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Using ungulate occurrence to evaluate community-based conservation within a biosphere reserve model

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Abstract

Conservation areas in tropical forests protect the most diverse and threatened ecosystems on the planet. In the Amazon, ungulates are important determinants of forest structure and plant diversity, as well as being a resource for rural communities. Using occupancy-based methods, we estimated the occurrence of white-lipped peccary *Tayassu pecari*, collared peccary *Pecari tajacu*, lowland tapir *Tapirus terrestris* and red brocket deer *Mazama americana* in and around protected areas reserve in Tambopata, Peru, to evaluate how different management designation, anthropogenic influences and habitat type influenced the occurrence of each species. We used a combination of track surveys ($n = 258$) and camera surveys ($n = 256$) to estimate ungulate presence at 55 sites in a national reserve, a native community and adjacent buffer areas from May 2008 to March 2009. We found that prediction of the occurrence of white-lipped peccary, lowland tapir and red brocket deer was best accomplished using travel time from the nearest city (a measure of an area's accessibility). The occurrence of ungulates differed little between buffer and reserves, but community lands managed by indigenous peoples showed reduced probabilities of ungulate occurrence. Our results indicate that passive protection afforded by inaccessibility might be an effective management strategy for this region; however, we doubt that this is tenable as a long-term solution.

Introduction

Moist tropical forests cover 6% of the Earth's land surface and contain more than half of all species and are the most rapidly depleted ecosystems on the planet (Wilson, 2003). The Amazon rain forest is home to numerous endemic and endangered species (Kress *et al*., 2004), which have been threatened directly and indirectly by anthropogenic activities including hunting, agriculture, deforestation, fossil fuel development, mining, road construction and climate change (Killeen, 2007). Conservation efforts in the region have attempted to balance the delicate relationship between human development and biodiversity.

Protected areas have been widely accepted as the most effective means of preserving biodiversity (MacKinnon *et al*., 1986; International Union for Conservation of Nature and Natural Resources, 1994). The biosphere reserve model has been applied for the selection and management of 553 protected areas in 170 countries worldwide (United Nations Education Scientific and Cultural Organization, 2010). It integrates a core area dedicated to conservation with intermediate buffer zones used for low-impact activities such as tourism and research and outer transition zones for high-impact activities such as agriculture and human settlement (Batisse, 1986; MacKinnon *et al*., 1986). The biosphere reserve model represents a compromise between beliefs that conservation and development occupy separate realms and that the two are inextricably linked (Wells & Brandon, 1993; Adams *et al*., 2004). Ideally, under the biosphere model, the loss of economic opportunities to local peoples in core areas would be offset by permitted activities in the buffer zone (Naughton-Treves, Buck Holland & Brandon, 2005). Nonetheless, strict interpretation and enforcement of the biosphere reserve concept has been difficult in the face of complex social, economic and biological forces (Wells & Brandon, 1993).

There has been a growing consensus that protected areas can only function with the cooperation of local people (Wells & Brandon, 1993; Fitzgibbon, Mogaka & Fanshawe, 2000) and that 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). This realization and the failures of exclusionary conservation have helped the concept of community-based conservation gain traction as a conservation management strategy (Berkes, 2004, 2007). In the Amazon, the concept of community-based conservation has helped to spawn the creation of officially designated reserves owned and managed by indigenous inhabitants. However, there is considerable debate on the effectiveness of self-managed indigenous lands for conserving wildlife (Schwatzman, Nepstad & Moreira, 2000; Berkes, 2007). The major conservation challenges to self-managed indigenous lands and other protected areas in the Amazon come from anthropogenic encroachment (Peres & Terborgh, 1995). Specifically, human accessibility to protected areas has been shown to increase hunting pressure on wildlife populations (Hill *et al*., 1997).

Ungulate species play a vital role in the Amazon ecosystem. Ungulates influence forest structure and plant diversity through seed dispersal, seed predation and herbivory (Redford, 1992) and are prey for large predators (Weckel, Giuliano & Silver, 2006). The ungulate assemblage in the Amazon includes the white-lipped peccary *Tayassu pecari*, collared peccary *Peccari tajacu*, lowland tapir *Tapirus terrestris*, red brocket deer *Mazama americana*) and grey brocket deer (*M. gouazoubira*). These five species provide a food source for rural communities (Robinson & Bodmer, 1999) and the sale of meat brings revenue for rural hunters (Bodmer & Puertas, 2000). Subsistence hunters exhibit a preference for large game because they are the most efficiently hunted prey items (Alvard, 1993). The loss of ungulate species results in gradual yet profound shifts in the nature of plant communities and a loss of biodiversity (Redford, 1992). When ungulates can no longer perform their ecological function, large seeded plant species experience reduced dispersal and increased conspecific competition (Muller-Landau, 2007; Stoner *et al*., 2007).

In Peru, efforts to protect the wildlife and other natural resource in Amazonian include national parks, reserves and indigenous community reserves covering *c*. 15% of the nation's total area (Peruvian Ministry of the Environment, 2010). Specifically, the Department of Madre de Dios in south-eastern Peru, completely within the Amazon basin, contains a mosaic of protected areas. This mosaic includes the Manu Biosphere Reserve and a group of protected areas in the Tambopata region that utilize the biosphere reserve model to conserve the regions wildlife resources.

In order to preserve ungulates and the overall biodiversity in the Amazon, it is important to evaluate the efficacy of current management strategies. Additionally, there is still a need to determine the factors that influence the occurrence of animals in this ecosystem. The goal of our study was to determine whether area designation, anthropogenic factors or habitat characteristics influenced the occurrence of ungulates in the Amazon rainforest of south-eastern Peru. Our objectives were to (1) determine whether community-based conservation within a biosphere reserve framework influenced the occurrence of lowland tapir, white-lipped peccary, collared peccary, red brocket deer and grey brocket deer; (2) determine how human access to the forest influenced ungulate occurrence; (3) identify habitat characteristics influencing ungulate occurrence; (4) make recommendations for the selection of protected areas and management of Neotropical ungulates.

Methods and materials

Study area

We conducted this study in the Department of Madre de Dios, Tambopata Province, Peru (Fig. 1). Our study 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 moist subtropical life zone boundary (Holdridge, 1967). The vegetation of the region has been characterized as primary tropical moist forest made up of terrace (terra firme) and floodplain forest (várzea; Griscom & Ashton, 2003). Dominant tree families in this region are Arecaceae, Moraceae, Euphorbiaceae, Myristaceae, Sapotaceae, Violaceae and Rubiaceae (Pitman *et al*., 2001). Predators of ungulates in the area included pumas *Felis concolor* and jaguars *Panthera onca*. The altitude of the study site was *c*. 250 m and annual rainfall was 3200 mm, with a weak dry season from April to September (Brightsmith, 2004).

Our study area fit the biosphere reserve model with a national park adjacent to a national reserve surrounded by a buffer zone. The core area consists of the 1 091 416 ha Bahuaja-Sonene National Park (hereafter, park) and the 274 690 ha Tambopata National Reserve (hereafter,

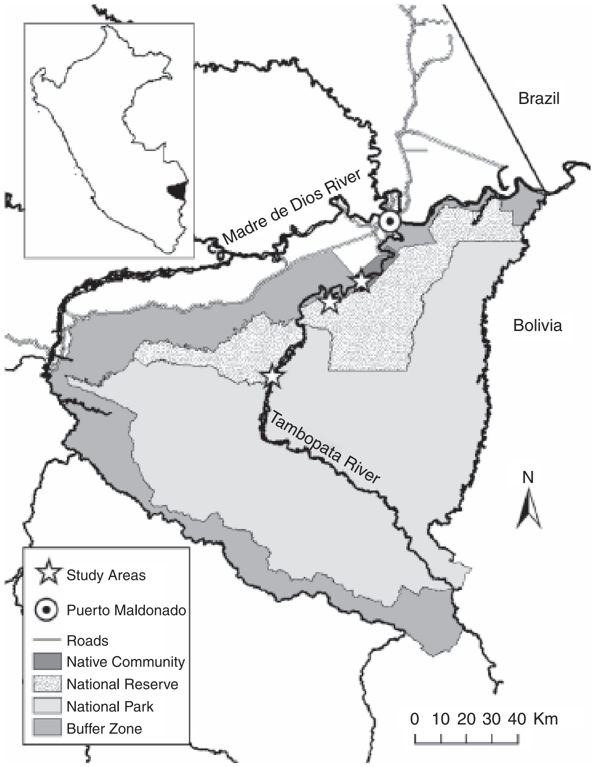

Figure 1 Map of three study areas and four management designations (native community, national reserve, national park and buffer zone) in Tambopata, Peru.

reserve). Both of these areas have been protected from most extractive activities since 1990 and were officially recognized in 2000. Subsistence hunting, Brazil nut collection by indigenous people and ecotourism have been allowed in the reserve.

The park and reserve are surrounded by an *c.* 262 000 ha buffer zone that has allowed low levels of agriculture, logging, mining and hunting (INRENA, 2003). Adjacent to the buffer area was the Native Community of Infierno (hereafter, community) owned and managed by the indigenous Ese'Eja and Mestizo community members that contains 10 000 ha, of which 4000 ha has been set aside exclusively for ecotourism (Brightsmith & Aramburú Muñoz-Najar, 2004). There was 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 was Puerto Maldonado, the department capital (Fig. 1).

Site selection

We worked in three study areas based around three access points into the forest (Fig. 1). These areas were selected because they provided entry to different management designation and provide a gradient of accessibility to the rainforest for humans. 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. Our third study area was located near the border of the park and provided access to the reserve. At each study area, we used areas that we could reach on foot in <6 h from three access points as the total study area. Within the study areas, we systematically created 1 km^2 sampling units completely within 1 of the 2 major forest types (terra firme or várzea). Because of the fact that our sampling was constrained by the areas we could access on foot, we had an unbalanced study design with 55 sampling units: 32 in the reserve, 10 in the community and 13 in the adjacent buffer zone.

Data collection

We conducted camera and track surveys of the sampling units during three seasons to account for the seasonal variation in ungulate occurrence. We conducted surveys during the dry season (May–August 2008), the transition period from the wet to dry seasons (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 considered a secondary sampling occasion. We created 1 km transects bisecting each sample unit by making paths through the forest, cutting only enough vegetation to allow us to see the ground while minimizing the disturbance or the chance of attracting animals to the transect. We walked (1–2 km h^{-1}) each transect scanning for tracks two to three times during each season. We recorded each of the five ungulate species as either present or absent. We walked on or otherwise erased tracks after detection to avoid re-detecting them on a subsequent survey. Surveys were conducted ≥ 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.

We used Cuddeback C3000 infrared-triggered digital cameras (NonTypical, Park Falls, WI, USA) to conduct 3 consecutive four-night camera surveys on each transect during each season. We placed cameras on or adjacent to the transects in areas with the greatest probability of capturing an animal (game trails, claylicks or water holes). We placed cameras *c.* 3 m from the spot where an animal was most likely to pass, with the aperture of the camera *c.* 75 cm from the ground. We anchored the camera to a tree with a screw and a steel cable. To protect the cameras from moisture, we sealed them with silicone, placed 15 g of silica gel desiccant inside and covered them with a canopy of leaves. We recorded a species as present if it was photographed ≥ 1 time during the survey and absent if it was not photographed.

Variables

We used two different classification schemes to evaluate the influence of management designations on the probability of ungulate occurrence. First, we classified each designation separately (reserve, buffer, community) to determine whether each designation had different probabilities of ungulate occurrence. Alternatively, we classified the area into two different management designations (reserve-buffer and community) to determine whether the probabilities of ungulate occurrence only differed between protected area and the community designation.

To quantify the accessibility of each sampling unit, we measured boat and walking travel time from Puerto Maldonado to each survey site. To calculate the total travel time, we 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 h^{-1}. These combined measurements provided an overall travel time and an index of the accessibility of each study site, which we used as a proxy for the relative human activity, and human population density of an area, as both decreased with greater distance from the city. Additionally, there were no settlements located down river from (south) or in between our study areas (Fig. 1)

We also measured habitat variables that could influence ungulate occurrence. We classified the forest types as either terra firme or várzea (described earlier) because of forest type's potential to influence ungulate distributions (McShea *et al.*, 2001). We quantify the influence of claylicks on ungulate's probability of occurrence by geo-referencing all known claylicks around the study areas (Donald Brightsmith, Texas A&M University, unpubl. data), placing them into a Geographic Information System and using ArcMap 9.2 to measure linear distance from the center of the sampling unit to the closest claylicks. From visual observations, we also recorded whether there was a waterhole present within the sampling unit. Both claylicks and waterholes are important resources for ungulates in the Amazon (McShea *et al.*, 2001; Montenegro, 2004). Claylick are natural areas with high clay concentrations in the soil that, when ingested, can reduce the effects of plant toxins, acidosis and intestinal infections in wildlife (Klaus & Schmid, 1998). Water holes are especially important for ungulates during the water-limited dry season (McShea *et al.*, 2001).

Occupancy and detection estimation

We used the occupancy modeling methodology (MacKenzie *et al.*, 2006) to evaluate the factors influencing the occurrence of ungulates. We estimated species-specific occupancy (ψ) while accounting for the detection (p) rate for two survey methods (track and camera). We treated each four-night camera session and, each time, a transect was sampled as a secondary sampling occasion and used multi-season models with the initial parameterization (which holds colonization and extinction constant) in all analyses, except for red brocket deer (MacKenzie *et al.*, 2006). Because of limited detections in the transition and wet seasons, we only modeled red brocket deer during the dry season using a single season model (MacKenzie *et al.*, 2006). We evaluated candidate models and estimated parameters using the program PRESENCE 2.2 (Hines, 2006). Before evaluating occupancy for each species, we 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 (Norman *et al.*, 2004) (Table 1).

We evaluated models with five detection parameters. These parameters included four survey-specific variables (can change across secondary sampling occasions), method (M; camera or track survey), whether a camera was placed at a water hole (H) or a claylick (P) and the categorical variable rain or no rain within 24 h (R). We also evaluated one site-specific variable (remaining constant over sampling occasions) distance to the nearest clay lick (D) because claylicks are often in open areas with heavy animal traffic and might influence the detection rates.

We selected the model with the lowest Akaike's Information Criterion adjusted for a small sample size (AIC_c) as the best representation of the data (Burnham & Anderson, 2002). We examined the relevance of each parameter in the top-ranked detection models by examining 95% confidence intervals (CIs) to see whether they contained 0 (Burnham & Anderson, 2002). We used the best model with relevant predictors in all subsequent models to evaluate species occurrence.

We evaluated a suite of 13 *a priori* models using the previously described detection parameterization to understand ungulate occurrence (Table 2). We evaluated models with three management designations (reserve, buffer, community; 3areas) and two management designations (reserve-buffer and community; area) travel time from Puerto Maldonado (time), distance to nearest claylick (lick), presence of a water hole (hole) and forest type (veg).

To select the best approximating models in each model each set of candidate models, we ranked models using their AIC_c value, their relative difference from the best model (ΔAIC_c) and Akaike weights (w_i) (Burnham & Anderson,

Table 1 The number of parameters (K), AIC_c and ΔAIC_c values for *a priori* detection (p) models of four ungulate species in Tambopata, Peru

	Species[a]											
	WLP			CP			LT			RBD[b, c]		
Model	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
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 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, (H) camera placement at a waterhole and p (.) null model.

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

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

WLP, white-lipped peccary; CP, collared peccary; LT, lowland tapir; RBD, red brocket deer.

Table 2 Number of parameters (*K*), AIC$_c$ and ΔAIC$_c$ values for *a priori* occupancy (ψ) models of four ungulate species in Tambopata, Peru

	Species											
	WLP			CP			LT			RBD[b]		
Model[a]	*K*	AIC$_c$	ΔAIC$_c$	*K*	AIC$_c$	ΔAIC$_c$	*K*	AIC$_c$	ΔAIC$_c$	*K*	AIC$_c$	ΔAIC$_c$
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
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

[a] Parameter definitions: (3areas) three management designations (reserve, buffer and community), (area) two 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] Modeled using only dry season (May–August) detection data.

WLP, white-lipped peccary; CP, collared peccary; LT, lowland tapir; RBD, red brocket deer.

2002). We model averaged maximum likelihood estimates of occupancy (Burnham & Anderson, 2002) and graphically displayed the relationship between ψ and the relevant parameters for each species (Donovan & Hines, 2007).

Results

We conducted 258, 1 km transect track surveys and 256, four-night camera surveys during this study. We detected white-lipped peccary, collared peccary, lowland tapir and red brocket deer on 42, 28, 25 and 20% track surveys and 19, 7, 13 and 11% camera surveys, respectively. Grey brocket deer were only detected once on a track survey and twice during a camera survey and were excluded from further analysis.

We selected a different parameterization for the detection of each of the four species modeled based on AIC$_c$ values (Table 1). Each method (M) had a unique detection probability for all four species. Rain within 24 h of a track survey (R) decreased the detection for all species except red brocket deer, which was not affected by rain as it was modeled only during the dry season (Table 1). Distance from the transect to the nearest known claylick (D) and camera placement at a claylick (P) had an additive effect on the detection of white-lipped peccary, lowland tapir and red brocket deer and camera placement at a waterhole (H) affected the detection of collared peccary (Tables 1 and 3).

Models with two management designations (reserve-buffer and community) were ranked higher than models with three management designations (reserve, buffer and community) for collared peccary and red brocket deer (Table 2). The best model for collared peccary included only management designation as a covariate and the probability of occurrence was higher in the reserve-buffer than in the community during the dry season for both collared peccary [$\psi_{\text{reserve-buffer}} = 0.929$ (SE $= 0.098$), $\psi_{\text{community}} = 0.480$ (SE $= 0.178$)] and red brocket deer [$\psi_{\text{reserve-buffer}} = 1.00$ (SE $= 0$), $\psi_{\text{community}} = 0.3340$ (SE $= 0.161$)] (Table 4).

The best-fitting models for white-lipped peccary ($w_i > 0.773$), lowland tapir ($w_i > 0.8157$) and red brocket deer ($w_i > 0.3329$) occurrence included only travel time as a covariate (Table 2). Travel time was not a covariate in the best model for collared peccary; however, it appeared as a covariate in 4 of 8 top-ranked models ($\Delta\text{AIC}_c \leq 2$, $w_i > 0.3557$) for this species (Table 2). For all four species, model-averaged estimates of travel time were positive and 95% CIs did not include 0, indicating its relevance as a predictor of species occurrence (Table 4). Examining occupancy rates as a function of travel time for all species showed increased species presence as the travel time increased from 2 to 6–8 h (Fig. 2).

Few of the best competing models included habitat characteristic as parameters. Nonetheless, competing models for the collared peccary included (lick) distance to the nearest claylick (Table 2). There were positive relationships between distance to the nearest claylick (MLE = 0.3009, 95% CI = 0.1869, 0.4150, Table 4) and probability of collared peccary occurrence.

Discussion

There is no clear consensus on the most effective way to preserve wildlife resources in the Amazon rain forest (Schwatzman *et al.*, 2000). The concept of community-based conservation is attractive because it includes indigenous

Table 3 Maximum likelihood estimates (MLE) and upper (↑ 95%) and lower (↓ 95%) 95% confidence intervals for parameters of the best detection model for each of four ungulate species in Tambopata, Peru

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

[a] 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.

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

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

WLP, white-lipped peccary; CP, collared peccary; LT, lowland tapir; RBD, red brocket deer.

Table 4 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 four ungulate species in Tambopata, Peru

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

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

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

WLP, white-lipped peccary; CP, collared peccary; LT, lowland tapir; RBD, red brocket deer.

peoples and local ecological knowledge in the management of the surrounding resources (Berkes, 2004). Nonetheless, we found reduced probabilities of ungulates occurring within the community owned reserve, providing little evidence that community-based conservation was the most effective means for preserving wildlife resources. However, we cannot rule out the possibility that the reduced occupancy rates found in the community reserve were in part a function of its location close to a population center. We found that accessibility, measured as travel time, was the most important factor influencing the occupancy of three ungulate species (and an important factor influencing the occupancy of a fourth ungulate species) in the protected areas of Tambopata, Peru, regardless of the management designation of an area.

The biosphere reserve model integrates humans into the ecosystem and attempts to incorporate social and economic development with biodiversity conservation (Wells & Brandon, 1993; Naughton-Treves *et al*., 2005). We found mixed support for the biosphere reserve model, regulating varying degrees of access and extraction. For all four species, our results showed no significant differences between the rates of occurrence in the reserve and buffer zone, indicating that the distinction between the two had little relevance to ungulate occurrence. Nonetheless, our study did suggest that decreased accessibility to an area increased the probability of ungulates occurring, and this does support the basic premise that limited accessibility to the core area of a biosphere reserve can be an effective management design. Concordant with our work, Peres & Lake (1995) found that areas ≥6 km

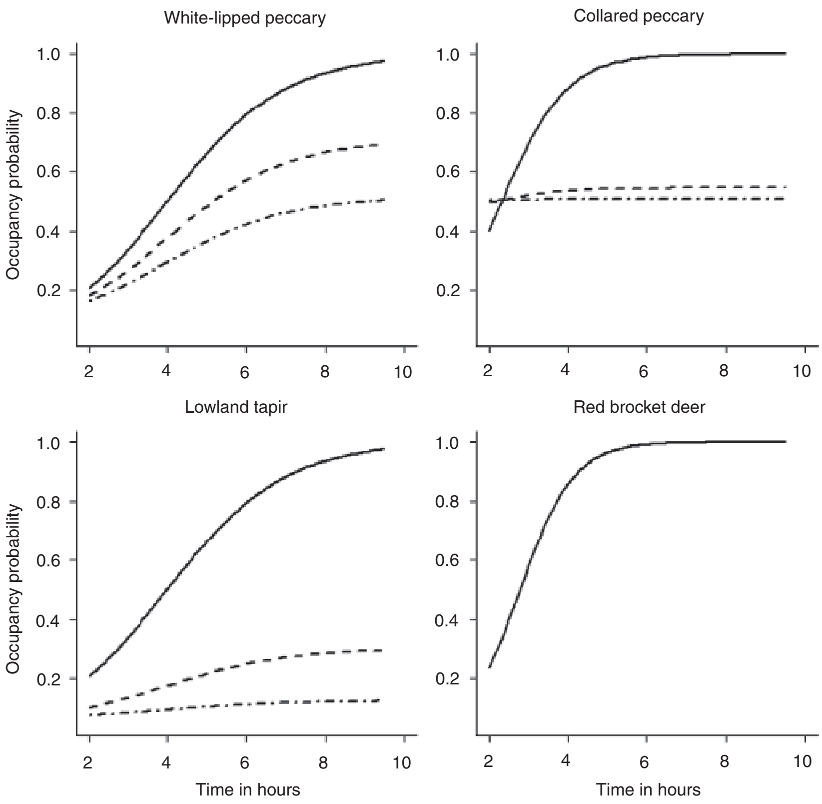

Figure 2 Occupancy estimates of white-lipped peccary *Tayassu pecari*, collared peccary *Peccari tajacu*, lowland tapir *Tapirus terrestris* and red brocket deer *Mazama americana* as a function of travel time from each study site to Puerto Maldonado, Peru, during the dry season (May–August 2008; solid lines), transition (September–November 2008, dashed lines) and wet season (January–March 2009, dashed and dotted line). Red brocket deer occupancy could only be estimated for the dry season.

from a river or road were passively protected from extractive activities by the practical limits of distance. Similar patterns have been demonstrated with the biosphere reserve model in Brazil and Cameroon, where ungulates have been found in higher densities in core protected areas compared with more accessible outer areas (Fimbel, Curran & Usongo, 2000; Peres, 2001). Our results also corroborate the findings of Bruner *et al.* (2001), who found that most of the 93 tropical protected areas they examined experienced smaller reductions in game populations than the surrounding areas. Together, our findings reiterate the importance of locating protected areas in remote and thereby passively protected sites (Peres & Terborgh, 1995).

Currently, travel time by river provides a realistic measurement of accessibility for these areas of Tambopata; however, this could change as more roads are built and become more important means of transportation in our study region (Delgado, 2008). The paving of the Inter-Oceanic Highway (abutting our study area to the north) and the subsequent immigration and development it will bring should be a primary conservation concern for the region, and its impacts on wildlife should be investigated.

Interestingly, our study only provided limited information on how the basic habitat features of the Amazon (claylicks, forest type and waterholes) influence the occurrence of ungulates in the forest. Recent research has suggested that the white-lipped peccary select for floodplain forest habitats (Tobler, Carrillo-Percastegui & Powell, 2009). We have little doubt that some if not all the habitat features evaluated in this study influence the occurrence of ungulates in the rain forest on some scale, but these features were likely irrelevant, given the influence of human accessibility to the area. Possibly, fine-scale measures of vegetative structure or microhabitat conditions not included in this study would have better elucidated the influences of habitat on ungulate occurrence in the Amazon. It is also important to note that occupancy modeling does not account for different densities of animals within sampling units. Thus, it is possible that ungulate abundances varied between occupied sampling unit and that our estimates were not reflective of population responses to the environment variables measured. However, the relatively low densities at which these ungulate occur make this an unlikely scenario and this does not limit our conclusions of the factor that influences the occurrence of ungulates.

We did find a positive relationship between distance to claylicks and collared peccary presence, suggesting that collared peccaries may avoid claylicks frequented by white-lipped peccaries. One plausible explanation for our findings is avoidance behavior or habitat partitioning between these two congeners (Fragoso, 1999). Although our results showed little support for distance to claylicks as an important variable of white-lipped peccary occurrence, out of 48 total camera survey detections, 20 occurred at only four claylicks.

Because of the fact that seasonal migration of Neotropical ungulates has not been observed, lower occupancy estimates of the four ungulate species examined during the transition and wet seasons were most likely an effect of unmodeled heterogeneity in detection (Fragoso, 1999; Noss *et al*., 2003; Keuroghlian, Eaton & Longland, 2004). We 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 ungulate occurrence in the Amazon.

Management implications

Our study suggests that community-based conservation was not the most effective strategy for the management of ungulates (Berkes, 2007). Still, it is important to note that all ungulate species in this study were detected in the community reserve and the clear economic and social benefits to this model may make community-based conservation more tenable in the long term.

Our study does show the benefits of passively protecting wildlife in the Amazon rain forest. For this simple concept to succeed, with or without a biosphere reserve framework, it will be critical to consider the location of protected 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 & Terborgh, 1995). However, remote placement is a luxury that few conservation areas have and as development in this region continues, it will be more difficult to locate protected areas away from human impacts. Given this reality, the buffering concept of the biosphere reserve model might be practical. Additionally, as access into the Amazon increases so will the need for stakeholders to be more active in the management and protection of wildlife resources. Clearly agreed upon conservation goals as well as demarcated boundaries, public awareness of laws and the presence of guards may become necessary for the conservation of wildlife (Bruner *et al*., 2001).

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