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An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals

M. W. Tobler[1], S. E. Carrillo-Percastegui[2], R. Leite Pitman[3], R. Mares[2] & G. Powell[2]

1 Botanical Research Institute of Texas, Andes to Amazon Biodiversity Program, Fort Worth, TX, USA/Texas A&M University, Department of Wildlife and Fisheries Sciences, College Station TX, USA
2 World Wildlife Fund, Washington, DC, USA
3 Duke University Center for Tropical Conservation/Instituto Procarnivoros/Oxford University Wildlife and Research Conservation Unit, Durham, NC, USA

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Correspondence
Mathias W. Tobler Botanical Research Institute of Texas, 509 Pecan Street, Fort Worth, TX 76102-4060, USA.
Email: matobler@brit.org

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Abstract

Mammal inventories in tropical forests are often difficult to carry out, and many elusive species are missed or only reported from interviews with local people. Camera traps offer a new tool for conducting inventories of large- and medium-sized terrestrial mammals. We evaluated the efficiency of camera traps based on data from two surveys carried out at a single site during 2 consecutive years. The survey efforts were 1440 and 2340 camera days, and 75 and 86% of the 28 large- and medium-sized terrestrial mammal species known to occur at the site were recorded. Capture frequencies for different species were highly correlated between the surveys, and the capture probability for animals that passed in front of the cameras decreased with decreasing size of the species. Camera spacing and total survey area had little influence on the number of species recorded, with survey effort being the main factor determining the number of recorded species. Using a model we demonstrated the exponential increase in survey effort required to record the most elusive species. We evaluated the performance of different species richness estimators on this dataset and found the Jackknife estimators generally to perform best. We give recommendations on how to increase efficiency of camera trap surveys exclusively targeted at species inventories.

Introduction

Mammal inventories serve a multitude of purposes: they show the diversity at a specific site, allow for comparison among sites, help refine distribution maps for individual species and can be used to evaluate the impact of human activities on mammal communities. A good knowledge of the presence and distribution of species is crucial for planning and evaluating conservation strategies for a region. However, despite years of research throughout the Amazon, there are few complete mammal inventories and our knowledge on the distributions of rare and elusive species is still poor (Voss & Emmons, 1996). The methods commonly used for mammal inventories are line transects, direct observations, identification of tracks and feces, trapping and interviews with local people (Voss & Emmons, 1996; Voss, Lunde & Simmons, 2001; Trolle, 2003*a*; Mendes Pontes, 2004; Haugaasen & Peres, 2005). While line transects can be used to survey the density of relatively abundant mammal species, they often fail to record rare and elusive species such as small carnivores, anteaters and armadillos (Voss & Emmons, 1996).

The use of camera traps for studying terrestrial mammals has become increasingly popular in recent years as camera technology has improved and equipment costs have decreased. Applications range from collecting species inventories (Maffei, Cuéllar & Noss, 2002; Silveira, Jacomo & Diniz, 2003; Trolle, 2003*b*; Srbek-Araujo & Garcia, 2005; Azlan & Lading, 2006) to studying activity patterns (van Schaik & Griffiths, 1996; Gómez *et al.*, 2005; Azlan & Sharma, 2006) and estimating animal density (Mace *et al.*, 1994; Karanth & Nichols, 1998; Sweitzer *et al.*, 2000; Trolle & Kéry, 2003; Silver *et al.*, 2004). Silveira *et al.* (2003) concluded that camera trap surveys were the most appropriate and accurate method for mammal inventories in the open savannas of Emas National Park in Brazil when compared with line transects and track counts. In a study on forest antelopes in the Udzungwa Mountains of Tanzania, camera traps recorded species rarely encountered in census walks (Rovero, Jones & Sanderson, 2005). Records from camera traps in Tanzania significantly extended the known range for the endangered Jackson's mongoose *Bdeogale jacksoni* (De Luca & Rovero, 2006). Photographs from camera traps provide reliable records of a species presence, and they can be sent out for verification by experts (see Meijaard, Kitchener & Smeenk, 2006).

When conducting any inventory, it is important to evaluate its completeness to estimate how many more species might be detected by further sampling effort (Magurran, 1988). An estimate of the completeness of an inventory is especially important when comparing species diversity among sites or when looking at changes in species composition over time. Species accumulation curves and diversity estimators are commonly used to address this issue (Soberon & Llorente, 1993; Colwell & Coddington, 1994). Species accumulation curves plot the cumulative number of species detected against the sampling effort per unit time, which in the case of camera traps can be survey days or camera days (the number of survey days multiplied by the number of cameras used). The curve reaches an asymptote when all species from the focal taxa have been recorded. Various methods have been developed to estimate the true number of species in an incomplete survey and to assess the completeness of the inventory (Soberon & Llorente, 1993; Colwell & Coddington, 1994; Colwell, Mao & Chang, 2004). These methods can be divided into two broad classes: species richness estimators based on extrapolation of species accumulation curves and non-parametric estimators related to capture–recapture models (Colwell & Coddington, 1994). The latter usually perform better in comparative studies (Walther & Moore, 2005). In this study we report the results of two camera trap-based inventories, evaluate the survey effort needed to record a certain percentage of the total species assemblage and test the performance of different non-parametric estimators to evaluate completeness of camera trap surveys.

Study area

This study was carried out in mostly primary lowland Amazonian moist forest in southeastern Peru. About two-thirds of the study site were within the Los Amigos Conservation Concession (12°30′–12°36′S and 70°02′–70°09′W, elevation 250–320 m), a 1400 km^2 privately managed protected area, with the remainder falling within two active logging concessions. The mean annual rainfall is between 2500 and 3500 mm with a marked dry season from June to September and a rainy season during the months of November through February. The mean annual temperature is 24 °C with a range from 10 to 38 °C.

Three major vegetation types can be distinguished in the study area: terra firme forests, floodplain forest and palm swamps dominated by the palm *Mauritia flexuosa*. Cameras were placed in terra firme and floodplain forests only, because the extent of palm swamps is very limited within the study area. The floodplain forest is occasionally inundated during the rainy season from December to March, but there was no inundation during the time of the surveys reported here.

Materials and methods

Camera trap surveys

Two 60-day camera trap surveys were carried out from 14 September to 13 November 2005 and from 16 August to 15 October 2006, at the end of the dry season and the beginning of the rainy season. The surveys were designed to meet the requirements for estimating jaguar *Panthera onca* density (Silver, 2004). In the 2005 survey, 24 camera stations were set out in a 2 km grid along the study site's trail system (Fig. 1) covering an area of *c.* 50 km^2. For the 2006 survey, we used the same camera locations as in 2005, but added 16 more camera stations at a 1-km interval in a central sub-area. In 2006 we excluded one camera station from the analysis because the cameras were malfunctioning, leaving a total of 39 stations.

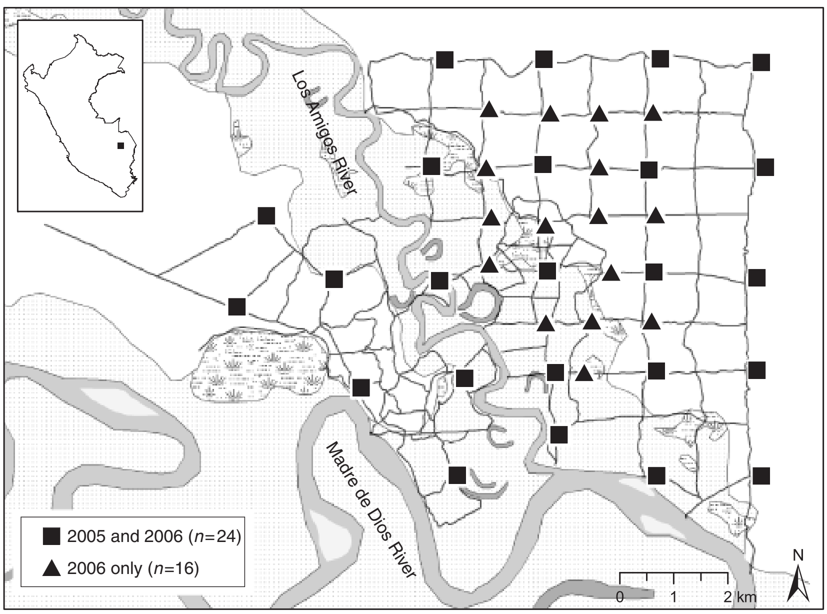

Figure 1 Study area and location of camera stations along the trail system. Dotted area indicates floodplain forest while the white area is terra firme forest.

Each camera station included paired cameras facing one another on respective sides of a trail, allowing the cameras to photograph both sides of an animal. Cameras were set at an average height of 50 cm above the ground. We used Deercam (NonTypical Inc., Park Falls, WI, USA) passive infrared cameras, which were sealed with extra silicon and equipped with an aluminum roof for better protection from rain. Small silica bags were placed inside the camera housing to further reduce damage from moisture. The delay between pictures was set to 5 min and the sensitivity of the infrared sensor was set to high. Cameras were operating 24 h a day and were checked every 5 days to replace film and batteries if necessary.

Data analysis

All images were scanned and entered into Camera Base, an Access database designed for managing camera trap survey data (Tobler, 2007). For every photograph, the station, date, time and the species were recorded.

To evaluate the effectiveness of our camera trap surveys for inventorying mammal species, a subset of all photographs including only large- and medium-sized (weight >1 kg) terrestrial mammals were used, therefore excluding arboreal species, small rodent species, and mostly aquatic or riverine species (*Pteronura brasiliensis, Lontra longicaudis* and *Hydrochoerus hydrochaeris*).

We calculated the capture frequency of a given species as the number of photos/1000 camera days, and used a Spearman rank correlation for comparisons between the two surveys. The data were filtered to exclude images of the same species at the same station within a period of 1 h in order to make sure that events were independent, because some species (e.g. white-lipped peccaries, *Tayassu pecari*) would spend a long period of time in front of a camera.

To evaluate the effect of species size on their capture probability, we calculated the percentage of times both cameras took a picture versus only one of the two cameras at a station and compared that to body weight based on data taken from Emmons & Feer (1997). Data from both surveys were pooled for the analysis, and we only included the 14 species with samples of 15 photos or more, after excluding cases where an animal had walked behind one of the cameras at the station. We used a Spearman rank correlation to evaluate the relationship between body weight and percentage of events with pictures from both cameras.

To look at the effect of camera spacing and grid size on the inventory results, we subsampled the data from 2006 into two groups. The first group contained 22 stations spaced out in a regular grid at 1-km interval, covering an area of *c.* 15 km^2. The second grid contained 23 stations spaced out at 2 km covering the full study area. Both grids had the same number of cameras in each habitat type.

We compared the performance of eight species diversity estimators: the non-parametric abundance-based estimators ACE and Chao 1, and the non-parametric incidence-based estimators ICE, Chao 2, Jackknife 1, Jackknife 2, Jackknife 3 and Jackknife 4 (Chao, 2004). Because non-parametric species richness estimators are directly related to closed population capture–recapture models, they underlie some of the same assumptions. They assume that the community composition does not change over the time of the study (closure), and the Jackknife estimators assume that there is no temporal variation in capture probability for all species (Burnham & Overton, 1979; Chao, 2004). With survey length of 60 days these assumptions should be met. We used EstimateS (Colwell, 2006) to calculate rarefaction curves and most of the species estimators. The Jack 3 and Jack 4 estimators were implemented with visual basic for applications in Excel. For all randomizations we used 1000 runs. To calculate different incidence-based species richness estimators, we treated each survey day as a sample resulting in 60 samples for each survey. To compare the two surveys, we plotted the results against the number of camera days. To evaluate the completeness of our surveys and the accuracy of the total number of species estimated by different estimators, we compared the number of species against a list of known species from the study area (Leite Pitman, unpubl. data).

To investigate the relationship between capture frequency and the number of camera days required to register a species, we used a simple binominal model

$$P(X = k) = \frac{n!}{k!(n-k)!}p^k(1-p)^{n-k}$$

where k is the number of successes, n the number of trials and P the probability of success.

In our case, p is the average number of pictures per camera day for a given species and n is the total number of camera days. By using a 5% probability of taking no photograph at all, we determined the number of camera days needed to collect at least one photograph for a species with a specific capture frequency, within a 95% confidence limit. For this case, $k = 0$ and $P\,(X = 0) = 0.05$ reducing the equation to:

$$0.05 = (1-p)^n$$

Solving the equation for n gives the following relationship:

$$n = \frac{\ln(0.05)^*}{\ln(1-p)}$$

Results

Capture frequencies and species list

During the 2005 survey, we obtained 508 photographs of 21 species of mammals, during a total of 1440 camera days (Table 1). In 2006 we obtained 814 photographs of 27 species of mammals, during a total of 2340 camera days. We excluded three species of mammals from our analysis of the 2006 survey because they were arboreal or small mammals: the common squirrel monkey *Saimiri boliviensis*, the South-American red squirrel *Sciurus spadiceus* and the spiny

*Correction added after publication 15 April 2008: the equation was changed from '$n = \frac{\ln(0.05)}{\ln(p)}\ln(l-p)$' to '$n = \frac{\ln(0.05)}{\ln(1-p)}$'.

Table 1 Number of captures and capture frequency (number of photos/1000 trap nights) for all species observed during two camera trap surveys at Los Amigos

	Species	Common name	2005	2006	Habit
Didelphimorphia					
Didelphidae	*Didelphis marsupialis*	Common opossum	21 (14.6)	16 (6.8)	T
Pilosa					
Myrmecophagidae	*Myrmecophaga tridactyla*	Giant Anteater	–	2 (0.9)	T
	Tamandua tetradactyla	Collared anteater	1 (0.7)	3 (0.9)	T, Ar
Cingulata					
Dasypodidae	*Cabassous unicinctus*	Southern naked-tailed armadillo	–	–	T
	Dasypus kappleri	Great long-nosed armadillo	2 (1.4)	9 (3.8)	T
	Dasypus novemcinctus	Nine-banded long-nosed armadillo	1 (0.7)	2 (0.9)	T
	Dasypus spp.	Long-nosed armadillo	–	10 (4.3)	
	Priodontes maximus	Giant armadillo	5 (3.5)	7 (3.0)	T
Primates					
Cebidae	*Saimiri boliviensis*	Common squirrel monkey	–	1 (0.4)	Ar[a]
Carnivora					
Canidae	*Atelocynus microtis*	Short-eared dog	4 (2.8)	7 (3.0)	T
	Speothos venaticus	Bush dog	–	–	T
Procyonidae	*Procyon cancrivorus*	Crab-eating raccoon	–	1 (0.4)	T
	Nasua nasua	Coati	2 (1.4)	2 (0.9)	T
Mustelidae	*Eira barbara*	Tayra	3 (2.1)	8 (3.4)	T
	Galictis vittata	Grison	–	–	T
	Lontra longicaudis	Neotropical otter	–	–	Aq[a]
	Mustela african	Amazon weasel	–	–	T, Ar[a]
	Pteronura brasiliensis	Giant otter	–	–	Aq[a]
Felidae	*Puma yagouarundi*	Jaguarundi	1 (0.7)	1 (0.4)	T
	Leopardus pardalis	Ocelot	15 (10.4)	31 (13.2)	T
	Leopardus wiedii	Margay	2 (1.4)	13 (5.6)	T, Ar
	Panthera onca	Jaguar	14 (9.7)	37 (15.8)	T
	Puma concolor	Puma	14 (9.7)	11 (4.7)	T
Perissodactyla					
Tapiridae	*Tapirus terrestris*	Lowland tapir	39 (27.1)	63 (26.9)	T
Artiodactyla					
Cervidae	*Mazama americana*	Red brocket deer	8 (5.6)	31 (13.2)	T
	Mazama gouazoubira	Grey brocket deer	17 (11.8)	36 (15.4)	T
Tayassuidae	*Tayassu pecari*	White-lipped peccary	95 (66)	115 (49.1)	T
	Pecari tajacu	Collared peccary	23 (16.0)	19 (8.1)	T
Rodentia					
Dasyproctidae	*Dasyprocta punctata*	Brown agouti	50 (34.7)	48 (20.5)	T
	Myoprocta acouchy	Green acouchy	2 (1.4)	15 (6.4)	T
Sciuridae	*Sciurus spadiceus*	Southern Amazonian red squirrel	–	5 (2.1)	Ar
Caviidae	*Hydrochoerus hydrochaeris*	Capybara	–	–	T, Aq[a]
Dinomyidae	*Dinomys branickii*	Pacarana	–	–	T
Cuniculidae	*Cuniculus paca*	Paca	14 (9.7)	33 (14.1)	T
Echimyidae	*Proechimys* sp.	Spiny rat	–	9 (3.4)	T[a]
Lagomorpha					
Leporidae	*Sylvilagus brasiliensis*	Brazilian rabbit	–	3 (1.3)	T
Aves	*Crypturellus undulaus yapura*	Undulated tinamou	4 (2.8)	25 (10.3)	[a]
	Mitu tuberosa	Razor-billed curassow	28 (19.4)	26 (11.1)	[a]
	Penelope jacquacu	Spix's guan	7 (4.9)	6 (2.6)	[a]
	Psophia leucoptera	Pale-winged trumpeter	56 (38.9)	140 (59.8)	[a]
Terrestrial mammals			21	24	
All mammals			21	27	

T, terrestrial; Ar, arboreal; Aq, aquatic.

[a]Species not included in the analysis.

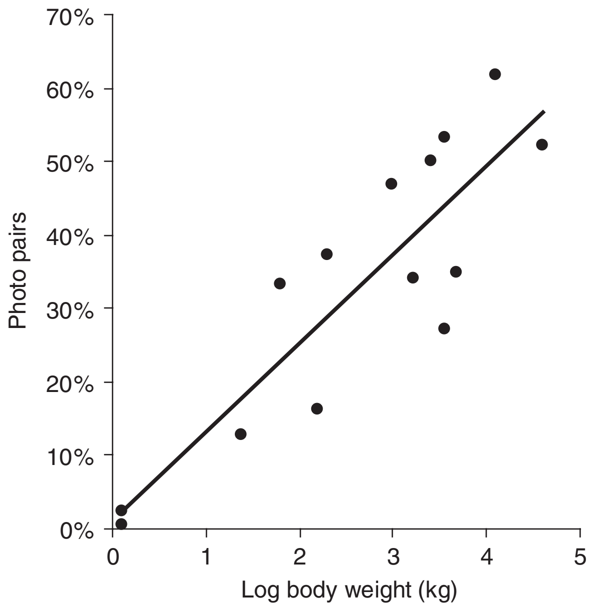

Figure 2 Relation between body weight and the percentage that both cameras at a station took a picture (Spearman's $\rho = 0.811$, $P < 0.0001$, $n = 14$).

rat *Proechimys* sp. A total of 28 species of large- and medium-sized terrestrial mammals have been reported for the area (Leite Pitman, unpubl. data). The camera traps successfully registered all species of large mammals, with an overall completeness of the surveys of 75% (2005) and 86% (2006) for large- and medium-sized mammals. The most commonly photographed species were white-lipped peccaries, lowland tapirs *Tapirus terrestris* and brown agoutis *Dasyprocta punctata*. The most commonly photographed cat species were jaguars and ocelots *Leopardus pardalis*. All species recorded exclusively in 2006 were represented by only one to three photographs, indicating their low capture probabilities. Capture frequencies for all species were highly correlated for the two surveys, (Spearman's $\rho = 0.883$, $P < 0.0001$, $n = 24$) indicating that capture frequencies are species specific.

Our data show that body weight had a strong positive correlation with the number of times both cameras at a station took a picture (Fig. 2; Spearman's $\rho = 0.811$, $P < 0.0001$, $n = 14$). This indicates that small animals are more likely to pass in front of a camera without triggering a picture and will therefore have a lower capture probability.

Camera spacing and grid size did not influence the survey success (Table 2). With identical survey effort, almost the same number of species was obtained with the two different designs. All species recorded by only one of the two grids (jaguarundi *Puma yagouarundi*, crab-eating raccoon *Procyon cancrivorus* and Brazilian rabbit *Sylvilagus brasiliensis*) had very low overall capture rates.

Species richness estimators

The rarefied species accumulation curves for the 2005 and 2006 surveys have very similar shapes. Neither of the curves

Table 2 The influence of camera trap spacing on the number of medium and large terrestrial mammal species registered during a 60-day survey in the Peruvian Amazon

	Stations	Camera days	Floodplain	Terra Firme	Species	Terrestrial mammals
2 km grid	23	1380	8	15	32	23
1 km grid	22	1320	8	14	30	22
Total	39	2340	14	25	33	24

The data comes from two nested camera grids run simultaneously in the same area, one with 2 km camera spacing and the other one with cameras set 1 km apart.

had leveled off, but the 2006 survey was clearly more complete than the 2005 survey. Figure 3 shows the behavior of the different species richness estimators with increasing survey effort. ACE and ICE are almost identical, probably because the number of individuals per sample most of the time is zero or one and hardly ever more than three or four, adding little extra information by using abundance instead of incidents. For the 2006 survey these estimators reach an asymptote at around 2000 camera days, but the estimated total number of species is very low. Chao 1 and Chao 2 are also almost identical. The estimated number of species reaches a maximum, slightly below the known number of species, at around 1600 camera days and then declines as the survey coverage increases. The Jackknife estimators show an interesting pattern. The higher order estimators (Jack 4 and Jack 3) give good results for the 2005 survey and up to about 1200 camera days in the 2006 survey, but then become increasingly unreliable and actually show estimated values smaller than the number of observed species (S_{obs}). Jack1 gives the most reliable estimates for large numbers of camera days. Table 3 gives an overview of the performance of different estimators under different sample coverage (percentage of species detected in a survey). We can see that most estimators are lower than the true number of 28 species. However, all estimators perform better than S_{obs} except for the two estimators Jack 3 and Jack 4 at a sample coverage of 80% and higher. In general, the Jackknife estimators seem to give the best results followed by the ICE and ACE estimators. The two Chao estimators performed poorly.

Model for capture probability

The species accumulation curves show that it takes only 400–500 camera days to obtain a record of the most common species. It is the more elusive species that determine how much time is needed to complete a survey, and often those are the species of most interest. Figure 4 graphically shows the relationship between capture frequency and the time needed to obtain at least one photograph. We can see that the required sampling effort drastically increases once the frequency drops below 3/1000 camera nights. For a frequency of 2/1000 camera nights 1500 camera nights are required, and for a frequency of 1/1000 camera nights 3000

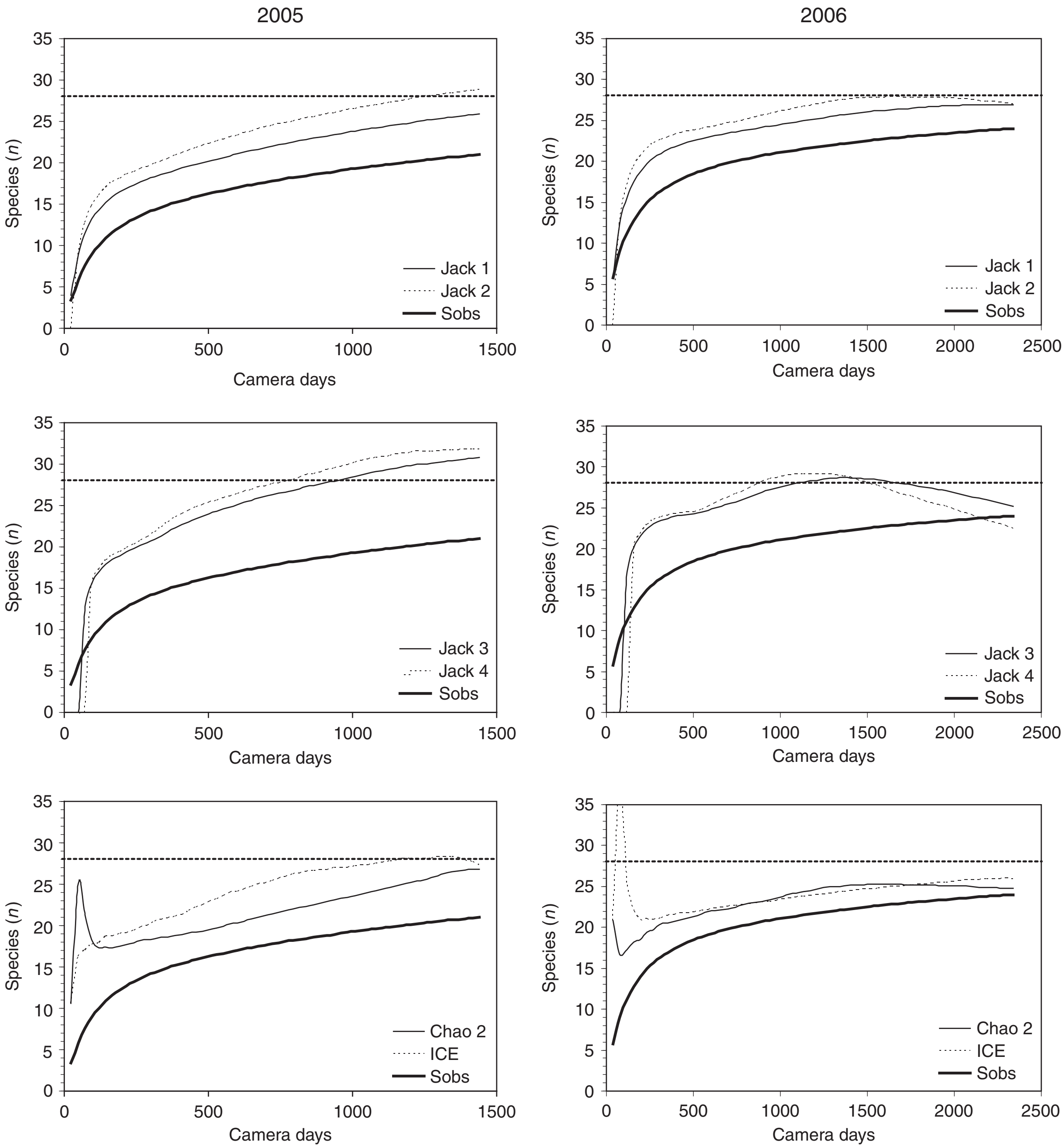

Figure 3 Comparison of different species estimators for two camera trap surveys carried out at the same site in two different years. The known number of species for the site is 28.

camera nights are needed to register the species with a 95% probability.

Looking at the capture frequencies (Table 1), we see that in our case about half of the species are fairly common with a capture frequency of four and above; however, the other half of the species can be considered elusive and will require a large sampling effort. We calculated the probability to obtain at least one photograph based on the sampling effort for the 2005 and 2006 survey for the six rarest species and found that all the species missed in 2005 had a very low capture probability (Table 4).

Discussion

Inventory efficiency

Our results demonstrate the effectiveness of camera traps for inventorying large- and medium-sized terrestrial

Table 3 Observed and estimated species richness under different sampling intensity for two camera trap surveys in the Peruvian Amazon. Bold numbers indicate the least biased species richness estimation

	2005				2006						
Days	8	17	33	60	5	7	13	26	36	51	60
Camera days	192	408	792	1440	195	273	507	1014	1404	1989	2340
S_{obs}	12.2	15.4	18.2	21.0	13.4	15.3	18.5	21.1	22.3	23.5	24.0
Individuals	33	70	135	246	30	42	77	155	124	304	357
Chao 1	16.7	18.6	22.0	26.9	18.5	19.8	21.4	23.9	25.2	25.1	24.8
Chao 2	17.5	18.9	26.2	26.8	18.6	19.8	21.4	23.8	25.2	25.1	24.7
ACE	18.9	21.4	26.2	**27.3**	19.2	19.9	21.4	23.4	24.4	25.6	26.1
ICE	19.0	21.4	22.7	**27.3**	21.0	21.0	21.8	23.5	24.5	25.6	25.9
Jack 1	16.5	19.4	22.5	25.9	18.7	20.4	22.6	24.6	25.8	26.8	**27.0**
Jack 2	18.1	21.2	25.0	28.8	20.7	22.2	23.8	26.2	**27.6**	**27.7**	27.0
Jack 3	18.9	22.7	26.8	30.8	21.5	23.1	24.2	**27.6**	28.7	26.9	25.2
Jack 4	**19.4**	**24.0**	**28.1**	31.8	**21.9**	**23.6**	**24.5**	28.9	28.7	24.8	22.5
Coverage	44%	55%	65%	75%	48%	55%	66%	75%	80%	84%	86%

The number of species believed to be present in the study area is 28.

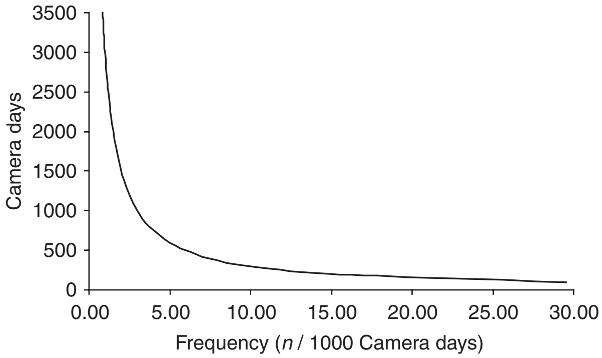

Figure 4 Number of camera days required to register a species with a 95% probability given a certain capture frequency.

mammals in tropical forests. Our cameras successfully registered 86% of the species known for the area during a period of only 2 months. Of the remaining species, all are extremely rare and are only known from one or two records in the study area. The pacarana *Dinomys branickii* has been photographed in the study area before, but might occur at a low density. Grisons *Galictis vittata* and southern naked-tailed armadillos *Cabassous unicinctus* were recorded in camera trap studies at other sites (Leite Pitman, 2007, G. Ayala and A. Paviolo pers. com.), but seem to be rare at our site with very few sightings over the last several years. Bush dogs *Speothos venaticus* have only been observed twice over the last 3 years. All of these species are poorly known by local people. Out of three published inventories from the same region, only one reported records of the bush dog and the southern naked-tailed armadillo, thus showing the difficulty of recording these species (Voss & Emmons, 1996). The sampling period for those three inventories were 2, 3 and 21 years and the total number of large- and medium-sized mammals reported were 19, 25 and 27, respectively. This shows the high efficiency of camera traps for rapid inventories.

Our results show that it takes a substantial survey effort to register some species. Several species had less than three photos taken during the 3840 camera days of both surveys combined. Other studies using camera traps for species inventories recorded 57% of the total number of species (16 of 28 species, 1035 camera days) in Emas National Park, Brazil (Silveira *et al.*, 2003), and 81% (17 of 21 species, 1849 camera days) in the Atlantic forest of Brazil (Srbek-Araujo & Garcia, 2005). Trolle & Kery (2005) recorded 23 species of large- and medium-sized mammals in only 504 camera days in the Pantanal of Brazil. In a survey of a secondary forest in Malaysia, the species accumulation curve leveled off at 25 species after about 4600 camera days (Azlan, 2006). Maffei *et al.* (2002) registered between 14 and 23 species at three sites in the Bolivian Chaco, and the number of species was clearly related to the survey effort. However, even at a site with 4815 camera days and 23 species, there were several species that were only represented by one photograph, showing the difficulty of detecting rare species. For programs that aim to monitor the presence of a species or the community composition over time or compare species diversity between different areas, it is important to keep in mind that a large survey effort is needed to register certain species and that the lack of photographs of a species does not automatically mean that the species is not present.

Capture frequencies for our two surveys were highly correlated, indicating that these frequencies are species specific. While capture frequencies can give an idea of the relative abundance of different species, there is an ongoing discussion among scientists about the reliability of this index (Carbone *et al.*, 2001, 2002; Jennelle, Runge & MacKenzie, 2002). We believe that capture frequencies are a relatively poor index for relative abundance among surveys or for comparing relative abundance of species within surveys because of a variety of factors such as species-specific behavior [e.g. use or avoidance of trails (Trolle & Kery, 2005), partly arboreal versus exclusively terrestrial, or habitat specialist versus generalist],

Table 4 The probability of obtaining at least one photograph for the most elusive species in our study site for 1440 and 2340 camera days based on a binomial model

Species	2005	2006	Frequency total	Probability 2005	Probability 2006
Procyon cancrivorus		1 (0.43)	0.26	0.32	0.46
Myrmecophaga tridactyla		2 (0.85)	0.53	0.53	0.71
Puma yagouarundi	1 (0.69)	1 (0.43)	0.53	0.53	0.71
Dasypus novemcinctus	1 (0.69)	2 (0.85)	0.79	0.68	0.84
Sylvilagus brasiliensis		3 (1.28)	0.79	0.68	0.84
Tamandua tetradactyla	1 (0.69)	2 (0.85)	0.79	0.68	0.84
Nasua nasua	2 (1.39)	2 (0.85)	1.06	0.78	0.92

The first two columns show the number of events and capture frequencies (captures/1000 camera days) registered for the two surveys (2005 and 2006). The third column shows the combined capture frequencies from the two surveys, which were used to calculate the probabilities.

species size (large animals are more likely to trigger the cameras), home range size (animals with larger home ranges move around more and have more cameras within their home ranges) or simply stochastic variation as can be seen when looking at the large differences in capture frequencies for several species between the two surveys in this study.

Performance of species richness estimators

All species richness estimators had a negative bias, but correctly indicated that some species were still missing in the samples. Our data show a very high heterogeneity in capture frequencies among species, with capture frequencies ranging from 0.4 to 66. The performance of the different estimators for this dataset supports results obtained from simulated data, where the Jackknife estimators performed best when heterogeneity in capture probability due to spatial distribution or movement of animals was introduced to the data (Brose, Martinez & Williams, 2003; Brose & Martinez, 2004). In such circumstances, Brose *et al.* (2003) recommend using Jack 4 for sample coverage of 26–35%, Jack 3 for coverage up to 50%, Jack 2 for coverage up to 74% and Jack 1 for samples with a coverage of 75–96%. This sequence of using lower order Jackknife estimators with increasing sample coverage works well for our data, and the point at which switching to a lower order Jackknife estimator is necessary can usually be determined by a decline in the estimated number of species. For our data, Jack 4 performs well up to a sample coverage of *c*. 65%.

Survey design

Camera traps are still most frequently used in surveys to estimate the abundance of large cats (Wallace *et al.*, 2003; Silver *et al.*, 2004; Di Bitetti, Paviolo & De Angelo, 2006; Jackson *et al.*, 2006; Karanth *et al.*, 2006). However, these surveys often produce a reliable inventory of all large- and medium-sized mammals as a useful by-product. Our survey was designed to meet the requirements needed for estimating jaguar density using capture–recapture models (Silver, 2004; Silver *et al.*, 2004) with camera stations set at regular intervals on trails, in pairs to photograph both sides of the animal and not being moved during the 2-month survey period. If the goal of a survey is exclusively to produce a species inventory, it is possible to use a more flexible design and reduce costs while increasing efficiency. Each station could be equipped with a single camera instead of a pair of cameras, reducing the number of cameras needed by half. Based on our data this will reduce the capture probability especially for small species; however, for most species this reduction will be $<50\%$ and therefore will increase efficiency.

Our data indicate that camera spacing and the area covered have little impact on the survey results. Therefore, surveys for inventory purposes can be conducted on a relatively small trail system with a high camera density to achieve the required camera days. It is important, however, to make sure that all the major habitat types are covered because some species might be more abundant or even restricted to one habitat type.

To increase the probability of catching species that rarely use trails or are habitat specialists, cameras can be set at sites targeting specific species such as animal trails, little streams, mineral licks, dens and fruiting trees. Other options are to bait camera stations to attract animals (Long *et al.*, 2003; Trolle & Kery, 2005) or to move cameras if the number of photos is very low or it seems that a large number of photographs result from a single species or individual passing by the camera repeatedly (Srbek-Araujo & Garcia, 2005). Unfortunately some of these designs may violate assumptions for the species richness estimators, resulting in more biased estimates.

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