USING UNGULATE OCCUPANCY TO EVALUATE A BIOSPHERE RESERVE DESIGN IN TAMBOPATA, PERU

A Thesis

by

MIGUEL MARIO LICONA

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2009

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Co-Chairs of Committee,	Roel R. Lopez
	Robert A. McCleery
Committee Member,	Donald J. Brightsmith
Head of Department,	Thomas A. Lacher

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ABSTRACT

Using Ungulate Occupancy to Evaluate a Biosphere Reserve Design in Tambopata, Peru. (August 2009)

Miguel Mario Licona, B.A., Dartmouth College

Co-Chairs of Advisory Committee: Dr. Roel R. Lopez
Dr. Robert A. McCleery

Conservation areas in tropical forests protect the most diverse and threatened ecosystems on the planet. In the Amazon, ungulates are important to forest structure and diversity, but are also food for rural people. I estimated occupancy of white-lipped peccary (*Tayassu pecari*), collared peccary (*T. tajacu*), lowland tapir (*Tapirus terrestris*), and red brocket deer (*Mazama americana*) in Tambopata, Peru to evaluate how different management designations along with anthropogenic and habitat factors influenced the distribution of these species. I used track surveys (n = 258) and camera surveys (n = 256) to estimate ungulate occupancy and detection at 55 sites in a national reserve, a native community, and adjacent buffer areas from May 2008 to March 2009. The best approximating model for white-lipped peccary, lowland tapir, and red brocket deer included only a variable of travel time from the nearest city (a measure of an area's accessibility). Management designation also had some influence on occupancy. I found significantly higher occupancy for collared peccary and red brocket deer in reserve and buffer areas than in the native community but there was no significant difference in occupancy between the reserve and buffer. These results indicate that passive protection might be an adequate management strategy for inaccessible areas of this region. However, as the Amazon continues to be developed, more active enforcement of park boundaries and regulations should be enacted if wildlife conservation is to be effective.

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I want to thank Bob McCleery for providing me with the framework and the freedom to complete this research project. I appreciate his frank advice on matters professional and personal. Thank you to Roel Lopez for his guidance and support. I also want to thank Don Brightsmith for helping me find a study area and support in the field.

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Thank you to all the women who raised me: Patti, Kandy, Laura, Evi, Mikela, Rebeca, and Grace. Thank you Daddy for getting me started in science. Thank you to my Peruvian family for being my second home. Thank you to Lorena and Flavia for your patience and understanding. Finally, thank you Gloria for accompanying me in the field and in life.

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INTRODUCTION

Moist tropical forests cover 6% of the Earth's land surface and contain more than half of all species, but are one of the most rapidly depleted ecosystems on the planet (Wilson 2003). The Amazon rain forest exemplifies the delicate relationship between human development and biodiversity in the tropics. It is the largest rainforest in the world and a center of biodiversity; home to numerous endemic and endangered species (Kress et al. 2004). The Amazon's biodiversity is threatened from numerous anthropogenic activities including hunting, agriculture, deforestation, fossil fuel development, mining, road construction, and climate change (Killeen 2007).

Protected areas have been widely accepted as the most effective means of preserving biodiversity (MacKinnon et al. 1986, IUCN 1994). The concept of a biosphere reserve is a model that has been applied to selection and management of 261 protected areas in 70 countries worldwide (Batisse 1986). It integrates a core area dedicated to conservation with an intermediate buffer zone used for low impact activities such as tourism and research and an outer transition zone for high impact activities such as agriculture and human settlement (Batisse 1986, MacKinnon et al. 1986). However, strict interpretation and enforcement of the biosphere reserve concept has been difficult in the face of complex social, economic, and biological forces (Wells and Brandon 1993).

This thesis follows the style of The Journal of Wildlife Management.

There is a growing debate regarding the establishment of protected areas, the impacts they have on regional economies, and the role of local people in the decision making process (Adams et al. 2004, Sanderson and Redford 2004, Wilkie et al. 2006). On one end of the continuum of there is the belief that conservation and development occupy separate realms and at the other it is believed the two are inextricably tied together (Adams et al. 2004). The biosphere reserve model has been developed as a compromise between these two conservation paradigms (Wells and Brandon 1993). It is intended to maintain a core conservation area where human impacts are minimized or eliminated. Ideally, the loss of economic opportunities in the core area would be offset by permitted activities in the buffer zone (Naughton-Treves et al. 2005).

Anthropogenic encroachment has been cited as a major factor mitigating the effectiveness of protected areas (Peres and Terborgh 1995). Roads open remote areas to logging, agricultural conversion and hunting (Chomitz and Gray 1996, Peres 2001, Laurance et al. 2006). There has been a direct causal relationship drawn between road building and loss of forest cover in tropical areas (Mäki et al. 2001), although substantially lower rates of deforestation were found in protected areas compared to surrounding areas (Sánchez-Azofeifa et al. 1999). Human accessibility to protected areas has also been shown to increase hunting pressure on wildlife populations (Hill et al. 1997). In the Congo Basin of Africa, distinct patterns have been demonstrated between ungulate densities and distance to roads (Fimbel et al. 2000). In the Amazon, it has been shown that areas ≥6 km from a river or road are passively protected from extractive activities by the practical limits of distance (Peres and Lake 2002). In many parts of the

Amazon, rivers replace roads as the primary means of access to otherwise remote and inaccessible areas (Peres and Terborgh 1995).

In Peru, several national parks, reserves and indigenous communities have been established to preserve its tropical forests. The Department of Madre de Dios contains a group of protected areas following the biosphere reserve model. This complex of protected areas contains 2 core areas consisting of Bahuaja-Sonene National Park and Tambopata National Reserve surrounded by a buffer zone and several native community reserves (Instituto Nacional de Recursos Naturales [INRENA] 2003). This area forms part of a 30 million ha complex of 18 protected areas across Peru and Bolivia known as the Vilcabamba-Amboró Conservation Corridor (Conservation International 2009).

The Inter-Oceanic Highway which borders these protected areas and bisects the corridor is currently being paved. This road was originally constructed in the 1960's to populate and exploit remote parts of the Amazon, and in 1979, an agreement was signed with Brazil to extend the road to the Peruvian coast (Naughton-Treves et al. 2005). Greater accessibility has led to increased immigration to the region and potentially detrimental impacts on the structure and resources of the forest (Oliveira et al. 2007). It has been predicted that deforestation rates will increase with the completion of this project, however the direct cause of this will not be the road itself, but its concomitant population growth and construction of secondary road networks (Naughton-Treves et al. 2005).

Ungulates are an ecologically and socially important group that contributes to biomass and diversity of ecosystems worldwide (Emmons and Feer 1997). In the

Amazon, this assemblage consists of white-lipped peccary (*Tayassu pecari*), collared peccary (*T. tajacu*), lowland tapir (*Tapirus terrestris*), red brocket deer (*Mazama americana*), and grey brocket deer (*M. gouazoubira*). These 5 species provide a food source for rural communities (Robinson and Bodmer 1999) and the sale of their meat brings revenue for rural hunters (Bodmer and Puertas 2000). Subsistence hunters exhibit a preference for large game because they are the most efficiently hunted prey items (Alvard 1993). This preference can be a problem for ungulates because large-bodied animals tend to have long life-spans and low reproductive rates (Robinson and Redford 1986).

Ungulates play vital roles in the Amazon ecosystem. They influence forest structure and plant diversity through seed dispersal, seed predation, and herbivory (Redford 1992) and are prey for large predators (Weckel et al. 2006). The loss of these species results in gradual yet profound shifts in the character of the plant community and a major loss of biodiversity (Redford 1992). The removal of large mammal species from an otherwise intact tropical ecosystem results in an “empty forest” which is more difficult to detect and quantify than deforestation (Redford 1992). When ungulates can no longer perform their ecological functions, the large seeded species experience reduced dispersal and increased conspecific competition (Stoner et al. 2007).

Two important resources for ungulates in the Amazon are claylicks and waterholes (McShea et al. 2001, Montenegro 2004). Claylicks are exposed areas where animals consume soil. These soils have high concentrations of minerals, principally sodium, but also calcium, magnesium, and phosphorus that supplement the animals’ diets (Montenegro 2004). Claylick soils also have high clay concentrations that can reduce the effects of plant toxins, acidosis, and intestinal infections in wildlife (Klaus and Schmid 1998). Water holes have also been shown to be important resources for tropical ungulates, especially in the water-limited dry season (McShea et al. 2001).

In order to preserve biodiversity in the Amazon, it is important to evaluate the efficacy of current management efforts. Further, we need to determine and address the factors that are influencing the presence and distribution of animals in this ecosystem. The goal of this study was to determine if area designation in a biosphere reserve, anthropogenic factors or habitat characteristics influenced the distribution of ungulates in the Amazon rainforest of southeastern Peru. Specifically, my objectives were to 1) determine if the management designation within a biosphere reserve framework influence the occupancy of lowland tapir, white-lipped peccary, collared peccary, red brocket deer, and grey brocket deer; 2) how the proximity to roads, deforestation, and human populations influence ungulate distribution in the biosphere reserve; 3) Identify habitat characteristics with the greatest effects on ungulate occupancy; and 4) make recommendations for selection of protected areas and management of Neotropical ungulates.

STUDY AREA

I conducted this study in the Department of Madre de Dios, Tambopata Province, Peru (Figure 1). This area lies at the foot of the Andes Mountains, at the western edge of the Amazon basin, in the moist tropical life zone, near the edge of the moist subtropical life zone boundary (Holdridge 1967). The vegetation of this region has been characterized as primary tropical moist forest made up of terrace (terra firme), and floodplain forest (várzea; Griscom and Ashton 2003). The dominant tree families in this region have been identified as Arecaceae, Moraceae, Euphorbiaceae, Myristaceae, Sapotaceae, Violaceae, and Rubiaceae (Pitman et al. 2001). Altitude is approximately 250 m and annual rainfall has been recorded as 3,200 mm with a weak dry season from April–September (Brightsmith and Bravos 2006).

This area fits the biosphere reserve model with 2 levels of core protected areas consisting of a national park adjacent to a national reserve surrounded by a buffer zone. Bahuaja-Sonene National Park (hereafter, park) contains 1,091,000 ha and has been protected from all forms of extractive activities, except for low levels of hunting by indigenous people. Tambopata National Reserve (hereafter, reserve) contains 275,000 ha and has the same restrictions as the park; however, ecotourism and Brazil nut collection are permitted. The buffer zone surrounding these areas contains 262,000 ha that can be used for low levels of agriculture, logging, mining, and hunting (INRENA 2003). The Native Community of Infierno (hereafter, community) is a reserve owned and managed by the indigenous Ese’Eja and mestizo community members that contains 10,000 ha, of which 4,000 ha has been set aside exclusively for ecotourism (Brightsmith and Muñoz-Najar 2004). There is one guard station administered by INRENA between the community and the reserve and a second one between the reserve and the park. The nearest urban center is Puerto Maldonado, the department capital (Figure 1).

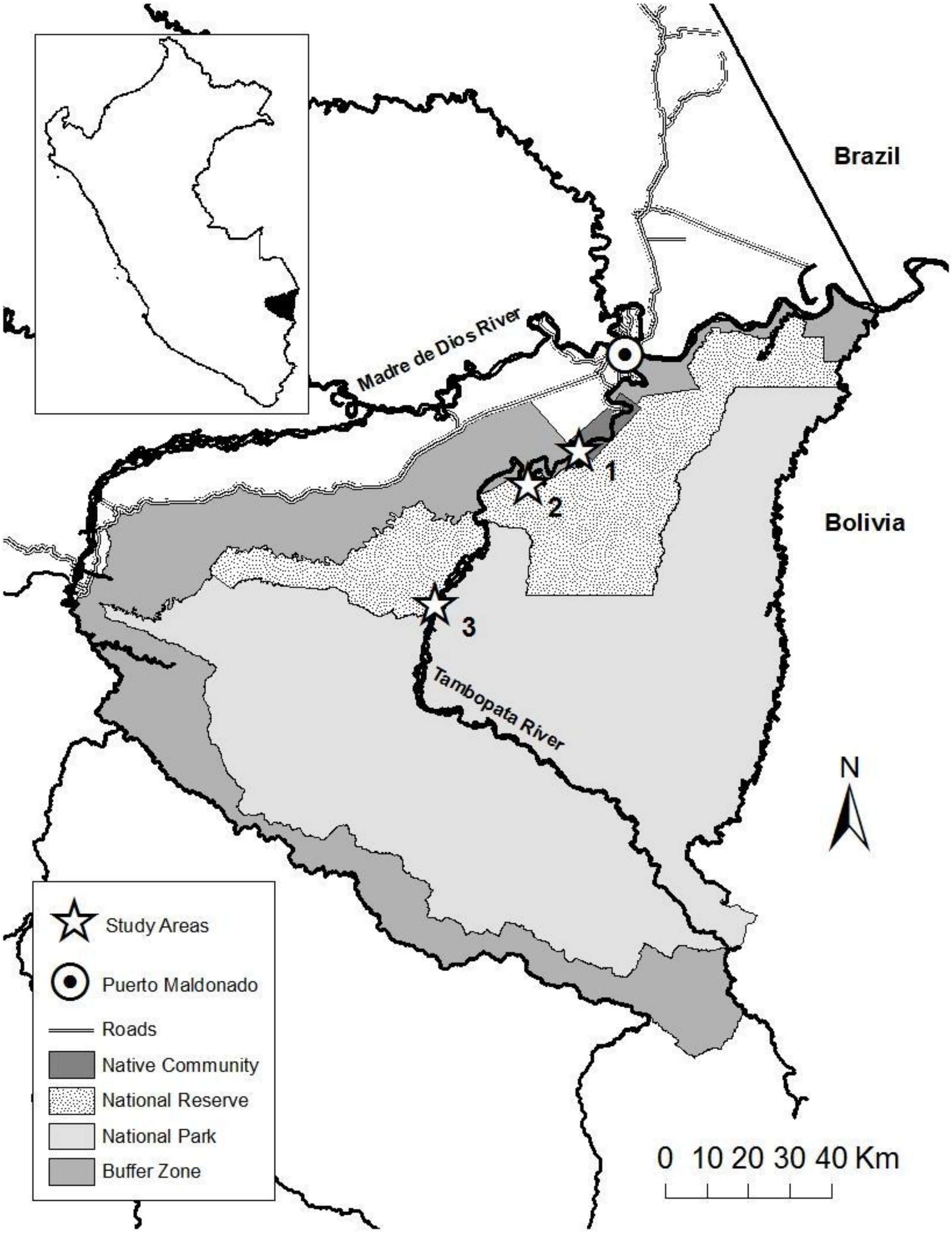

Figure 1. Map of 3 study areas and 4 management designations (native community, national reserve, national park, and buffer zone) in Tambopata, Peru.

METHODS

Site selection

I selected a total of 55 sites; 32 in the reserve, 10 in the community, and 13 in the adjacent buffer zone to survey. I worked in 3 study areas based around 3 access points into the forest areas (Figures 2–4). Study area 1 was located in the community and study area 2 was located in the buffer zone. Study areas 1 and 2 also provided access to areas within the reserve. The third study area was located near the border of the park and provided access to the reserve. I established the area that I could reach on foot in <6 hours from my 3 access points as my total study area. Within this area, I systematically placed 1 km transects approximately ≥0.5 km apart to ensure independence.

I conducted camera and track surveys during 3 seasons of the year to distinguish differences in occupancy by season, and to account for seasonal variation in detection probability. I conducted surveys during the dry season (May–August 2008), the transition period (September –November 2008), and the wet season (January–March 2009). Each season was defined as a primary sampling occasion and each track or camera survey was the secondary sampling occasion.

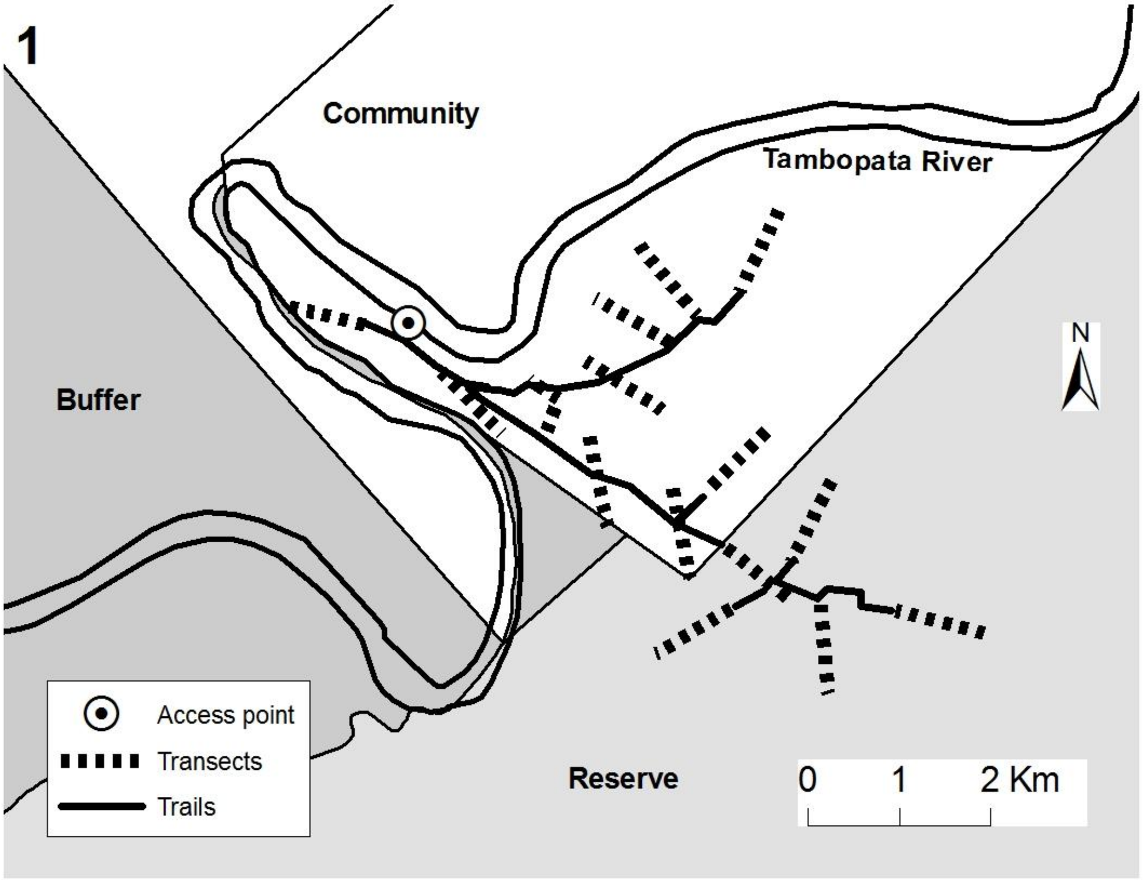

Figure 2. Map of study area 1 including survey sites in the community and reserve and access point in Tambopata, Peru

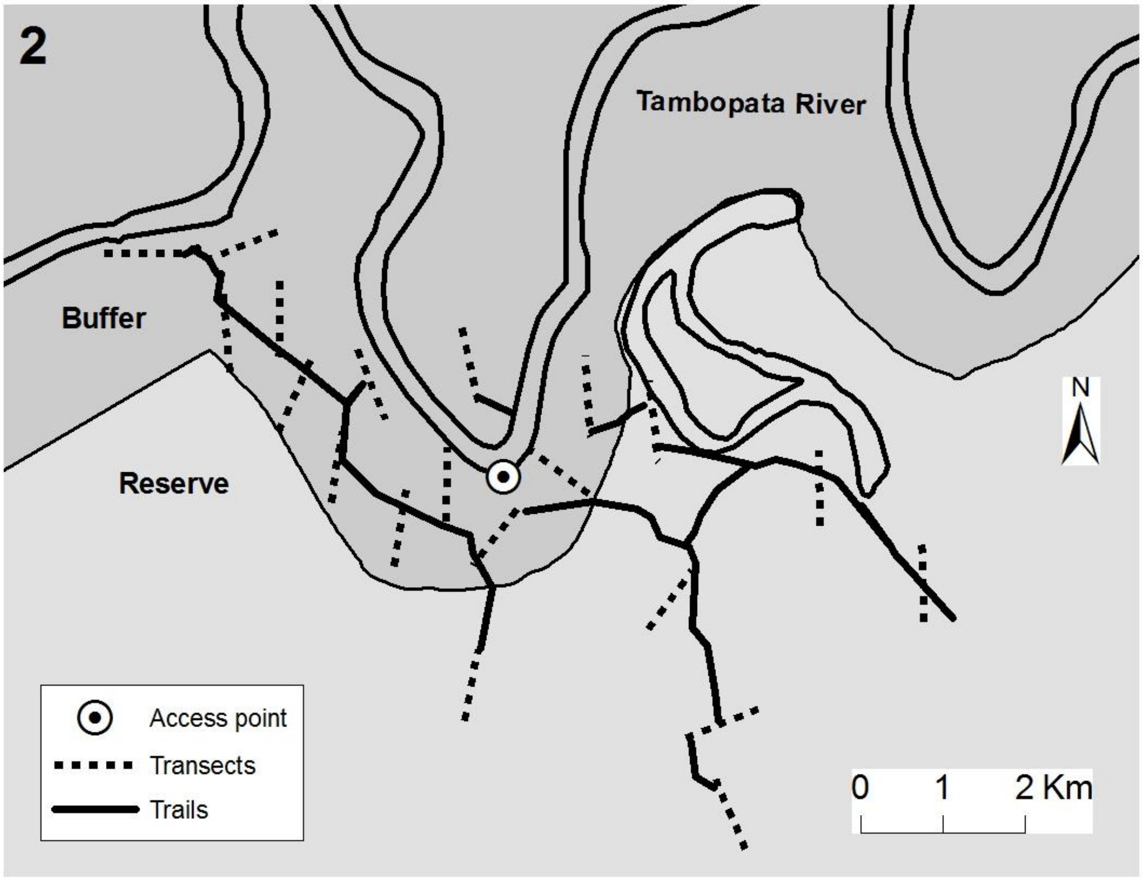

Figure 3. Map of study area 2 including survey sites in the reserve and buffer and access point in Tambopata, Peru.

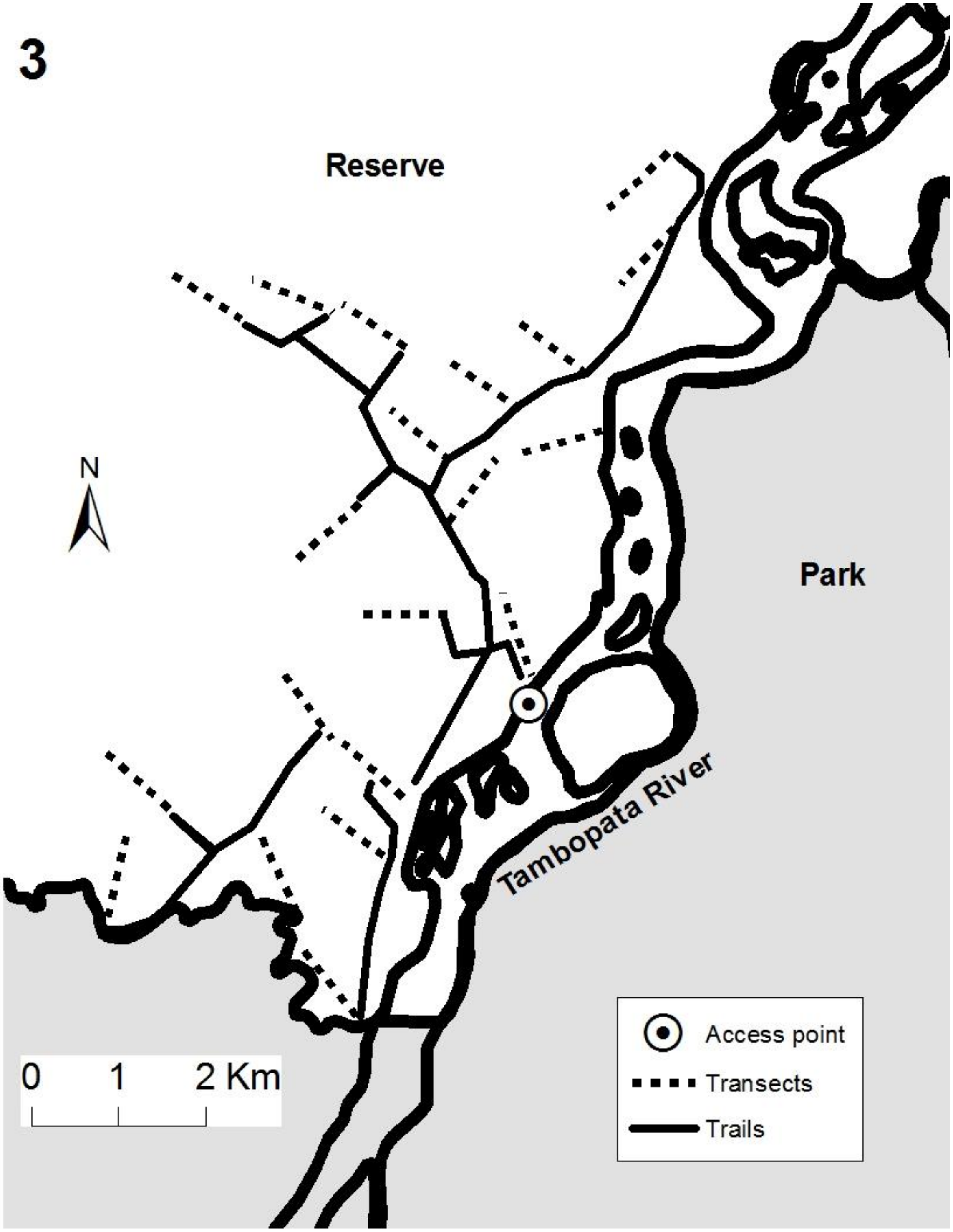

Figure 4. Map of study area 3 including survey sites in the reserve and access point in Tambopata, Peru.

Track surveys

I cut only enough vegetation to allow me to walk each 1 km transect and to see the ground, while minimizing disturbance or the chance of attracting animals to the transect. I walked (1–2 km per hour) each transect scanning for tracks 2–3 times during each season. I recorded each of the 5 ungulate species as either detected or not detected. I walked on or otherwise erased tracks after detection to avoid re-detecting them on a subsequent survey. Surveys were conducted approximately 1 week apart to allow reasonable time for animals to leave new tracks. Nonetheless, all surveys within each season were conducted over <1 month to ensure closure. I also recorded site and survey specific data that could have influenced ungulate occupancy and detection. I recorded rain within 24 hr (R), forest type (terra firme or várzea; veg) and whether the transect intersected a water hole (hole) or aguaje palm swamp (palm).

Camera surveys

I used 13 Cuddeback C3000 infrared-triggered digital cameras (NonTypical, Park Falls, Wisconsin) to conduct 3 consecutive camera surveys for 4 nights on each survey block during each season. A species was recorded as detected if it was photographed ≥1 time during the survey. I placed cameras traps along the same transects used for track surveys on the randomly chosen blocks. Within each block, I subjectively placed cameras in areas where they had the greatest probability of capturing an animal such as game trails, claylicks, or water holes. If the camera was placed at a water hole (H) or a claylick (P), I recorded this to account for possible differences in detection.

I placed the camera approx. 3 m from the spot where an animal was most likely to pass, with the aperture of the camera approx. 75 cm from the ground. I anchored the camera to a tree with a screw and a steel cable. To protect the cameras from moisture, I sealed them with silicon, placed 15 g of silica gel desiccant inside, and covered them with a canopy of leaves.

Spatial analysis

I recorded the location of each survey site and claylicks with a handheld eTrex Venture HC Global Positioning System [GPS] (Garmin International, Inc., Olathe, Kansas). I acquired local knowledge from area residents and other researchers to find the location of known claylicks (Donald Brightsmith, Texas A&M University, unpublished data). I used Landsat Thematic Mapper images (2005–2006) to map roads and deforestation in the region. All spatial information was placed into a Geographic Information System [GIS] database. I then used ArcMap 9.2 GIS to measure linear distance from each survey site to claylicks (lick, D), roads (road), and contiguous areas of deforestation >1 km^2 (edge). To quantify the accessibility of each study block (time), I measured boat and walking travel time from Puerto Maldonado to each survey site. To calculate total travel time, I combined the average travel time upriver by boat with a 55 hp outboard motor from Puerto Maldonado to the port closest to each access point and the walking time to the study block from the port estimated as the perpendicular distance at 3 km per hour. These combined measurements provided an overall travel time and an index of the accessibility of each study site. This measurement was also a proxy for the relative human activity, and human population density of an area, as both decreased with greater distance from the city.

Occupancy and detection estimation

I estimated species-specific occupancy (ψ) while accounting for detection (p) probabilities from 2 survey methods (track and camera) using occupancy modeling methodologies described by MacKenzie et al. (2006). I used multi-season models with the initial parameterization in all analyses, except for red brocket deer (MacKenzie et al. 2006). Due to limited detection in the transition and wet seasons, I only modeled red brocket deer during the dry season using a single season model (MacKenzie et al. 2006). I evaluated all candidate models and estimated parameters using the program PRESENCE 2.2 (Hines 2006). Before evaluating occupancy for each species I compared 16 a priori models with a constant ψ and different parameterizations of p to determine which models accounted for the most variability in detection (Table 1).

To examine differences in detection, I evaluated models with 5 detection parameters including cameras or track survey method (M), rain within 24 hours (R), distance to the nearest claylick (D), camera placement at a claylick (P), and camera placement at a waterhole (H). I selected the model with the lowest Akaike's Information Criterion adjusted for small sample size (AIC_c) as the best representation of the data (Burnham and Anderson 2002). I examined the relevance of each parameter in the top ranked detection models by examining its 95% confidence interval (CI) to see if it contained 0 (Burnham and Anderson 2002). I then used the best model with relevant predictors in all subsequent models used to evaluated occupancy.

To determine what factors had the greatest influence on the occupancy of each ungulate species, I evaluated 15 a priori occupancy models (Table 2) with the best detection parameterization (see above). I evaluated models with 3 management designations (reserve, buffer, community; 3area) and 2 management designations (reserve-buffer and community; area) to determine if occupancy differed between the reserve and buffer designation.

Table 1. Notation and descriptions of a priori detection models for 4 ungulate species in Tambopata, Peru.

Model notation	Description of detection covariates and models
p(.)	constant detection across all surveys
p(M)	track or camera method
p(R)	rain within 24 h of track survey
p(D)	distance from a claylick to transect
p(P)	camera placement at a claylick
p(H)	camera placement at a waterhole
p(MR)	track or camera method and rain within 24 h of track survey
p(MD)	track or camera method and distance from a claylick to transect
p(MP)	track or camera method and camera placement at a claylick
p(MH)	track or camera method and camera placement at a waterhole
p(MRP)	track or camera method, rain within 24 h of track survey, and camera placement at a claylick
p(MDP)	track or camera method, distance from a claylick to transect, and camera placement at a claylick
p(MRH)	track or camera method, rain within 24 h of track survey, and camera placement at a waterhole
p(MRD)	track or camera method, rain within 24 h of track survey, and distance from a claylick to transect

Table 1. Continued

Model notation	Description of detection covariates and models
p(MRDP)	track or camera method, rain within 24 h of track survey, distance from a claylick to transect, and camera placement at a claylick
p(MRDPH)	track or camera method, rain within 24 h of track survey, distance from a claylick to transect, camera placement at a claylick, and camera placement at a waterhole

Table 2. Notation and descriptions of a priori occupancy models for 4 ungulate species in Tambopata, Peru.

Model notation	Description of occupancy covariates and models
ψ(.)	occupancy is constant
ψ(3areas)	site has 1 of 3 management designations (reserve, buffer, or community)
ψ(area)	site has 1 of 2 management designations (reserve-buffer or community)
ψ(time)	travel time from Puerto Maldonado to each site
ψ(road)	distance to the nearest road
ψ(edge)	distance to the nearest deforested area >1 km^2
ψ(lick)	distance to the nearest claylick
ψ(time+area)	travel time and 2 management designations
ψ(time+3areas)	travel time and 3 management designations
ψ(time+lick)	travel time and distance to the nearest claylick
ψ(time+hole)	travel time and presence of a waterhole
ψ(area+lick)	2 management designations and distance to the nearest claylick
ψ(time+area+lick)	travel time, 2 management designations, and distance to the nearest claylick
ψ(hole)	presence of a waterhole
ψ(veg)	site located in terra firme or várzea forest

I also evaluated models with travel time from Puerto Maldonado (time), linear distance to the nearest road (road) and deforested area (edge) to assess other potential anthropogenic impacts on ungulate occupancy. Distance to the nearest claylick (lick), presence of a water hole (hole), and forest type (veg) were modeled as habitat components that could potentially influence occupancy. To select the best approximating models in each model set, I ranked models using their AICc value their relative difference from the best model (ΔAIC_c) and Akaike weights (w_i) (Burnham and Anderson 2002). I considered models ≤2 AIC_c units to compete with the best models and discarded models >2 AIC_c units as unlikely representations of the data (Burnham and Anderson 2002).

After selecting top ranked models, I model averaged their maximum likelihood estimates of occupancy and evaluated their relevance by examining whether their 95% CIs contained 0 (Burnham and Anderson 2002). Then, I graphically displayed the relationship between ψ and relevant parameters for each species (Donovan and Hines 2007).

RESULTS

I conducted 258, 1 km transect surveys and 256, 4 night camera surveys during this study. I detected white-lipped peccary, collared peccary, lowland tapir, and red brocket deer on 108, 71, 65, and 51 track surveys and 48, 18, 34, and 27 camera surveys, respectively (Table 3). Grey brocket deer were only detected once on a track survey and twice during a camera survey.

I selected a different parameterization for detection of each of the 4 species based on AIC_c values (Table 4). Each method (M) had a unique detection probability for all 4 species. Rain within 24 hours of a track survey (R) decreased detection for all 4 species except red brocket deer which was not affected by rain and modeled only during the dry season (Table 5). Distance from the transect to the nearest known claylick (D) and camera placement at a claylick (P) had an additive effect on detection of white-lipped peccary, lowland tapir and red brocket deer and camera placement at a waterhole (H) affected detection of collared peccary (Table 4).

The best fitting models of occupancy for white-lipped peccary (w_i >0.773), lowland tapir (w_i >0.8157), and red brocket deer (w_i >0.3329) included only travel time as a covariate (Tables 6 and 7). Travel time was not a covariate in the best model for collared peccary occupancy, however it appeared as a covariate in 4 of 8 top ranked models ($\Delta AIC_c \leq 2$, w_i >0.3557) for this species (Tables 6 and 7). For all 4 species, model averaged estimates of travel time were positive and 95% CIs did not include 0, indicating its relevance as a predictor of occupancy (Table 8). Examining occupancy as a function of travel time for all species showed increased occupancy from 2 to 6–8 hours of travel time (Figures 5–8). Collared peccary and red brocket deer occupancy approached 1 when travel time was approximately 6 hours. White-lipped peccary and lowland tapir occupancy approached 1 when travel time was approximately 8 hours.

Table 3. Number of detections of 4 ungulate species in 3 management designations using track (T) and camera (C) survey methods during the dry season (May–August 2008), transition (September –November 2008), and wet season (January–March 2009) in Tambopata, Peru. Detection data was collected at 32 sites in the reserve, 13 sites in the buffer, and 10 sites in the community using 258, 1 km track surveys and 256, 4 night camera surveys (1,024 nights).

	Dry season		Transition		Wet season		**Total**	
	T	C	T	C	T	C	T	C
WLP								
Reserve	29	10	20	20	24	8	**73**	**38**
Buffer	11	0	0	0	3	0	**14**	**0**
Community	10	6	1	1	10	3	**21**	**10**
Total	**50**	**16**	**21**	**21**	**37**	**11**	**108**	**48**
CP								
Reserve	24	2	10	6	11	3	**45**	**11**
Buffer	12	1	2	3	5	0	**19**	**4**
Community	5	0	0	0	2	3	**7**	**3**
Total	**41**	**3**	**12**	**9**	**18**	**6**	**71**	**18**
LT								
Reserve	23	11	14	10	13	3	**36**	**24**
Buffer	7	2	0	0	0	0	**7**	**4**
Community	3	2	1	1	4	3	**8**	**6**
Total	**33**	**15**	**15**	**13**	**17**	**6**	**65**	**34**

Table 3. Continued

	Dry season		Transition		Wet season		**Total**	
	T	C	T	C	T	C	T	C
RBD								
Reserve	26	8	3	9	6	3	**35**	**20**
Buffer	14	2	0	1	1	0	**15**	**3**
Community	0	3	1	0	0	1	**1**	**4**
Total	**40**	**13**	**4**	**10**	**7**	**4**	**51**	**27**

Table 4. The number of parameters (K), AIC_c, and ΔAIC_c values for a priori detection models of 4 ungulate species in Tambopata, Peru.

	Species[b]											
	WLP			CP			LT			RBD[c]		
Detection model[a]	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c
p(MRDP)	8	430.20	0.00	8	418.12	9.98	8	430.64	0.00	6	190.56	2.50
p(MRP)	7	431.36	1.16	7	415.54	7.40	7	431.36	0.72	5	191.16	3.10
p(MRDPH)	9	432.97	2.77	9	411.51	3.37	9	433.41	2.77	7	190.42	2.36
p(MDP)	7	434.18	3.98	7	425.21	17.07	7	434.75	4.11	5	188.06	0.00
p(MP)	6	436.64	6.44	6	422.95	14.81	6	436.64	6.00	4	189.32	1.26
p(MRD)	7	436.95	6.75	7	418.40	10.26	7	437.42	6.78	4	192.20	4.14
p(MR)	6	438.42	8.22	6	415.83	7.69	6	438.42	7.78	4	194.41	6.35
p(MRH)	7	440.34	10.14	7	408.14	0.00	7	440.34	9.70	5	194.72	6.66
p(D)	5	441.00	10.80	5	437.60	29.46	5	441.65	11.01	3	192.24	4.19

Table 4. Continued

	Species[b]											
	WLP			CP			LT			RBD[c]		
Detection model[a]	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c
p(MD)	6	441.28	11.08	6	425.84	17.70	6	441.88	11.24	4	190.82	2.76
p(M)	5	444.07	13.87	5	423.53	15.39	5	444.07	13.43	3	192.67	4.62
p(MH)	6	445.79	15.59	6	415.41	7.27	6	445.79	15.15	4	192.77	4.71
p(H)	5	460.82	30.62	5	472.06	63.92	5	460.82	30.18	3	219.07	31.02
p(P)	5	462.58	32.38	5	463.00	54.86	5	462.58	31.94	3	188.77	0.72
p(.)	4	462.59	32.39	4	470.69	62.55	4	462.59	31.95	2	223.12	35.06
p(R)	5	463.15	32.95	5	472.51	64.37	5	463.15	32.51	3	225.17	37.12

[a] Parameter abbreviations: (M) camera or track method, (R) rain within 24 h of the track survey, (D) distance from a claylick to the transect, (P) camera placement at a claylick, (H) camera placement at a waterhole, and (.) constant detection.

[b] Species abbreviations: (WLP) white-lipped peccary, (CP) collared peccary, (LT) lowland tapir, and (RBD) red brocket deer.

[c] Modeled using only dry season (May–August) detection data.

Table 5. Maximum likelihood estimates (MLE) and upper (↑95%) and lower (↓95%) 95% confidence intervals for parameters of the best detection model for each of 4 ungulate species in Tambopata, Peru.

		p		p(M)		p(R)		p(D)		p(P)[c]		p(H)	
Species[a]	Model[b]	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%
WLP	p(MRDP)	0.1766	0.2470 0.1062	0.7578	0.9113 0.6042	0.1935	0.3683 0.0186	0.5763	0.6548 0.4978	0.8195	0.9594 0.6797		
CP	p(MRH)	0.0738	0.1179 0.0297	0.9321	0.9786 0.8856	0.1969	0.3422 0.0517					0.8760	0.9990 0.7530
LT	p(MRDP)	0.1766	0.2478 0.1054	0.7688	0.9147 0.6229	0.1919	0.3660 0.0178	0.5689	0.6447 0.4930	0.8194	0.9599 0.6789		
RBD[d]	p(MDP)	0.3491	0.6071 0.0912	0.5294	0.8754 0.1833			0.3587	0.4876 0.2298	0.5942	0.6915 0.4969		

[a] Species abbreviations: (WLP) white-lipped peccary, (CP) collared peccary, (LT) lowland tapir, and (RBD) red brocket deer.

[b] Parameter definitions: (M) camera or track method, (R) rain within 24 h of the track survey, (D) distance from a claylick to the transect, (P) camera placement at a claylick, and (H) camera placement at a waterhole.

[c] Modeled effect of distance to a claylick on camera detection for RBD only.

[d] Modeled using only dry season (May–August) detection data.

Models with 2 management designations (reserve-buffer and community) were ranked higher than models with 3 management designations (reserve, buffer, and community) and a variable in best competing models ($\Delta AIC_c \leq 2$) for collared peccary and red brocket deer (Table 6). For collared peccary and red brocket deer, the 95% CI of parameter estimates of 2 management designations did not include 0, indicating its relevance as a predictor of occupancy (Table 8). Occupancy was higher in the reserve-buffer than in the community during the dry season for both collared peccary (ψ reserve-buffer = 0.9290, ψ community = 0.4809) and red brocket deer (ψ reserve-buffer = 1.000, ψ community = 0.3340; Figure 9). The best model for collared peccary included only management designation as a covariate and the second best model included the additive effect of management designation and distance to claylicks (lick) which appears to be a relevant predictor of occupancy (MLE = 0.3009, 95% CI = 0.1869, 0.4150). Examining claylicks as a function of occupancy, there was clearly a positive relationship between distance to claylicks and occupancy of collared peccary (Figure 10). Another top ranked model contained presence of a waterhole (hole) as a covariate which was also a relevant predictor of occupancy (MLE = 0.0806, 95% CI = 0.0806, 0.0806, Figure 11).

Table 6. The number of parameters (K), AIC_c, and $\Delta\mathrm{AIC}_c$ values for a priori occupancy models of 4 ungulate species in Tambopata, Peru.

	Species[b]											
	WLP			CP			LT			RBD[c]		
Occupancy model[a]	K	AIC_c	$\Delta\mathrm{AIC}_c$	K	AIC_c	$\Delta\mathrm{AIC}_c$	K	AIC_c	$\Delta\mathrm{AIC}_c$	K	AIC_c	$\Delta\mathrm{AIC}_c$
ψ(time)	9	419.50	0.00	8	407.05	0.68	9	419.5	0.00	6	177.81	0.00
ψ(time+3areas)	11	420.13	0.63	10	412.12	5.75	11	420.61	1.11	8	183.69	5.88
ψ(time+area)	10	421.15	1.65	9	408.78	2.41	10	421.15	1.65	7	180.96	3.15
ψ(time+lick)	10	421.97	2.47	9	407.85	1.48	10	422.45	2.95	7	180.88	3.07
ψ(time+hole)	10	422.34	2.84	9	407.94	1.57	10	422.78	3.28	7	180.44	2.63
ψ(time+area+lick)	11	424.82	5.32	10	408.37	1.20	11	424.02	4.52	8	184.15	6.34
ψ(veg)	9	427.94	8.44	8	410.76	4.39	9	428.38	8.88	6	191.27	13.46
ψ(hole)	9	430.03	10.53	8	409.63	3.26	9	430.48	10.98	6	191.13	13.32
ψ(.)	8	430.09	10.59	7	408.14	1.77	8	430.64	11.14	5	188.34	10.53

Table 6. Continued

	Species[b]											
	WLP			CP			LT			RBD[c]		
Occupancy model[a]	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c	K	AIC_c	ΔAIC_c
ψ(area)	9	430.18	10.68	8	406.37	0.00	9	430.69	11.19	6	178.47	0.66
ψ(area+lick)	10	431.92	12.42	9	406.85	0.48	10	432.42	12.92	7	181.00	3.19
ψ(3areas)	10	432.03	12.53	9	409.08	2.71	10	432.55	13.05	7	180.31	2.50
ψ(lick)	9	433.26	13.76	8	408.27	1.90	9	433.26	13.76	6	190.42	12.61
ψ(road)	9	447.65	28.15	8	413.54	7.17	9	448.18	28.68	6	194.03	16.22
ψ(edge)	9	447.65	28.15	8	413.54	7.17	9	448.18	28.68	6	194.03	16.22

[a] Parameter definitions: (3areas) 3 management designations (reserve, buffer, and community), (area) 2 management designations (reserve-buffer and community), (time) travel time from the nearest city, (lick) distance to the nearest claylick, (hole) presence of a waterhole, (road) distance to the nearest road, (edge) distance to the nearest deforested area >1 km^2, (veg) forest type, and (.) constant occupancy.

[b] Species abbreviations: (WLP) white-lipped peccary, (CP) collared peccary, (LT) lowland tapir, and (RBD) red brocket deer.

[c] Modeled using only dry season (May–August) detection data.

Table 7. Ranking of best a priori models ($\Delta AIC_c \leq 2$) used to examine the effects of management designation, anthropogenic factors, and habitat characteristics on occupancy of 4 ungulate species in Tambopata, Peru. Included are the number of parameters (K), -2 log likelihood (-2lnL), AIC_c, ΔAIC_c, and Akaike weights (w_i) of each model.

Species[a]	Model[b]	K	-2lnL	AIC_c	ΔAIC_c	w_i
WLP	ψ(time)p(MRDP)	9	397.50	419.50	0.00	0.3565
	ψ(time+3areas)p(MRDP)	11	391.99	420.13	0.63	0.2602
	ψ(time+area)p(MRDP)	10	396.15	421.15	1.65	0.1562
CP	ψ(area)p(MRH)	8	387.24	406.37	0.00	0.1767
	ψ(area+lick)p(MRH)	9	384.85	406.85	0.48	0.1390
	ψ(time)p(MRH)	8	387.92	407.05	0.68	0.1258
	ψ(time+lick)p(MRH)	9	385.85	407.85	1.48	0.0843
	ψ(time+hole)p(MRH)	9	385.94	407.94	1.57	0.0806
	ψ(.)p(MRH)	7	391.76	408.14	1.77	0.0728
	ψ(lick)p(MRH)	8	389.14	408.27	1.90	0.0683
	ψ(time+area+lick)p(MRH)	10	383.37	408.37	2.00	0.0650
LT	ψ(time)p(MRDP)	9	396.47	419.50	0.00	0.5561
	ψ(time+3areas)p(MRDP)	10	396.15	420.61	1.11	0.1456
	ψ(time+area)p(MRDP)	11	393.50	421.15	1.65	0.1140

Table 7. Continued

Species[a]	Model[b]	K	-2lnL	AIC_c	ΔAIC_c	w_i
RBD[c]	ψ(time)p(MDP)	6	162.81	177.81	0.00	0.3329
	ψ(area)p(MDP)	6	163.47	178.47	0.66	0.2394

[a] Species abbreviations: (WLP) white-lipped peccary, (CP) collared peccary, (LT) lowland tapir, and (RBD) red brocket deer.

[b] Parameter definitions: effects of (3areas) 3 management designations (reserve, buffer, and community), (area) 2 management designations (reserve-buffer and community), (time) travel time from the nearest city, (lick) distance to the nearest claylick, and (hole) presence of a waterhole on occupancy, and (M) camera or track method, (R) rain within 24 h of the track survey, (D) distance from a claylick to the transect, (P) camera placement at a claylick, and (H) camera placement at a waterhole on detection.

[c] Modeled using only dry season (May–August) detection data.

Table 8. Model averaged maximum likelihood estimates (MLE) and upper (↑95%) and lower (↓95%) 95% confidence intervals for parameters of top ranked occupancy models ($\Delta AIC_c \leq 2$) for each of 4 ungulate species in Tambopata, Peru.

	Parameter[b]													
	ψ		ψ (time)		ψ (area)		ψ (lick)		ψ (hole)		ψ (reserve)		ψ (buffer)	
Species[a]	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%	MLE	↑95% ↓95%
WLP	0.0392	0.1250 -0.0467	0.5550	0.6732 0.4368	0.0302	0.0892 -0.0288					0.0055	0.0281 -0.0170	0.0455	0.1534 -0.0623
CP	0.2346	0.5861 -0.1170	0.2505	0.3827 0.1183	0.3661	0.4199 0.3122	0.3009	0.4150 0.1869	0.0806	0.0806 0.0806				
LT	0.0476	0.1469 -0.0517	0.5633	0.6644 0.4623	0.0281	0.0843 -0.0280					0.0024	0.0123 -0.0075	0.0200	0.0673 -0.0273
RBD[c]	0.0851	0.2385 -0.0683	0.2718	0.4933 0.0502	0.2394	0.2394 0.2394								

[a] Species abbreviations: (WLP) white-lipped peccary, (CP) collared peccary, (LT) lowland tapir, and (RBD) red brocket deer.

[b] Parameter definitions: effects of (time) travel time from the nearest city, (area) 2 management designations, (lick) distance to the nearest claylick, (hole) presence of a waterhole, and (reserve and buffer) 3 management designations on occupancy.

[c] Modeled using only dry season (May–August) detection data.

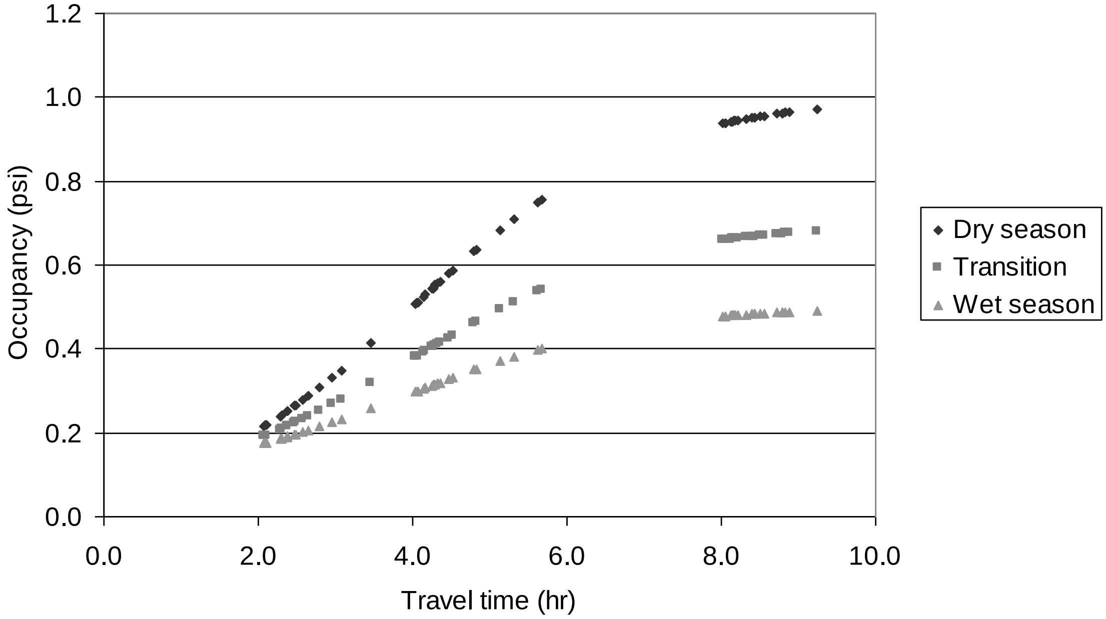

Figure 5. Occupancy estimates of white-lipped peccary as a function of travel time from each study site to Puerto Maldonado, Peru during the dry season (May–August 2008), transition (September –November 2008), and wet season (January–March 2009).

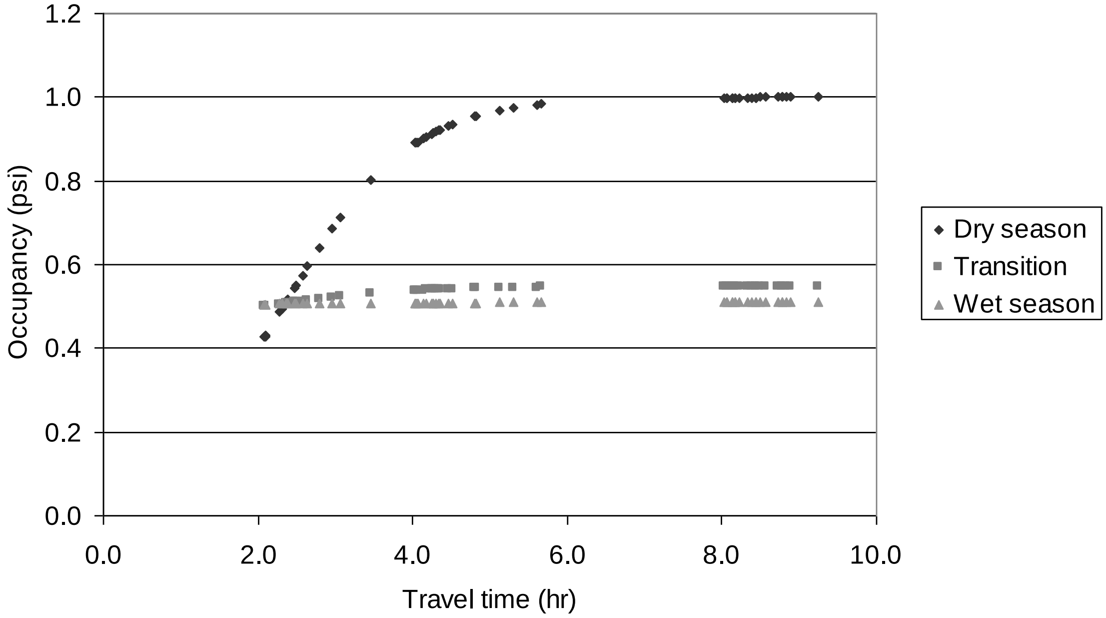

Figure 6. Occupancy estimates of collared peccary as a function of travel time from each study site to Puerto Maldonado, Peru during the dry season (May–August 2008), transition (September–November 2008), and wet season (January–March 2009).

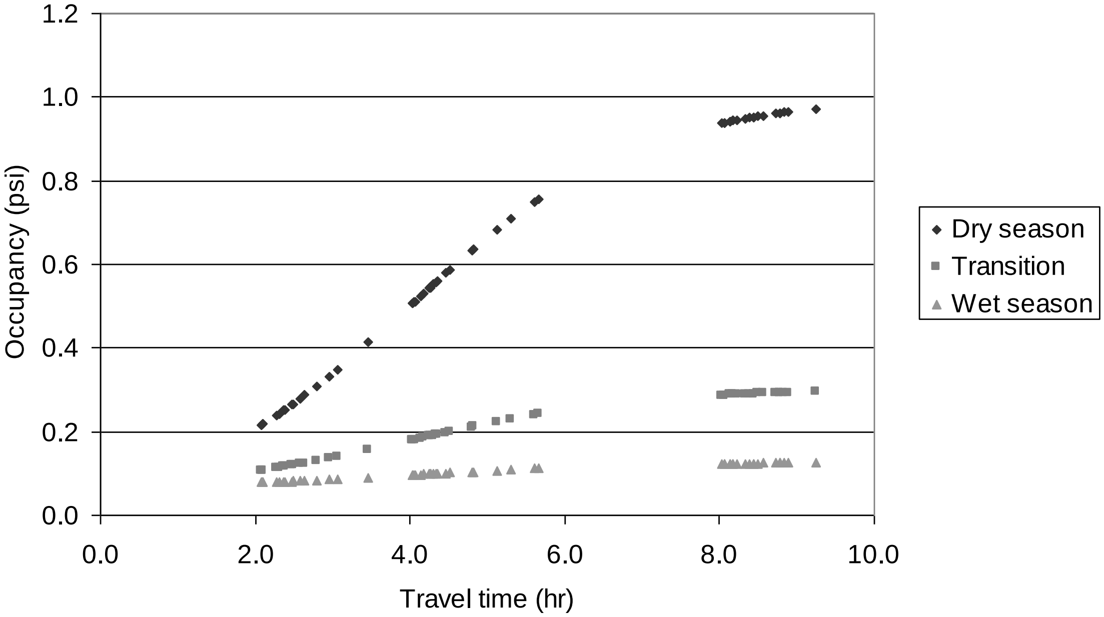

Figure 7. Occupancy estimates of lowland tapir as a function of travel time from each study site to Puerto Maldonado, Peru during the dry season (May–August 2008), transition (September–November 2008), and wet season (January–March 2009).

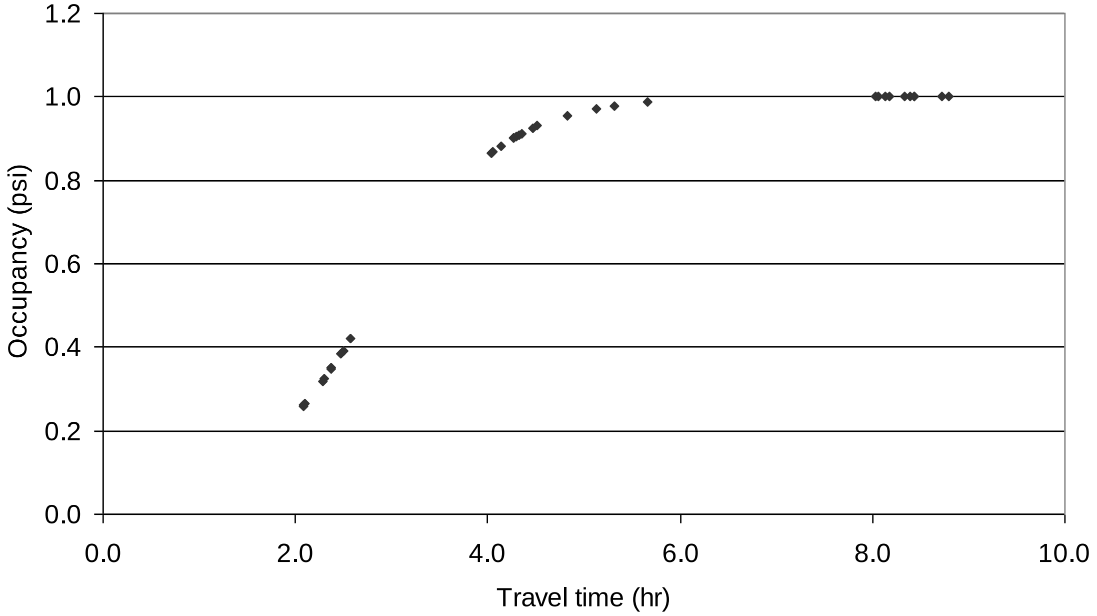

Figure 8. Occupancy estimates of red brocket deer as a function of travel time from each study site to Puerto Maldonado, Peru during the dry season (May–August 2008).

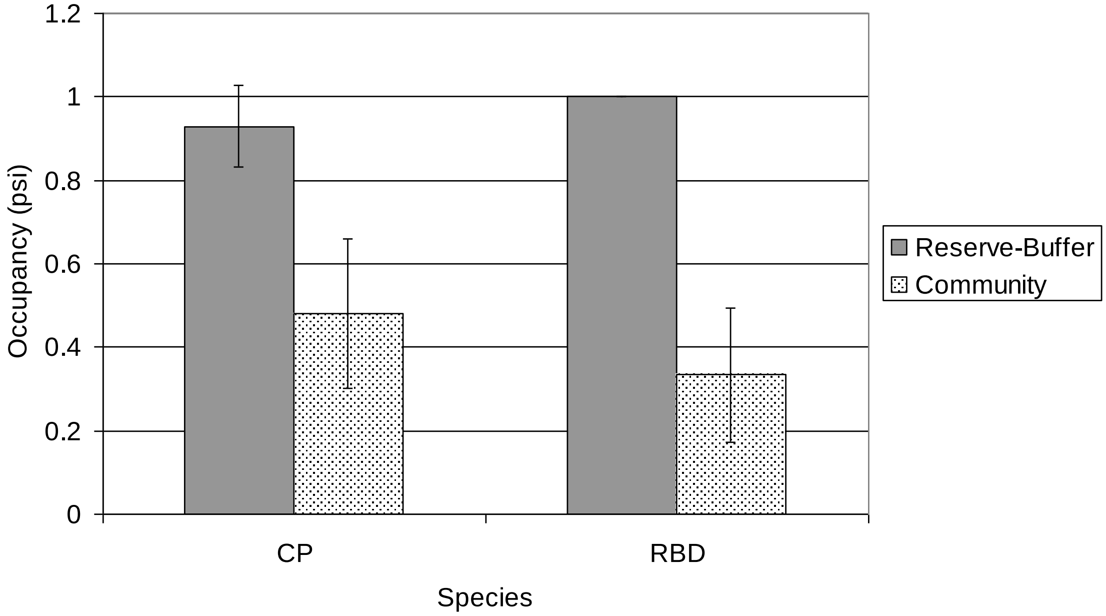

Figure 9. Occupancy and SE estimates of collared peccary (CP) and red brocket deer (RBD) in reserve-buffer and community areas in Tambopata, Peru during the dry season (May–August 2008).

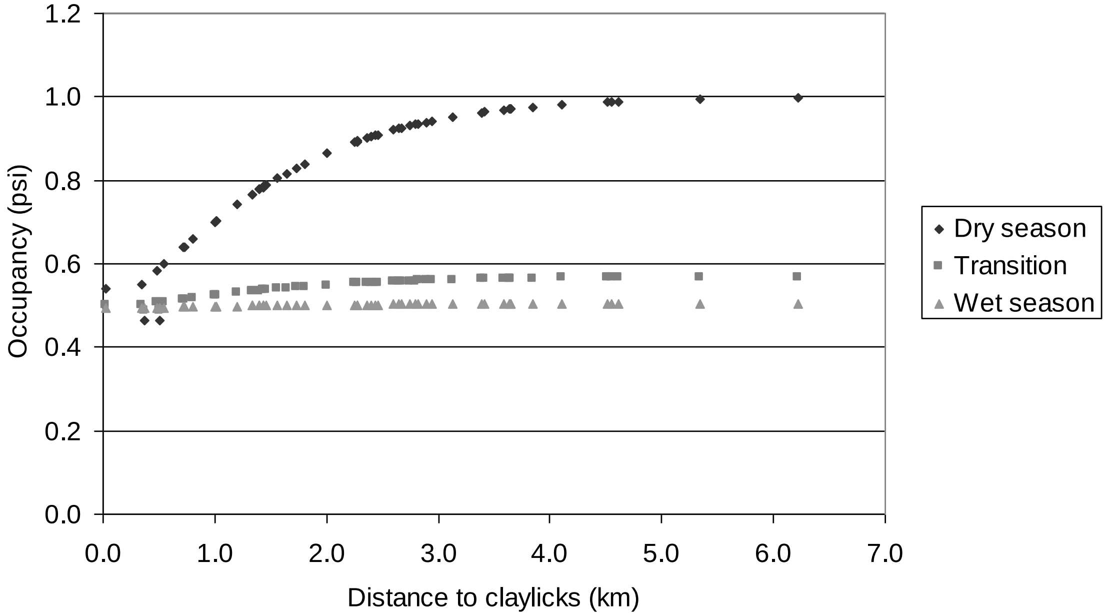

Figure 10. Collared peccary occupancy estimates as a function of distance to claylicks during the dry season (May–August 2008), transition (September–November 2008), and wet season (January–March 2009) in Tambopata, Peru.

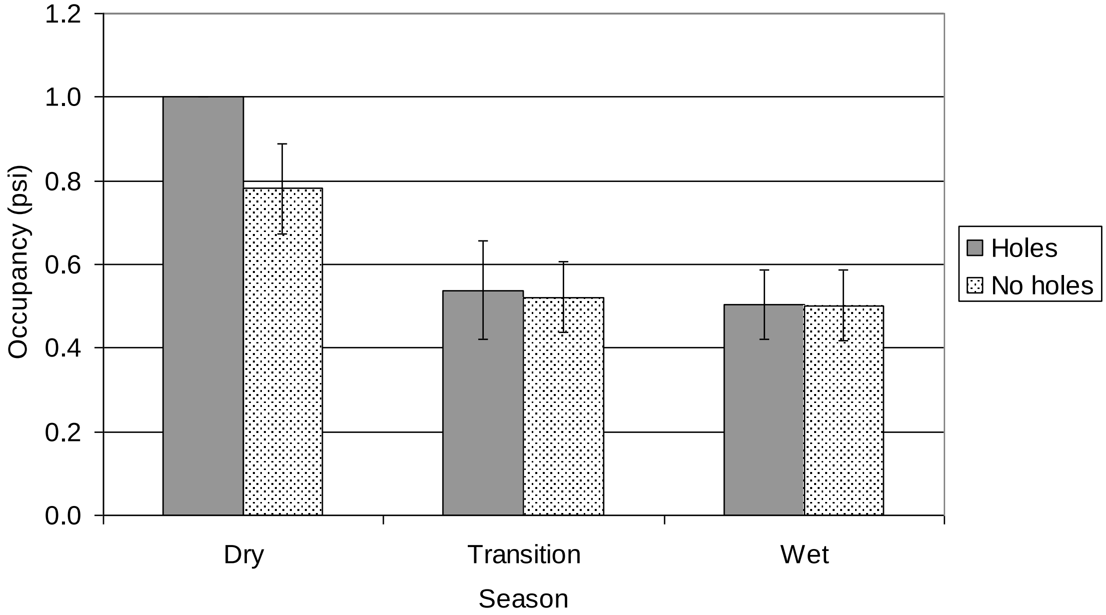

Figure 11. Collared peccary occupancy and SE estimates at sites with and without waterholes during the dry season (May–August 2008), transition (September–November 2008), and wet season (January–March 2009) in Tambopata, Peru.

DISCUSSION

Data from this study indicated that accessibility, measured as travel time, was the most important factor influencing occupancy of all 4 ungulate species in the protected areas of Tambopata, Peru. Similar patterns have been demonstrated by studies in Brazil and Cameroon that found higher ungulate densities in core protected areas compared to more accessible outer areas (Peres 2001, Fimbel et al. 2000). These results also confirm the findings of Bruner et al. (2001) which found that most of the 93 tropical protected areas they examined experienced smaller reductions in game populations than surrounding areas. These studies reiterate the importance of locating protected areas in remote and thereby passively protected sites (Peres and Terborgh 1995).

The results showing occupancy of collared peccary and red brocket deer approaching 1 sooner than white-lipped peccary corroborate the findings of Reyna-Hurtado and Tanner (2007). They reported that, in a Mexican biosphere reserve, collared peccary and red brocket deer were less sensitive to human activities and altered landscapes than white-lipped peccary. Whereas collared peccary and red brocket deer can actually thrive in fragmented habitats, white-lipped peccaries require large tracts of undisturbed forest (Fragoso 1999).

There is growing understanding that protected areas can only function with the cooperation of local people (Wells and Brandon 1993, Fitzgibbon et al. 2000). Top-down conservation plans that do not account for human needs will be viewed as contrary to local interests and destined to fail (Adams et al. 2004). Therefore, the cooperation of local communities, and their inclusion in planning and management of protected areas should greatly increase the success of any wildlife conservation program (Wells and Brandon 1993, Naughton-Treves et al. 2005).

A biosphere reserve is an attempt to incorporate social and economic development with biodiversity conservation (Wells and Brandon 1993, Naughton-Treves et al. 2005). Such areas should contain a core that is protected from all types of development and extractive activities surrounded by one or more buffers where higher impact activities are permitted (Wells and Brandon 1993). Therefore, it is to be expected that areas located on the outer perimeter of the biosphere reserve will experience greater effects of anthropogenic activity than the core area. In this study, these effects are reflected in the decreased occupancy of all 4 ungulate species in more accessible areas, especially the native community.

Results of modeling for all 4 species showed no significant differences between occupancy in the reserve and buffer zone, indicating that the distinction between the 2 has little relevance to ungulate distribution. However, the occupancy of collared peccary and red brocket deer in the combined reserve-buffer area was higher than in the native community. This may indicate that the reserve-buffer area received some benefit from its designation as protected, in addition to its lower accessibility.

Interestingly, no models showed evidence for higher ungulate occupancy with proximity to claylicks although all 4 species have been recorded visiting claylicks and actively consuming soil in this and other studies (Montenegro 2004). The positive relationship between distance to claylicks and collared peccary occupancy suggests that this species actually avoids claylicks. One plausible explanation for this result is avoidance behavior or habitat partitioning between these 2 congeners (Fragoso 1999). Although modeling showed little support for distance to claylicks as an important variable of white-lipped peccary occupancy, out of 48 total camera survey detections, 20 occurred at only 4 claylicks. Their frequent use of claylicks exemplifies the importance of this resource to white-lipped peccaries. It is possible that undiscovered claylicks existed within the study area, which could have resulted in unmodeled changes in occupancy. Collared peccary occupancy was also influenced by the presence of waterholes at survey sites, which demonstrates the importance of this resource.

The data showed no support for the influence of roads and associated deforestation on ungulate occupancy in this study, although there is considerable evidence for the negative impact of roads on tropical forests and wildlife (Chomitz and Gray 1996, Mäki et al. 2001, Laurance et al. 2006). The paving of the Inter-Oceanic Highway and the inevitable, subsequent immigration and development should be a primary conservation concern for the region and their impacts on wildlife should continue to be investigated. Travel time by river provides a realistic measurement of accessibility for these areas of Tambopata at the current time, which is why distance to roads was only measured in linear distance and not time. However, this could change as more roads are built in this region and become more important means of transportation (Delgado 2008).

There were a number of methodological considerations in this study that affected detection and my ability to model occupancy with more precision. I used 2 different methods, camera and track surveys, in this study and they showed clear differences in detection probabilities that highlight the trade-offs between the 2. Although track surveys use a cheap, primitive method to collect more detection data than cameras, establishing and maintaining transects in rainforest vegetation requires considerable effort. Camera surveys require relatively less effort, but require a large investment of equipment and batteries. In the rainforest, they are also susceptible to damage from moisture, termites, and flash floods. Overall, sample size was constrained by the considerable amount of time and effort required to establish a survey site and conduct repeat surveys.

Proximity of claylicks to a transect or placement of a camera at a claylick strongly influenced the detection of white-lipped peccaries, lowland tapir, and red brocket deer because these areas are important resources, resulting in predictable visitation by these species (Montenegro 2004). Placement of a camera at a water hole had a significant effect on collared peccary detection because they frequented these areas, and were difficult to detect elsewhere. Greater survey effort or novel methods would be necessary to estimate occupancy of grey brocket deer.

Lower occupancy estimates of these species in the transition and wet seasons is most likely an effect of unmodeled differences in detection. Higher occupancy estimates in the dry season indicate higher detection during this time, because seasonal migration of Neotropical ungulates has not been observed (Fragoso 1999, Noss et al. 2003, Keuroghlian et al. 2004). I attempted to account for this difference by including rain as a detection covariate, however this did not reflect the cumulative effect of several consecutive days of rain on track detection. Therefore, concentrating data collection in the dry season could be a more efficient method for monitoring ungulates in the Amazon.

CONCLUSION

Because most protected areas in the Amazon are only passively protected, their location has been a critical consideration in planning and managing such areas. It has been suggested that upper watersheds are optimal locations for protected areas in the Amazon because natural watershed boundaries represent the least accessible points on the landscape (Peres and Terborgh 1995). However, as development continues in this region, it will be more difficult to locate protected areas away from human impacts so more active protection measures will be necessary.

Clearly demarcated boundaries, public awareness of laws, and presence of guards have been found to increase effectiveness of protected areas in the tropics (Bruner et al. 2001). Monitoring of river or road access to protected areas should continue and be increased concomitantly with development in surrounding areas. If the biosphere reserve model is to be an effective tool for wildlife conservation in the future, design, location, and enforcement of protected areas will need to adapt to changing conditions. Increased public cooperation and involvement in decision making will improve chances of success of conservation efforts.

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APPENDIX

Figure A-1. Camera trap photograph of white-lipped peccaries at a claylick in Tambopata National Reserve, Peru.

Figure A-2. Camera trap photograph of collared peccaries in Tambopata, Peru.

Figure A-3. Camera trap photograph of a lowland tapir at a claylick in Tambopata National Reserve, Peru.

Figure A-4. Camera trap photograph of a red brocket deer in Tambopata, Peru.

Figure A-4. Camera trap photograph of a grey brocket deer in Tambopata National Reserve, Peru.

VITA

Name: Miguel Mario Licona

Address: Wildlife and Fisheries Sciences Department, Texas A&M University,
210 Nagle Hall, College Station, TX 77843-2258

Email Address: mlicona@tamu.edu

Education: B.A., Ecology, Dartmouth College, 2003
M.S., Wildlife and Fisheries Sciences, Texas A&M University, 2009

Experience: Expedition Biologist, Biosphere Expeditions-Peru, 2008
Wolf Biologist, U.S. Fish & Wildlife Service, 2007
Mammal Biologist, Wildlife Conservation Society-Bolivia, 2006
Research Associate, Teton Science School, 2004
Elk Biologist, Wyoming Game & Fish Department, 2004
Fisheries Biologist, Wyoming Game & Fish Department, 2004