species lives in smaller family units, but occasionally aggregate into herds larger than 300 animals corresponding to the mast fruiting of species such as *Dryobalanops aromatic* (camphor wood forest in Malaysia) or *Lithocarpus* spp (mountain oak in Sarawak) (Caldecott *et al.* 1993, Kawanishi *et al.* 2008). In contrast, our study suggests that group sizes in white-lipped peccary vary across the species range according to climatic, ecological, and human conditions with groups that are larger in areas that are far away from human and are apparently more productive in terms of fruit production. The importance of changing availability of food resources on affecting the size of groups or subgroups for social mammals is substantiated by research on several species of primates. For example, in a Costa Rican rain forest, spider monkey (*Ateles geoffroyi*) and mantled howler monkeys (*Alouatta palliata*) have larger groups in areas with higher food resources availability (Chapman 1989, 1990). Similar, Ugandan chimpanzees (*Pan troglodytes;* Chapman *et al.* 1995) and red colobus (*Procolobus rufomitratus;* Snaith & Chapman 2005) vary the size of foraging groups as a function of food resource availability. We need to further test if when white-lipped peccary groups divide in subgroups (which happen only in some specific areas of its distribution range; Carrillo *et al.* 2002, Keuroghlian *et al.* 2004) correlate with limited resources availability either spatially or temporally.

Contrary to what we expected, the indexes of seasonality alone were not significant predictors of group size across all sites studied but were part of the best models together with distances to nearest settlements and amount of rainfall. Our sample had only three dry or semi-dry sites (Chaco dry forests, Hato Piñero, and Calakmul region), but several sites where water is permanently available (*e.g.*, Manu National Park, Yasuni National Park, Maraca Island). The scarcity of standing water has, however, been shown to cause high mortality on this species, consequently reducing group size in some very seasonal sites or where there are not major source of standing or running water as the Yucatan peninsula in southern Mexico (Reyna-Hurtado *et al.* 2009).

In large undisturbed forest, we found that there is a positive relationship between rain and group size. This finding raises the possibility that white-lipped peccary will be affected by climate change. For example, in the Yucatan Peninsula in southern Mexico several climate models suggest that the area will experience a reduction in rainfall on average of 22 percent, which can further rise to 48 percent in 90 years (Magrin *et al.* 2007). If this scenario is correct, our study suggests that group size, and likely population size, would be negatively affected (Reyna-Hurtado *et al.* 2009). This is a serious conservation concern, considering that this area is the stronghold for white-lipped peccary population in Mexico (Reyna-Hurtado *et al.* 2009). However, for the Brazilian Pantanal an extended dry season scenario would mean less flooded habitat and consequently more dry land available for white-lipped peccary which may have positive effects on population density (Desbiez *et al.* 2010). These finding suggest also the possibility that white-lipped peccary populations are, and would be, site-specific affected (Figs. 3 and 4).

Our data ranged from white-lipped peccary most northern extent of distribution (Mexico) to its most southern extent (Argentina). However our results must be considered with caution, as there are no data for many areas within the large historic range (14 million km^2) of the species (Altrichter *et al.* 2012). Furthermore, recently, Keuroghlian *et al.* (2012) have gathered evidence of unexplained disappearances of entire populations of white-lipped peccary from areas considered pristine, demonstrating that there is a lot we do not understand about white-lipped peccary population dynamics. Despite these limitations, our results have contributed to understand why group sizes of white-lipped peccary vary across it geographic range that are subjected to different ecological and human conditions. Information on these relationships is a key to advance our understanding of the socio-ecological strategies of animal species living in groups and how these social factors are impacted by human activities and environmental variables.

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