Research Article

Using activity and occupancy to evaluate niche partitioning: the case of two peccary species in the Atlantic Rainforest, Brazil

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Abstract

Collared and white-lipped peccaries (*Pecari tajacu* and *Tayassu pecari*, respectively) are widely distributed, herd-forming ungulates that are sympatric in a variety of Neotropical ecosystems. Patterns of co-occurrence and niche partitioning are still poorly understood in sympatric peccary populations in the Atlantic Forest. We aimed to test the hypothesis that the collared and white-lipped peccary avoided each other by some degree of niche partitioning in the Vale Natural Reserve, Espírito Santo state, southeastern Brazil. Species-specific occupancy, detection, and activity patterns were estimated from camera-trap data collected at 39 sample sites over a 1-year period. We found that both peccary species respond to similar habitat covariates (palm density, distance to water resources, poaching intensity). We also quantified the probability of co-occurrence, or the Species Interaction Factor (*SIF*), using a two-species occupancy modelling approach. We found that the two species avoided each other in space ($SIF=0.41\pm0.02$), thus providing evidence for niche partitioning. Specifically, occupancy of the collared peccary was significantly lower at sites occupied by the white-lipped peccary ($\psi BA=0.24\pm0.08$) when compared to sites unoccupied by the white-lipped peccary ($\psi Ba=0.80\pm0.05$). We also found weak evidence for temporal niche partitioning, with the white-lipped peccary being more restricted to diurnal hours. Our results contribute to our knowledge of species ecology and the potential mechanisms of coexistence for peccary species in the Vale Natural Reserve.

Introduction

Interspecific competition is one of the main selective pressures affecting species distributions and depends on the evolutionary adaptations to reduce competition among closely related and/or sympatric species (Leibold, 1998; Bulmer, 1974; MacArthur and Levins, 1967). Generally, this competition relates primarily to the use of resources such as food and space, and specific morphological adaptations or behavioral patterns may have evolved to permit coexistence of the two species. Niche partitioning may include the use of distinct habitats (i.e., partitioning along a spatial axis) and dietary resources (i.e., trophic portioning), as well as different activity patterns (i.e., temporal partitioning; Abrams, 1983).

Peccaries are important components of the Neotropical ecosystems, serving as seed dispersers (Keuroghlian et al., 2009; Beck, 2006), ecosystem engineers (e.g., Keuroghlian et al., 2009), and prey items for large carnivores (e.g., Garla, 2001). Patterns of co-occurrence and niche partitioning are poorly understood in sympatric peccary populations in the Atlantic Forest. Here, we focus on interactions between two peccary species: the white-lipped (*Tayassu pecari*) and the collared peccary (*Pecari tajacu*). Collared and white-lipped peccaries are widely distributed herd-forming ungulates that are sympatric in a variety of Neotropical ecosystems (Keuroghlian et al., 2004; Sowls, 1997; Bodmer, 1990). Herds of white-lipped peccary typically exceed 50 individuals, whereas collared peccary herds rarely exceed 20 individuals (Fragoso, 1999; Sowls, 1997; Donkin, 1985). In the Neotropics, peccaries are generally frugivorous (Beck, 2006), presenting some level of

overlap in their diet (Desbiez et al., 2009a). The collared peccary occurs from northern Argentina to southern USA (Gongora et al., 2011), while white-lipped peccaries are confined to the Neotropical Region, from northern Argentina to southeastern Mexico (Keuroghlian et al., 2013). In Vale Natural Reserve, both peccary species constitute similar biomass (Ferreguetti et al., 2016a).

Both the white-lipped and collared peccary inhabit several types of tropical forests, xerophytic thorn forests, and open woodland vegetation in tropical floodplains and savannas (Keuroghlian et al., 2013; Gongora et al., 2011; Desbiez et al., 2009a). However, there appears to be some differences in habitat use. The white-lipped peccary is generally dependent on specific humid habitats, such as palm-dominated swamps (Beck, 2006; Fragoso, 1998) and riparian forests (Desbiez et al., 2009a,b; Keuroghlian et al., 2009; Reyna-Hurtado et al., 2009; Keuroghlian and Eaton, 2008a). In contrast, the collared peccary can be found in more open environments, including grasslands and small forest patches, as well as disturbed habitats, such as agricultural fields (Keuroghlian et al., 2009; Reyna-Hurtado and Tanner, 2005; Keuroghlian et al., 2004; Bodmer, 1990), while maintaining a degree of dependency on forested habitats (Desbiez et al., 2009a,b; Keuroghlian et al., 2009). White-lipped peccaries are considered as the dominant species in case of potential interference competition with collared peccaries because this species forms larger herds and is larger in body size (28–40 kg) compared to collared peccary (16–25 kg; Oliveira-Santos et al., 2011).

Camera trap surveys are a minimally-invasive method for studying species in remote areas across the world, such as Vale Natural Reserve (VNR) (Steenweg et al., 2017). The application of occupancy modeling

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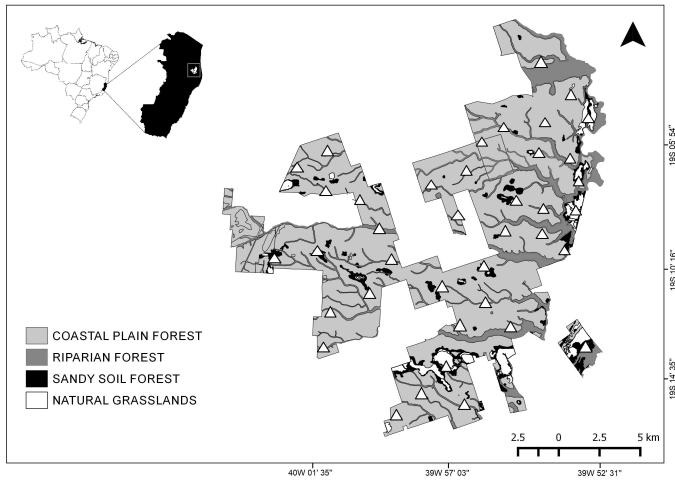*Email address:* atilla.ferreguetti@gmail.com (Atilla Colombo Ferreguetti)

Figure 1 – Habitat mosaics inside the Vale Natural Reserve, Espírito Santo, Brazil. White triangles represent the location of each camera trap.

to camera trap data can also allow us to better understand the patterns of species co-occurrence. This approach explicitly accounts for imperfect detection (i.e., if a species was present but not detected at a site) to estimate the true occupancy of each species (MacKenzie et al., 2004). Competition between species can then be inferred from differences in the temporal activity or spatial habitat use of one species in the presence and absence of the other (MacKenzie et al., 2006).

In addition to environmental factors and interspecific interactions, anthropogenic factors such as poaching may influence the occupancy of either or both of these peccary species. Moreover, our ability to detect these species may also be influenced by poaching, because these species may persist at lower abundances or exhibit behavioral responses to persecution in heavily poached areas (Reyna-Hurtado et al., 2016; Keuroghlian et al., 2013; Gongora et al., 2011; Cullen et al., 2001; Peres, 1996). At our study area, in particular, studies have already documented negative effects of poaching on the red brocket deer, *Mazama americana* (Ferreguetti et al., 2015), as well as the nine-banded (*Dasypus novemcintus*) and six banded (*Euphractus sexcinctus*) armadillos at VNR (Ferreguetti et al., 2016b). Peccaries are primarily poached for consumption, although poaching in VNR may not be as intensive as reported for other regions in the Neotropics (Mena et al., 2000; Sowls, 1997; Bodmer et al., 1994). Both peccary species are poached for consumption of their meat in their distribution, with white-lipped peccary being more vulnerable to poaching pressure (Keuroghlian et al., 2013; Gongora et al., 2011). Roads are also known to impact natural ecosystems, by reducing habitat quality and increasing edge effects, noise pollution and chemical and artificial lighting (McClure et al., 2013; Van Der Ree et al., 2011). Therefore, roads could have an impact on white lipped peccary abundance due to the direct or indirect effects associated with resultant habitat loss (Keuroghlian et al., 2013). In addition, roads may provide poachers with easy access to otherwise isolated areas (Barber et al., 2014; Laurance and Balmford, 2013).

Our goals were two-fold: 1) to understand the habitat relationships for each of these species to better understand their general ecology (i.e. occupancy and detectability); and 2) to identify the factors that facilitate co-occurrence of sympatric peccary species in an Atlantic Forest reserve in southeastern Brazil. We tested the hypothesis that shared diet preferences would result in either temporal (e.g., differences in peak activity period) or spatial (e.g., differences in habitat use) niche partitioning between collared and white-lipped peccaries. Specifically, we predicted that the collared peccary would avoid the sites occupied by the dominant white-lipped peccary. Additionally, since both species are often subjected to poaching (hunting has been outlawed in Brazil since 1967), we also evaluated how poaching may influence habitat use by examining its effect on the occupancy and detection probabilities of each species by comparing sites with different levels of poaching intensity in the Vale Natural Reserve.

Materials and methods

Study area

Our study was conducted in the Vale Natural Reserve (VNR), a protected area spanning over $235\,km^2$ in the neighboring municipalities of Linhares and Jaguaré (19°6′–19°18′ S and 39°45′–40°19′ W), in northeastern Espírito Santo state (Fig. 1). This reserve belongs to the Vale Company, a major mining enterprise in Brazil, and is composed of a main block of rainforest (approximately 98.1% of the total area), and a smaller fragment, known as Biribas Reserve, southwest of the main block. The VNR is covered by a mosaic of habitats with four main vegetation types (adapted from Jesus, 1987; Peixoto and Gentry, 1990): coastal plain, riparian, and sandy soil forests, and natural grasslands. The coastal plain forest has two or more upper strata and high densities of lianas and epiphytes, and covers approximately 70% of the reserve. The coastal plain forest is characterized by a tall canopy with an open, shaded understory. The riparian forest, which covers approximately 10% of the reserve, is a mixed vegetation type associated with streams, composed of widely-spaced trees and a predominance of palm species. Nearly 6% of the riparian habitat consists of wetlands (swamps) and streams. The sandy soil forest covers approximately 8% of the VNR and is comprised of woody vegetation found on sandy soils, physiognomically similar to the coastal plain forest at an early or intermediate stage of succession. The natural grasslands occur as enclaves within the forest, which, in the geological past were once the sites of shallow ponds, and cover approximately 6% of the VNR (Fig. 1).

Camera-trapping

We used camera-trapping to derive detection/non-detection data of target species, to model the occupancy probability for each species, as well as to document their respective activity patterns (Fig. 1). We selected 39 sites using a systematic design stratified by vegetation type to ensure that the four main vegetation types found in the VNR were represented. We placed a grid of $2\,km^2$ over a digital map of the reserve and identified sites to be surveyed by selecting grid cells at least 2 km from one another (e.g., Ancrenaz et al., 2012; Magnusson et al., 2005). This strategy resulted in an even site distribution within the VNR. At each site, we installed one passive infrared Bushnell® camera trap in picture function, approximately 40–50 cm above the ground. All cameras were checked every 20 to 25 days to change batteries, when necessary. The traps were programmed to operate 24 h/day and were sampled simultaneously with 200 days of trapping effort. We did not use bait to attract species to the sampled sites.

Model covariates

We selected 8 covariates that we hypothesized *a priori* could influence occupancy and/or detection of one or both peccary species. These covariates included: distance from the forest edge (edge), density of trees with a diameter at breast height (DBH) of >50 cm (dens_trees), the density of lianas (dens_liana), distance from water resource (water), density of palm species (palm), distance from paved roads (road), vegetation type (veg), and poaching intensity (poaching). We used a Pearson correlation matrix to examined correlations between all covariates and found that none were highly correlated, as indicated by a correlation coefficient of >0.5 (Tab. 2).

At each site, we established 30×50 m plots in each of the 4 cardinal directions at a distance of 50 m from the camera-trap. In each plot, we measured the Diameter at Breast Height (DBH) of each tree and counted the number of large trees (DBH>50 cm). We also counted the number of individual palms to quantify the density of palm species (individuals/km²). The density of lianas was based on the number of stems rooted within each four 10×50 m transects. We quantified 3 additional covariates — the distances to forest edge, water resource, and paved road — for each of the 39 sites using the ArcGIS software (ESRI ArcMap 10.1). The poaching intensity within the study area was calculated using a georeferenced database of 14 years of poaching records collected by the reserve's security guards. These records were used

to calculate a poaching intensity (records/km^2) for each grid square in which a camera was installed.

Single-species Occupancy Models

Occupancy modeling requires temporally– or spatially-replicated data to account for imperfect detection, thus allowing us to estimate the probability of detecting a species given that it was present at a site during sampling (MacKenzie et al., 2006). As such, we discretized our camera trapping data into sampling intervals of 5 consecutive days (40 occasions, in all) to construct a detection history (MacKenzie et al., 2006). For each species, we estimated site occupancy (ψ) and detection (p) probabilities, modeling our observations with three possible outcomes: (1) the site was occupied and the species was detected ($\psi \times p$); (2) the site was occupied but the species was not detected ($\psi \times [1-p]$), and (3) the site was unoccupied ($1-\psi$), and therefore the species was not detected. We used a single-species, single-season occupancy model to determine which of the 8 covariates mentioned above influence the habitat use and detectability of each species. We were interested in understanding the effects of a large number of covariates on occupancy and detection probabilities. As such, we split the occupancy modelling into 2 components (MacKenzie et al., 2006): 1) determining the "best-fit" model for detection probability while holding occupancy constant, and 2) determining the "best-fit" model for occupancy while modeling detection as determined by the "best-fit" model in component 1, above. This allowed us to evaluate differences in occupancy and detectability as determined by a single covariate or a set of covariates, which would contribute to an improvement in the model's performance. All single-species, single-season occupancy models were analyzed using the `unmarked` package in Program R (R Development Core Team, 2012; Fiske and Chandler, 2011). Our "best-fit" model was selected using Akaike's Information Criterion adjusted for small sample size (AICc) and all models with a ΔAICc value <2 were considered to be equivalent. We assessed the adjustment fit (z) and the over-dispersion parameter ($\hat{c}$) using 2000 bootstraps. All parameter estimates and standard errors are reported from the "best-fit" model with the lowest AICc.

Co-occurrence Models

Two-species occupancy modeling compares the spatial variation in occupancy to estimate a probability of co-occurrence between two species (MacKenzie et al., 2004). We used the conditional parameterization of the two-species model, developed by Richmond et al. (2010), which estimates 8 parameters: ψA, ψBa, ψBA, pA, pB, rA, rBa, and rBA (Tab. 1; Robinson et al., 2014). In our models, ψA represents the occupancy probability of the "dominant" species, the white-lipped peccary. ψBA is the occupancy probability of the collared peccary when the site is occupied by the white-lipped peccary. Thus, ψBa is the occupancy probability of the collared peccary when the site is not occupied by the white-lipped peccary. Detection probabilities are similarly modeled, where pA represents the probability of detecting the white-lipped peccary, and pB represents the probability of detecting the collared peccary at sites unoccupied by the white-lipped peccary. The additional detection parameters include: rA, the probability of detecting a white-lipped peccary when collared peccaries are present; rBA, the probability of detecting a collared peccary when white-lipped peccaries are present and detected; and rBa, the probability of detecting a collared peccary when both species are present but the white-lipped peccary is not detected. Two-species occupancy models also estimate the probability of two species co-occurring, or the species interaction factor (SIF; MacKenzie et al., 2006, 2004). Using the model parameterization described above, this can be written as: $\frac{(\psi A \times \psi BA)}{(\psi A \times (\psi A \times \psi BA + (1-\psi BA) \times Ba))}$. An SIF estimate of 1 would indicate that the two species occur independently, whereas a $SIF > 1$ would suggest the two species are more likely to co-occur than expected by random chance, and a $SIF < 1$ would suggest that the two species spatially avoid one another — i.e., the two species are less likely to co-occur than expected by random chance (Robinson et al., 2014; MacKenzie et al., 2004).

Table 1 – Parameters of the two-species occupancy model used to evaluate co-occurrence of Collared and White-lipped peccary in the Vale Natural Reserve, Espírito Santo state, Brazil.

Parameter	Definition
ψA	Species A, probability of occupancy
ψBa	Species B, probability of occupancy when species A absent
ψBA	Species B, probability of occupancy when species A present
pA	Species A, probability of detection when species B absent
pB	Species B, probability of detection when species A absent
rA	Species A, probability of detection when species B present
rBA	Species B, probability of detection when both species are present and species A is detected during sampling period
rBa	Species B, probability of detection when both species are present and species A is not detected during sampling period

We used the "best-fit" single-species occupancy models to inform the covariates of the co-occurrence models, which were constructed in program PRESENCE (Hines, 2012). We adopted this approach because few covariates are typically used in co-occurrence models (Reed, 2011; Bailey et al., 2009). As such, we restricted our analysis to the additive covariate effects from each of our "best-fit" single-species, single-season occupancy models, to examine the spatial relationships (i.e., co-occurrence) between these two-peccary species. We fit 6 co-occurrence models to test the relationships between occupancy and detection of collared peccaries in the presence or absence of white-lipped peccaries. For instance, if occupancy of the collared peccary was driven by the presence or absence of the white-lipped peccary, then $\psi BA \neq \psi Ba$. Similarly, if the probability of detecting the collared peccary was influenced by the presence and not the detection of the white-lipped peccary, $pB \neq rBA = rBa$. We report parameter estimates and standard errors from the "best-fit" model, as determined by AICc.

Activity Patterns

In addition to spatial interactions, we were also interested in quantifying and comparing temporal activity patterns of these two-peccary species. To accomplish this, we used the time at which animals were photographed and a conditional circular kernel density function to estimate overlap in activity patterns using the `circular` package in Program R (Oliveira-Santos et al., 2013; R Development Core Team, 2012). This circular kernel includes a smoothing parameter and a conditional density isopleth, defined as the threshold of probability that specifies the section of the function that accounts for a given proportion of the entire probability function (Oliveira-Santos et al., 2013).

Results

Single-species Occupancy Models

For clarity, we only present the top 10 models, based on ΔAICc, for occupancy of the white-lipped and collared peccaries, with the respective "best-fit" detection covariate structures in Tab. 2.

The collared peccary was observed at 25 of the 39 sampling sites, resulting in a naïve occupancy probability of 0.64. Estimated occupancy and detection probabilities for the VNR were 0.71 ± 0.07 and 0.21 ± 0.01, respectively. The "best-fit" model described occupancy probability as an additive function of the site's distance to water resources, density of palm species and poaching intensity, and detection probability as a function of poaching intensity (Tab. 2). Occupancy of the collared peccary was higher at sites closest to water resources (Fig. 2A) and at sites with high density (>1000 individuals/km^2) of palm species ($\psi = 0.84 \pm 0.04$, and $\psi > 0.65 \pm 0.03$, respectively; mean±SE; Fig. 2B). Occupancy was negatively affected by poaching intensity, with probabilities ranging from $\psi = 0.98 \pm 0.05$ to $\psi = 0.14 \pm 0.03$ (Fig. 2C). The probability of detecting this species was also negatively related to poaching intensity (Fig. 2D) and distance to water (Fig. 2E). Detection dropped from $p = 0.47 \pm 0.04$ to $p = 0.004 \pm 0.030$ in areas of low to high poaching intensity, respect-
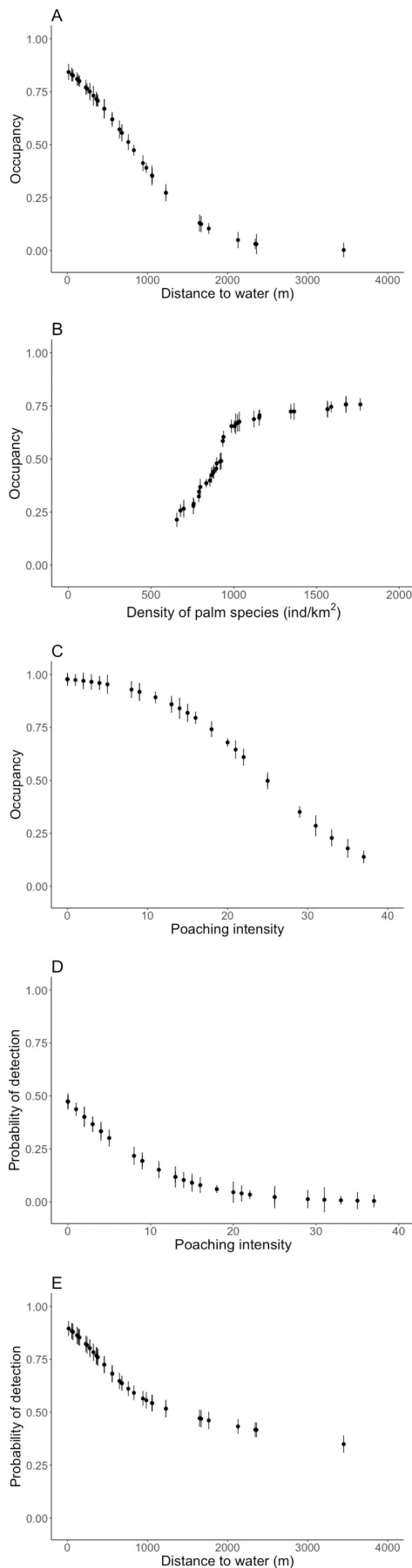
Figure 2 – Estimated effect of (A) distance from water resources; (B) density of palm species (ind/km²); and (C) poaching intensity on occupancy of Collared peccary. Estimated effect of (D) poaching intensity; and (E) distance to water resources on probability of detecting Collared peccary at a site occupied by the species.

Table 2 – Single-season occupancy and detectability models for Collared peccary and White-lipped peccary in the Vale Natural Reserve, Brazil, estimated using camera trap data between May 2013 and June 2014, grouped in sampling intervals of 5 consecutive days.

Model	ΔAICc	AICcw	param.
Collared peccary (*Pecari tajacu*) Linnaeus, 1758			
ψ(water; palm; poaching) p(water; poaching)	0.00	0.327	7
ψ(water; poaching) p(water; poaching)	0.03	0.148	6
ψ(palm; poaching) p(water; poaching)	0.79	0.144	6
ψ(water) p(water; poaching)	1.09	0.093	6
ψ(poaching) p(water; poaching)	1.89	0.091	5
ψ(palm) p(water; poaching)	2.06	0.086	5
ψ(water; poaching; road) p(water; poaching)	4.31	0.074	5
ψ(palm; poaching; road) p(water; poaching)	4.32	0.024	7
ψ(water; palm; poaching; veg) p(water; poaching)	4.35	0.004	7
ψ(water; road) p(water; poaching)	4.79	0.003	8
Model fit=0.23, $\hat{c}$=1.25 obtained with 2000 bootstraps			
White-lipped peccary (*Tayassu pecari*) Link, 1795			
ψ(water; palm; poaching; road; veg) p(poaching)	0.00	0.234	8
ψ(water; palm; poaching; road; palm) p(poaching)	0.02	0.129	7
ψ(water; palm; poaching; palm; veg) p(poaching)	0.18	0.110	7
ψ(water; poaching; road; veg) p(poaching)	1.46	0.052	7
ψ(water; poaching; veg) p(poaching)	1.48	0.050	6
ψ(water; palm; road; veg) p(poaching)	1.96	0.047	6
ψ(water; palm; poaching) p(poaching)	2.28	0.047	7
ψ(water; palm; poaching; road; veg) p(poaching)	2.81	0.041	6
ψ(water; poaching; road) p(poaching)	3.36	0.039	6
ψ(water; palm) p(poaching)	4.50	0.038	5
Model fit=0.16, $\hat{c}$=1.18 obtained with 2000 bootstraps			

Covariates include: distance to forest edge (edge); density of trees with diameter breast height > 50 cm (dens_tree); poaching intensity (poaching); density of palms species (palm); distance to road (road); density of liana (dens_liana); distance to water resources (water); and vegetation type (veg). ψ=occupancy, p=detection, AICcw=Akaike weight, param.=n°of parameters.

ively. Similarly, detection was highest at sites closest to water resources (p=0.90 ± 0.04) and lowest at sites furthest away (p=0.35 ± 0.04).

We observed the white-lipped peccary at 17 of 39 sampling sites, resulting in a naïve occupancy probability of 0.45. Estimated occupancy and detection probabilities were 0.51 ± 0.04 and 0.32 ± 0.03, respectively. The "best-fit" model described occupancy probability as a function of distance to water resources, density of palm species, poaching intensity, vegetation type, and distance to road. Detection was best modeled as a function of poaching intensity. Occupancy was higher (ψ=0.73 ± 0.02) at sites closest to water resources (Fig. 3A) and higher (ψ=0.96 ± 0.03) at sites with a high density of palm species (>1600 individuals/km²; Fig. 3B). Occupancy was negatively affected by poaching, with probabilities ranging from ψ=0.68 ± 0.06 to ψ=0.07 ± 0.03 at sites of low versus high intensity (Fig. 3C). The distance to the road had a positive influence on occupancy (Fig. 3D), with ψ>0.73 ± 0.03 at sites >1000 meters from roads. Occupancy probabilities for the white-lipped peccary also differed between vegetation types (Fig. 3E), with higher rates in riparian (ψ=0.94 ± 0.04) and coastal plain (ψ=0.88 ± 0.04) forests. Detection was also negatively related to poaching intensity (Fig. 3F), given that our probability of photographing this species dropped from 0.26 ± 0.06 to 0.007 ± 0.010.

Co-occurrence Models

We include the mean beta coefficient values in Tab. 3 for parameters ψA, ψBA, ψBa, pA, pB, rA, and $rBA = rBa$. The "best-fit" model indicated that the probability of detecting a collared peccary was independent of the detection of a white-lipped peccary (Tab. 4) yet was influenced by the presence of that species (i.e., $pB \neq rBA = rBa$). Similarly, occupancy of the collared peccary was strongly driven by the presence or absence of the white-lipped peccary (i.e., $\psi BA \neq \psi Ba$). Specifically, occupancy of the collared peccary was significantly lower
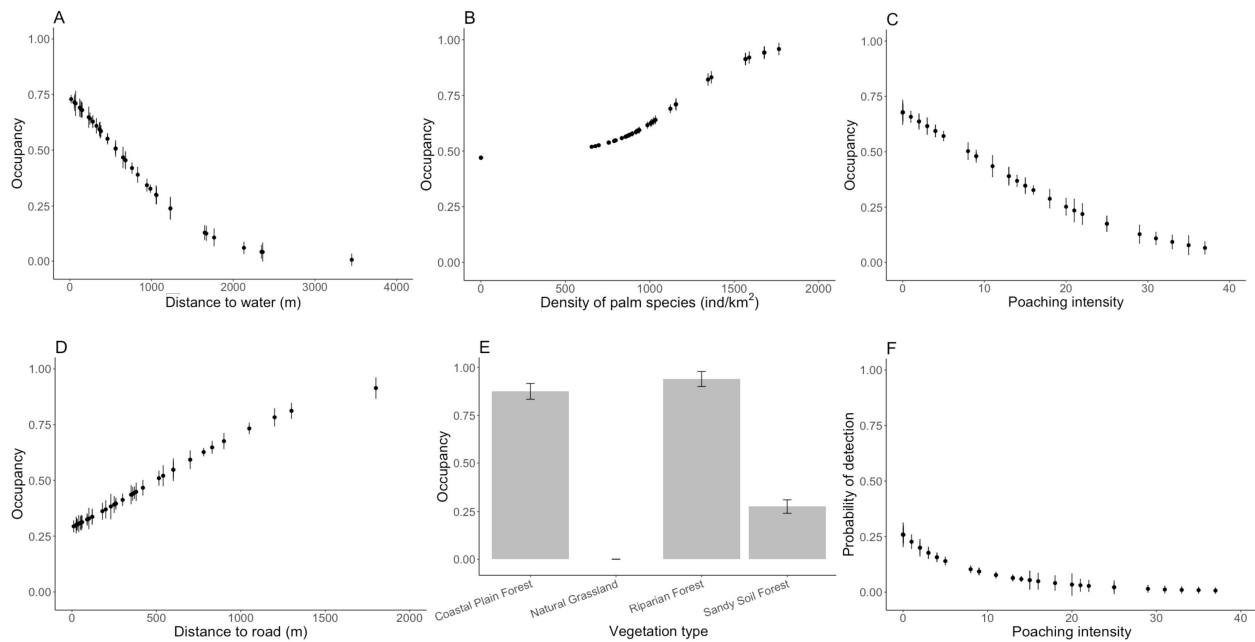
Figure 3 – Estimated effect of (A) distance from water resources; (B) density of palm species (ind/km^2); (C) poaching intensity; (D) distance to road; and (E) vegetation type on occupancy of White-lipped peccary. Estimated effect of (F) poaching intensity on probability of detecting White-lipped peccary at a site occupied by the species.

at sites occupied (Fig. 4, ψBA=0.24 ± 0.08) in comparison to sites unoccupied (ψBa=0.80 ± 0.05) by the white-lipped peccary. Based on this two-species modelling approach, we found support for the hypothesis that the two species avoid each other in space (SIF=0.41 ± 0.02).

Activity Patterns

We obtained 1234 photographic records of collared peccary and 823 of white-lipped peccary. The collared peccary was active for an average of 6.54 h/day, mainly during the day and at the beginning of the night. The white-lipped peccary was active for an average of 4.97 h/day and had primarily diurnal activity. The proportion of activity overlap between the two species was 0.51 (Fig. 5; smoothing parameter=37.4; isopleth=0.95). The overlap occurred between 06:00 h and 18:00 h, corresponding with sunrise and sunset hours, respectively.

Discussion

We estimated similar effects of habitat covariates on the occupancy of both peccary species. Despite this, our co-occurrence modeling approach suggested that the two species avoid each other in space. Spatial niche partitioning is a well-known mechanism to facilitate co-existence among ecologically-similar species (Gotelli et al., 2010; Hampton, 2004; Polis and Holt, 1992). Our results highlight a strong spatial niche partitioning between the white-lipped and collared peccary in the Vale Natural Reserve. Specifically, we demonstrated that the larger, and po-

tentially more dominant, white-lipped peccary had a higher occupancy probability associated with the forested areas in the VNR (i.e. coastal plain and riparian forests). Collared peccaries, on the other hand, occupied all vegetation types in the reserve (Desbiez et al., 2009a,b; Keuroghlian et al., 2009; Reyna-Hurtado et al., 2009; Reyna-Hurtado and Tanner, 2005; Keuroghlian et al., 2004). Both peccary species were strongly associated with environments closest to water, such as riparian forests, wetlands, and streams, but the white-lipped peccary appeared to be slightly more dependent on these water resources. In addition, palms represented a key habitat feature because occupancy probabilities of both species were positively associated with the density of palm species. Palm fruit has been shown to be a crucial food resource for both species (Keuroghlian and Eaton, 2008b; Beck, 2006; Fragoso, 1998). As a result, several studies have shown an intensive use of the palm forests by both white-lipped and collared peccaries (Keuroghlian et al., 2009; Beck, 2006; Fragoso, 1998).

Anthropogenic factors such as poaching also influenced the occupancy of both peccary species, as well as our ability to detect them. This may result from lower abundance and/or behavioral responses to persecution by poachers (Reyna-Hurtado et al., 2016; Keuroghlian et al., 2013; Gongora et al., 2011; Cullen et al., 2001; Peres, 1996). Peccaries from VNR are poached for consumption, although other Neotropical regions have reported higher rates of poaching than what we report here (Mena et al., 2000; Sowls, 1997; Bodmer et al., 1994). Occupancy of the white-lipped peccary was also positively associated with

Table 3 – Estimated beta coefficients and standard errors from the "best-fit" co-occurrence model for the Collared and White-lipped peccary in the Vale Natural Reserve, Espírito Santo state, Brasil.

Parameter[a]	Beta coefficient	SE
ψA[b]	0.4359	0.0794
ψBa	0.8183	0.0822
ψBA	0.6471	0.1159
pA	0.2914	0.0129
pB	0.1921	0.068
rA	0.4111	0.0328
$rBA = rBa$	0.4686	0.0458

[a] Estimated beta coefficients for covariate effects can be found in Fig. 4.
[b] White-lipped peccary assumed as the dominant species (species A).

Table 4 – Model selection results for the two-species conditional occupancy model examining the influence of the White-lipped peccary (species A) on the occupancy and detection of the Collared peccary (B) in the Vale Natural Reserve, Espírito Santo, Brazil.

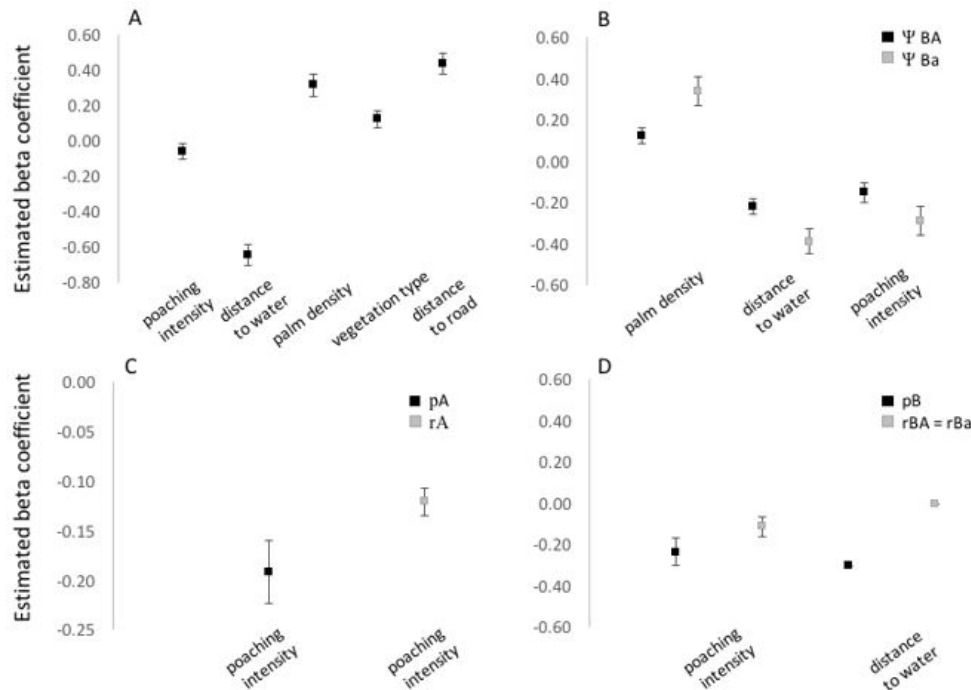| Occupancy	Detection	ΔAICc	AICcw	param.
$\psi BA \neq \psi Ba$	$pB \neq rBA = rBa$	0	0.85	24
$\psi BA \neq \psi Ba$	$pB = rBA = rBa$	21.35	0.09	20
$\psi BA \neq \psi Ba$	$pB \neq rBA \neq rBa$	23.99	0.05	27
$\psi BA = \psi Ba$	$pB \neq rBA = rBa$	35.1	0.01	19
$\psi BA = \psi Ba$	$pB = rBA = rBa$	59.75	0	16
$\psi BA = \psi Ba$	$pB \neq rBA = rBa$	65.05	0	22

Figure 4 – Estimated beta coefficients for covariate effects on occupancy of the (A) White-lipped; and (B) Collared peccary; and detection of the (C) White-lipped; and (D) Collared peccary. Reported estimates are from the "best-fit" two species occupancy model.

the distance to a road. This suggests that roads have a negative influence on at least one of our focal species, whether as a result of direct habitat loss (Keuroghlian et al., 2013) or indirect effects of roads on habitat quality (Barber et al., 2014; Laurance and Balmford, 2013; McClure et al., 2013; Van Der Ree et al., 2011) or an association with increased poaching activity near roads.

Our study is the first to show niche partitioning between these two peccary species within a co-occurrence modelling framework. Competitive interactions between collared and white-lipped peccaries is one possible explanation for the near-complete spatial niche partitioning we observed. In general, larger-bodied species either reduces the density of a smaller-bodied sympatric competitor or excludes it from the landscape (Rosenzweig, 1966). Reports from various regions have demonstrated that collared peccaries avoid contact with white-lipped peccaries and will even abandon feeding sites with the latter's arrival (Keuroghlian et al., 2004; Sowls, 1997). Agonistic relationships among peccaries have also been described in the Paraguayan Chaco where collared and chacoan peccaries (*Catagonus wagneri*) shifted their peak activity period to avoid encounters with white-lipped peccaries (Taber et al., 1994). In populations inhabiting fragmented forests, range ex-

pansions and concomitant shifts in the diet of collared peccaries were thought to be a strategy to avoid sympatric white-lipped peccaries (Keuroghlian et al., 2004). White-lipped peccaries are notoriously aggressive, and have been known to kill collared peccaries in captivity (Nogueira-Neto, 1973).

We found weak evidence for temporal niche partitioning between white-lipped and collared peccaries. We found that both species were mainly diurnal in VNR, and exhibited two activity peaks and a resting period from 10:00 h to 14:00 h. These observations coincide with patterns observed in previous studies (Galetti et al., 2015; Carrillo et al., 2002; Taber et al., 1994; Castellanos, 1983). However, the collared peccary was primarily active in the first hours of the night (i.e., 18:00 to 24:00 h), which is consistent with what (Taber et al., 1994) found in Paraguay. Temporal niche segregation did not appear to play an important role in reducing interspecific competition between collared and white-lipped peccaries.

We used camera trapping data and occupancy modeling to demonstrate similar habitat use and activity patterns of the collared and white-lipped peccary in VNR over a 1-year period. Our results suggest that, despite this large overlap in diet and habitat use (Desbiez et al., 2009a; Lees and Peres, 2008; Nowak, 1992), the collared and white-lipped peccary spatially avoid one another. However, our results also suggest that collared peccaries are more of a habitat generalist that uses a wide variety of habitats, while white-lipped peccaries are more restricted to forested habitats, especially riparian forests. This provides further evidence of spatial niche partitioning. Our results also suggest that the white-lipped peccary is more sensitive than the collared peccary to habitat alterations, particularly with regard to roads. Changes to the abundance or occupancy of white-lipped peccaries would undoubtedly influence the occupancy of collared peccaries. Long term studies are imperative in order to assess species vulnerabilities and how human activities may impact species interactions. Towards this end we provide a relevant contribution. ✍
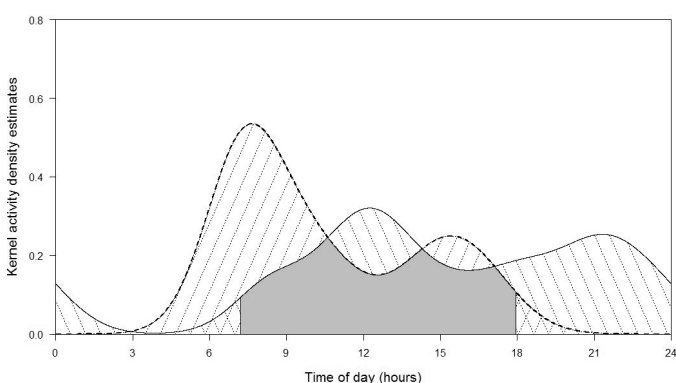

Figure 5 – Kernel activity density estimates for Collared peccary (solid line) and White-lipped peccary (dashed line) during a 24 h period. Gray areas represent periods of higher activity overlap (95% kernel) between the species in the study site, estimated using camera-trap survey data between May 2013 and June 2014. Sunrise and sunset hours were 06:00 and 18:00, respectively.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Pearson correlation matrix of the covariates used in the occupancy modelling.