

ORIGINAL RESEARCH

Estimating mammalian species richness and occupancy in tropical forest canopies with arboreal camera traps

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Abstract

Large and medium-bodied rainforest canopy mammals are typically surveyed using line transects, but these are labour intensive and usually ignore nocturnal species. Camera traps have become the preferred tool for assessing terrestrial mammal communities, but have rarely been used for arboreal species. Here, we compare the efficiency of arboreal camera trapping with line transects for inventorying medium and large-sized arboreal mammals, and assess the viability of using camera traps in trees to model habitat occupancy. We installed 42 camera traps, spaced 2 km apart, in the canopy of the Maijuna-Kichwa Regional Conservation Area, Peru and walked 2014 km of diurnal line transects on 22 trails at the same site. We compared the efficiency of each method using species accumulation curves. We applied a multi-species occupancy model, while examining the effect of camera height on detection probabilities, including the distance from a village and from a river as covariates to examine variability in habitat occupancy. In 3147 camera days, 18 species of arboreal medium and large-sized mammals were detected by cameras, while 11 species were recorded on line transects. Ten of these species were detected by both methods. Diurnal species were detected more quickly and with less effort using arboreal camera trapping than using diurnal line transects at the same site, although some species were more easily detected during line transects. Habitat occupancy was positively correlated with distance from the village for two species, and negatively correlated with distance from the river for one. Detection probabilities increased modestly with camera height. Practical limitations of arboreal camera trapping include the requirement for specialized climbing techniques, as well as increased potential for false triggers, requiring extended processing time. Arboreal camera trapping is an efficient method for inventorying arboreal mammals and a viable option for studying their distribution relative to environmental or anthropogenic variables when abundance or density estimates are not required.

Introduction

Tropical forest canopies contain about half the world's biodiversity (Lowman et al. 2013; Linsenmair et al. 2001; Lowman and Wittman 1996), three quarters of tropical forest vertebrates and a large proportion of the mammals (Kays and Allison 2001), but with the exception of a number of primate species, canopy mammals are poorly

known (Lowman et al. 2013; Kays and Allison 2001). Surveys of wildlife populations and distributions are central to conservation planning and management, but inventories of arboreal mammals are generally incomplete using current methods, often missing cryptic and nocturnal species. Furthermore, many recent monitoring programmes for tropical forest mammal populations consistently ignore arboreal species (Ahumada et al. 2013, 2011;

Rovero et al. 2014; Beaudrot et al. 2016), and therefore underestimate overall species richness and diversity, and risk overlooking declines in species that may be sensitive to habitat modification, anthropogenic factors or climate change.

While a range of methods are available for surveying terrestrial mammals in forests, including direct observation, tracks and signs, captures and camera traps (Voss and Emmons 1996; Haugaasen and Peres 2005; Norris et al. 2008; Tobler et al. 2008), arboreal mammals have traditionally been surveyed using line transects (Voss and Emmons 1996; Peres 2000). Line transect sampling can produce presence data, count indices, occupancy (Hines et al. 2010) or using the distance sampling method (Buckland et al. 2001), absolute densities. However, transects are labour intensive and observers often need to walk hundreds, if not thousands, of kilometres to obtain precise estimates of density (Peres 1999). Furthermore, the recommended sample of 10 or more lines, to ensure a good sample of habitat (Buckland et al. 2010), is rarely achieved. Line transects in tropical forests are often cut around camps and field stations covering a small portion of the study area (Peres 1999), limiting the inferences that can be made about distribution and density at the landscape scale.

Over the last decade, camera trapping has emerged as a preferred method for assessing terrestrial mammal populations, measuring species richness, occupancy, absolute density and activity patterns (McCallum 2013; O'Connell et al. 2011; Ahumada et al. 2011; Tobler et al. 2015) and their potential for standardization has led to the prioritization of their use in monitoring global biodiversity (O'Brien et al. 2010; Ahumada et al. 2013; Linkie et al. 2013). However, until recently, despite the availability of specialized equipment and climbing techniques (Houle et al. 2004), the use of camera traps in trees has been limited by false triggers caused by moving branches filling up cards and draining batteries. Limitations that have now been partially mitigated by the development of more efficient camera traps and larger memory cards (Gregory et al. 2014).

To date, camera traps have been used in trees to record the activity patterns and behaviour of small mammals (Oliveira-Santos et al. 2008) and blonde capuchin monkeys (*Sapajus flavius*) (Bezerra et al. 2014), and to monitor the use of particular habitat features such as feeding trees by Yakushima macaques (*Macaca fuscata yakui*) (Otani 2001) and Kinkajous (*Potos flavus*) (Schipper 2007), or natural canopy 'bridges' left over oil pipelines (Gregory et al. 2014). Although the potential advantages of using camera trapping to monitor primate populations have been extolled (Pebsworth and Lafleur 2014; Gerber et al. 2014), only a few studies have attempted to assess arboreal wildlife populations. These have sought to

determine presence at a given site (Méndez-Carvajal 2014; Olson et al. 2012), some using baited stations only a few metres off the ground (Kierulff et al. 2004; Cerbo and Biancardi 2012; Harley et al. 2014), and have not accounted for imperfect detection, as is necessary when interpreting camera trap data (Mackenzie et al. 2006). While some studies have used occupancy modelling for arboreal mammals, all have used direct observations (Keane et al. 2012; Baker et al. 2011; Hallam et al. 2015; Silveira 2014) or primate calls (Neilson et al. 2013) (Sales et al. 2016, 2015), with an observer present.

We used camera traps placed in trees at a moderately hunted site on the Rio Napo, Peru to: (1) assess the efficiency of camera traps for inventorying medium-sized and large arboreal mammals, compared to line transects at the same site and (2) test the viability of using camera trapping to measure occupancy and model the distribution of arboreal mammals in relation to covariates, using the distances from (1) an indigenous community of frequent hunters and (2) a major stream used by hunters for access, as proxies for human disturbance and hunting.

Materials and Methods

Study site

The Maijuna-Kichwa Regional Conservation Area (S 3.1° W 72.9°), on the lower Rio Napo, Loreto, Peru, is a 391 039 hectare area of continuous lowland rainforest that has been subjected to selective logging and hunting, although such pressures have been reduced since the expulsion of loggers and cessation of logging in 2007 (Gilmore et al. 2010). No forest cover was lost during selective logging activity (Gilmore et al. 2010). Using a hunted site enabled us to test the utility of our survey method under suboptimal conditions, where the abundance of hunted species might be low, since low abundance can lead to sparse data. This was important because survey methods are often employed to examine the effects of hunting or other anthropogenic pressures (Mace and Baillie 2007; Balmford et al. 2005). We surveyed forest on the Rio Sucusari near the indigenous community of Sucusari (145 inhabitants) (Fig. 1). The area has a tropical equatorial climate, hot and humid throughout the year, with slightly dryer months typically between June and November.

Camera trapping

Between November 2013 and December 2014, we set 42 *Bushnell Trophy Cam HD* camera traps with infrared flash, equipped with 32GB memory cards, on the intersections of a grid with 2 km between camera stations (Fig. 1). Two kilometres was chosen in an attempt to

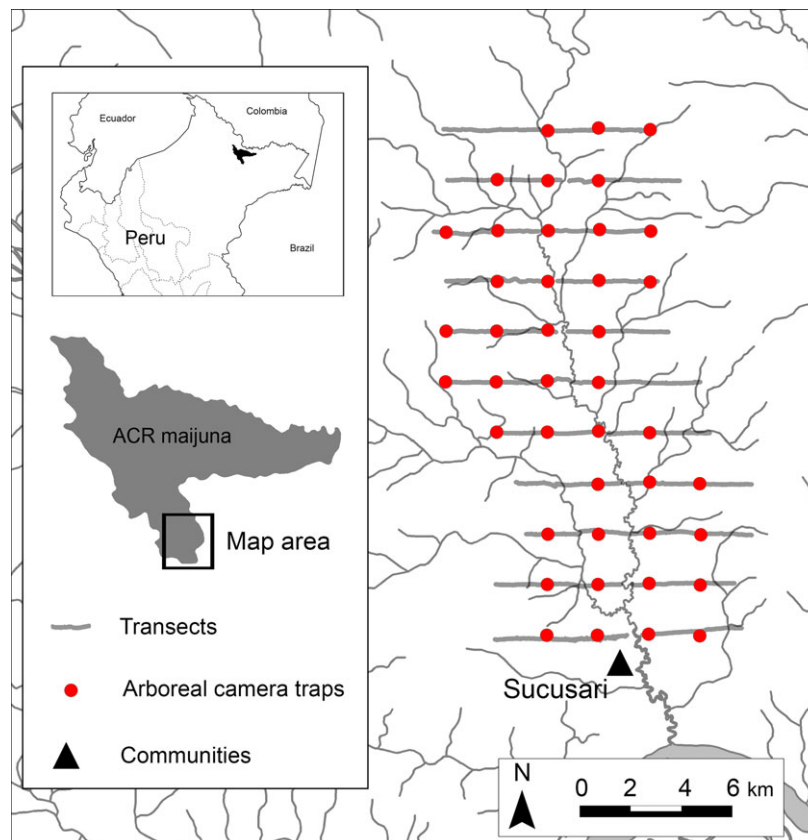


Figure 1. Arboreal camera trap and line transect trail locations on the Rio Sucusari, a tributary of the Rio Napo in northern Peru. Showing the indigenous community of Sucusari.

satisfy the assumption of ‘independence’ in occupancy models by exceeding the home-range size of target species (Mackenzie et al. 2006). We placed cameras in the nearest qualifying tree to each intersection of the grid. Qualifying trees were those safe for climbing, with branches suitable for camera positioning at a height >15 m [approximately, the mean height of the base of the crown of understory trees in Amazonia, (Asner et al. 2002)], and connected to at least one other tree by the proximity of its outer branches. Trees with these characteristics were common in the forest types surveyed, and all cameras were within 100 m of their respective grid intersection. To maximize detection probability, we positioned cameras to monitor branches or vines that had been subjectively assessed for potential arboreal mammal use, in that they reached other trees forming an aerial route through the canopy (Fig. 2). Trees and branches were not selected by species, height (apart from the minimum 15 m requirement), availability of fruit, presence of animal signs or any other criteria, and no baits or lures were used. The mean height of the camera positions was 22.5 ± 3.1 m (Mean \pm SD) and the range was 16.6–29.9 m. We set cameras to record 10-

sec video clips rather than stills because some similar nocturnal species (in particular kinkajous, *Potos flavus* and olingos, *Bassaricyon alleni*) are easier to distinguish in videos. We set an interval of 10 seconds between triggers. We also set cameras to record at noon each day using a time-lapse feature, so the dates of camera failures would be apparent. We attached cameras to trees using either two metal L-brackets with wing-nuts, or a commercially available ball mount to accurately point the camera in the desired direction (Fig. 3). Batteries, memory cards and damaged camera traps were all replaced between 16 May and 25 June 2014, and many of the ball mounts were also replaced with L-brackets and bolts due to superior resistance to animal interference.

Diurnal line transects

To compare the efficiency of camera trapping with line transects, for inventories of large and medium diurnal mammals, we cut 22 line transects of mean length 4.4 km (total length 96.7 km) running east–west on opposite banks of the Sucusari River on the same grid on which

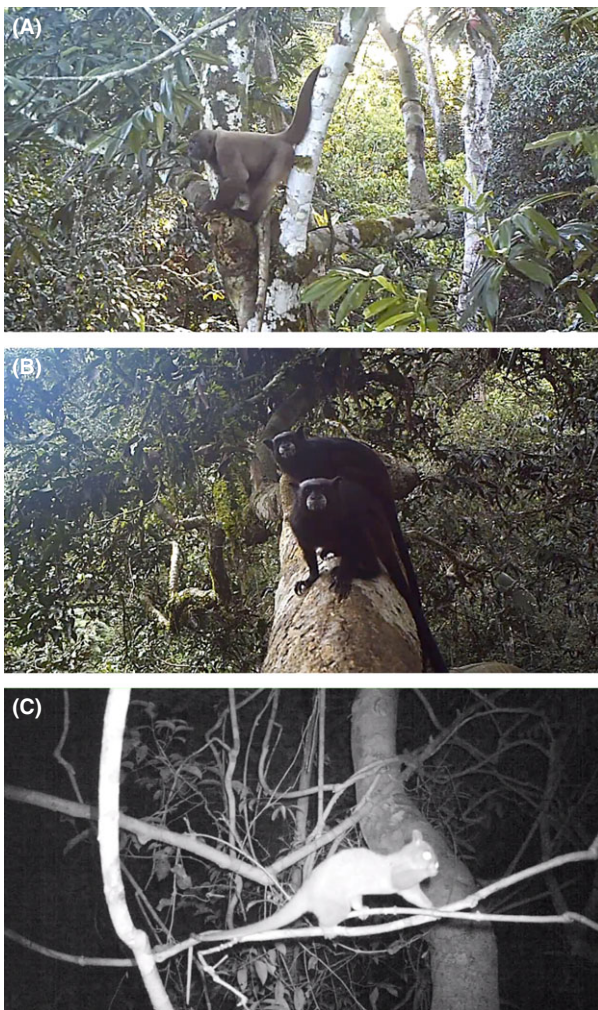


Figure 2. Camera placement monitoring (A) neighbouring tree, Humboldt's woolly monkey *Lagothrix lagothrica*, (B) along a horizontal bough, Black-mantled tamarin *Leontocebus nigricollis*, (C) a vine tangle, Western woolly opossum *Caluromys lanatus* (infrared lights at night).

we positioned the camera traps (Fig. 1). To achieve sufficient effort, each trail was walked multiple times during daylight hours within the months November and December 2013, and February March, June, July, October, November and December 2014, a period that extends beyond the period analysed for our camera traps. We accumulated a total effort of 2014 km, recording all direct sightings of medium and large mammals.

Data analysis

All camera trap videos were imported into *Camera Base* 1.7 (Tobler 2015) and for each, the station number, date, time and species were recorded. A total of 200 to 300 10-second videos can be processed per hour using *Camera Base*, which



Figure 3. Mounts used to attach arboreal camera traps on the Rio Sucusari, Peru; (A) ball and socket joint, (B) L-bracket system assembled on site to suit positioning. The majority of the ball mounts were replaced with L-brackets and bolts during the study due to their superior resistance to animal interference.

allows videos to be reviewed at double speed if required. Data were exported from *Camera Base* into the statistical software R (R Development Core Team, 2015). Records within 60 min were considered from the same 'event.'

A 90-day subset of data collected between 15 June and 12 September 2014 were analysed. This period represents a typical survey effort that other researchers can replicate, collected in the dry season when surveys will most commonly be done. Based on a preliminary analysis of the full dataset, we found detection probabilities were slightly higher during this period, which could be due to environmental conditions, initial avoidance of cameras by animals or improved positioning of cameras during resetting. Four cameras were excluded from the analysis due to malfunction during this period, when no data were produced, so 38 stations were used in the analysis.

Overall, 19 species of mammals detected by either cameras or transects were considered in our analysis,

including only large and medium-sized arboreal mammal species (>0.5 kg) (Table 1). Three species that were occasionally photographed in the canopy but mainly use lower heights up to 15 m were excluded from the study: margay (*Leopardus wiedii*, two events), coati (*Nasua nasua*, one event) and common opossum (*Didelphis marsupialis*, three events). All murid rodents were excluded as they fell below the body size cut-off level, but one primate, the pygmy marmoset (*Cebuella pygmaea*), was included despite being below the body-weight cut-off, in order to complete the dataset for the highly arboreal and generally large-bodied taxonomic group to which it belongs.

Inventory efficiency

To evaluate the survey effort needed to detect a certain number of species, we created rarefied species accumulation curves for the camera trap and transect data using the *vegan* package (Oksanen et al. 2015) in R (R Development Core Team, 2015). For the transect data, we only included diurnal species, because nocturnal species are not reliably detected during diurnal transects.

Occupancy modelling

Occupancy was modelled using a multi-species version of the Royle–Nichols (RN) occupancy model (Royle and Nichols 2003; Yamaura et al. 2011; Tobler et al. 2015). The RN model performs better than a standard binary model when there is heterogeneity in the detection probability, which is common in camera trap data (Tobler et al. 2015). This was confirmed for our dataset by comparing the goodness of fit for the RN model and a binomial multi-species occupancy model. Only the RN model resulted in an adequate fit (Bayesian P -value: 0.849, Lack-of-fit: 1.17, see below for further explanation of Bayesian P -values). To further reduce the issue of heterogeneity caused by short periods of high activity at some camera stations, data were pooled into 6-day sampling periods. Our data were represented by a summarized detection matrix y_{ij} that contains the number of 6-day sampling periods where species i was detected at site j at least once.

Instead of modelling the occurrence z_{ij} of each species i at each site j , the multi-species RN model models abundance a_{ij} using a Poisson distribution with a rate parameter λ_{ij} so that $a_{ij} \sim \text{Poisson}(\lambda_{ij})$. However, in our case, we do not interpret a_{ij} as true abundance and only use this formulation to cope with spatial heterogeneity in the detection history (Royle and Nichols 2003). Occupancy Ψ_{ij} is then calculated as the probability of at least one individual occurring at a site: $\Psi_{ij} = \Pr(a_{ij} \geq 0) = 1 - e^{-\lambda_{ij}}$. Covariates representing the distance from the village and the distance

from the river dividing the study area were added as a linear model with a *log* link:

$$\log(\lambda_{ij}) = \beta_{i,0} + \beta_{i,\text{dist.village}} \times \text{dist.village}_j + \beta_{i,\text{dist.river}} \times \text{dist.river}_j$$

where $\beta_{i,0}$ is the species-specific intercept and $\beta_{i,\text{dist}}$ are the species-specific regression coefficients for the distance covariates. The probability r_{ij} that an individual of species i was detected at site j was modelled as a function of the height the camera was placed in the tree. Our data y_{ij} then comes from a binomial distribution with the probability $p_{ij} = 1 - (1 - r_{ij})^{a_{ij}}$ being the probability that at least one individual is detected and k_j indicating the number of sampling occasions each camera was active.

$$\begin{aligned} \text{logit}(r_{ij}) &= \beta_{i,r} + \beta_{i,\text{height}} \times \text{height}_j \\ y_{ij} &\sim \text{Binomial}(k_j, 1 - (1 - r_{ij})^{a_{ij}}) \end{aligned}$$

Again, $\beta_{i,r}$ represents the species-specific intercept and $\beta_{i,\text{height}}$ the regression coefficient for height. All covariates were standardized by subtracting the mean and dividing by the standard deviation and coefficients were modelled as random effects coming from a normal hyperdistribution with a common mean and standard deviation (Zipkin et al. 2010). Significance of covariates was assessed by testing if the 95% credible intervals overlap zero. Since there was an assumption that the inventory was almost complete (based on knowledge of the arboreal mammal community at the site from our combined datasets), data augmentation was not used to estimate the number of unobserved species (Dorazio et al. 2006). The model was run in JAGS (Plummer 2003) using the R2Jags (Su and Yajima 2015) package in the program R (R Development Core Team, 2015). The model ran with three parallel chains with a length of 100 000 after a burn-in of 50 000 iterations and a thinning rate of 50. Convergence was then assessed by visually inspecting the chains and by examining the R-hat values for each parameter estimate. Model fit was assessed using Pearson's residuals χ^2 by comparing the observed residuals to residuals from data simulated under the model. We calculated the Bayesian P -value as $\Pr(\chi_{\text{obs}}^2 > \chi_{\text{sim}}^2)$ with values larger than 0.95 or smaller than 0.05 indicating a lack of fit as well as a 'lack-of-fit' statistics $\chi_{\text{obs}}^2 / \chi_{\text{sim}}^2$ which is expected to be equal to 1 if the model fits the data perfectly (Kéry and Schaub 2012).

Results

Species richness

During the 90-day period included in our analysis, the survey effort totalled 3147 camera days. Camera days were

Table 1. Total number of detections by camera traps for 6-day pooled data, mean per individual detection probabilities (r) and mean occupancy (ψ) in an arboreal camera trap survey on the Rio Sucusari, Peru. Detection probabilities and occupancy were estimated using a Royle–Nichols multi-species occupancy model.

	Detections in cameras	Naïve Occupancy	Mean occupancy (ψ)	Mean detection probability (r)	Activity	Detections on transects (2014 km)
Red howler monkey <i>Alouatta seniculus</i>	9	0.053	0.192	0.05	Diurnal	20
Humboldt's woolly monkey <i>Lagothrix lagothrica</i>	6	0.053	0.191	0.05	Diurnal	17
Yellow-handed titi monkey <i>Callicebus lucifer</i>	4	0.079	0.257	0.036	Diurnal	126
White-browed titi monkey <i>Callicebus discolor</i>	0	—	—	—	Diurnal	5
Hairy saki monkey <i>Pithecia hirsuta</i>	73	0.395	0.493	0.107	Diurnal	120
Spix's night monkey <i>Aotus vociferans</i>	26	0.263	0.406	0.062	Nocturnal	2
Marañon white-fronted capuchin <i>Cebus yuracus</i>	32	0.368	0.58	0.045	Diurnal	39
Common squirrel monkey <i>Saimiri macrodon</i>	63	0.421	0.529	0.103	Diurnal	58
Black-mantled tamarin <i>Leontocebus nigricollis</i>	28	0.237	0.322	0.099	Diurnal	312
Pygmy marmoset <i>Cebuella pygmaea</i>	1	0.026	0.184	0.038	Diurnal	0
Southern tamandua <i>Tamandua tetradactyla</i>	23	0.368	0.619	0.035	Nocturnal	6
Southern two-toed sloth <i>Choloepus didactylus</i>	13	0.158	0.28	0.067	Nocturnal	4
Amazonian red squirrel <i>Sciurus igniventris</i>	3	0.079	0.256	0.036	Diurnal	7
Streaked dwarf porcupine <i>Coendou cf. ichillus</i>	30	0.105	0.18	0.149	Nocturnal	0
Brazilian porcupine <i>Coendou prehensilis</i>	34	0.132	0.211	0.129	Nocturnal	0
Tayra <i>Eira barbara</i>	28	0.237	0.372	0.07	Diurnal	9
Kinkajou <i>Potos flavus</i>	169	0.605	0.682	0.118	Nocturnal	0
Allen's olingo <i>Bassaricyon alleni</i>	30	0.368	0.534	0.057	Nocturnal	0
Western woolly opossum <i>Caluromys lanatus</i>	127	0.447	0.531	0.151	Nocturnal	0

lost due to damage to cameras by animals or leaking batteries, and when batteries were exhausted. Cameras recorded 703 events for 18 of the large and medium mammal species considered in our analysis, and in addition, 355 images of small mammals, many of them unidentified rodents and opossums, 43 images of reptiles and 87 photographs of birds, predominantly larger species or those that forage on large boughs were recorded. Most notably, we recorded seven large eagles (harpy eagle, *Harpia harpyja* and crested eagle *Morphnus guianensi*). All large and medium-sized arboreal mammal species known

to occur were recorded, with the exception of two: the white-browed titi monkey (*Callicebus discolor*), which was recorded by line transects and the brown-throated three-toed sloth (*Bradypus tridactylus*), which was not recorded by any means. Both of these species appear to be restricted to riverine and secondary habitats represented by only four cameras, and the three-toed sloth appears to only be present close to the mouth of the Sucusari on the Napo River, which was not sampled in this study. One unexpected species was detected: a species of dwarf tree porcupine, possibly *Coendou cf. ichillus*, previously known

from only a handful of records in Ecuador and Peru (Gregory et al. 2015; Voss et al. 2013). Confirmation of the species would extend the known range beyond the eastern bank of the Rio Napo.

The species accumulation curve for camera trapping increased rapidly within the first 500 camera days (13.2 days for our 38 cameras) and within 1000 camera days, we can expect to record about 83% of species (CI: 72–95%, Fig. 4A). However, it takes substantially longer to obtain a complete inventory including the very rare species. No additional species were recorded in our full 1-year dataset with a survey effort of 9851 camera days. For diurnal species only, the species accumulation curve for camera traps (Fig. 4B) shows even faster accumulation of species with most species being recorded after 500 camera days, but the single detection of pygmy marmoset and the failure to detect the habitat specialist white-browed titi monkey means that the curve does not level out. In the species accumulation curve for diurnal line transects (Fig. 4C), most species are recorded within about 600 km of survey effort, which in our survey would have taken our four 2-person teams around 18.8 days to complete, but pygmy marmoset was never detected in 2014 km. Presumably, a similar effort would be required at night to detect nocturnal species; activity patterns taken from our camera trap data show that of the 18 species detected, eight were predominantly nocturnal and 10 predominantly diurnal (the undetected white-browed titi monkey is also diurnal (Campbell et al. 2011)).

Occupancy

Mean occupancy estimates for the 18 species detected by camera traps were highly variable (Table 1) ranging from 0.184 for pygmy marmoset to 0.683 for kinkajou. Occupancy had a positive relationship with distance from the village for all species (Fig. 5), although this was significant for only three species (Spix's night monkey: mean: 0.331, CI: 0.010–0.741; common squirrel monkey: mean: 0.475, CI: 0.147–0.972; western woolly opossum: mean: 0.336, CI: 0.053–0.668), and was almost significant for another four species (hairy saki monkey: mean: 0.258 CI: –0.064–0.580; Maraño white-fronted capuchin: mean: 0.256, CI: –0.078–0.606; Streaked dwarf porcupine: mean: 0.341, CI: –0.021–0.829; Allen's olingo: mean: 0.264 CI: –0.065–0.620). Occupancy had a negative relationship with distance from the river for all species, and this was significant for one species (common squirrel monkey: mean: –0.313, CI: –0.753–0.016) and almost significant for another species (Spix's night monkey: mean: –0.283, CI: –0.773–0.042). The relationship between the height of the camera placement in the tree and detection probability also showed a positive trend for all species, but was

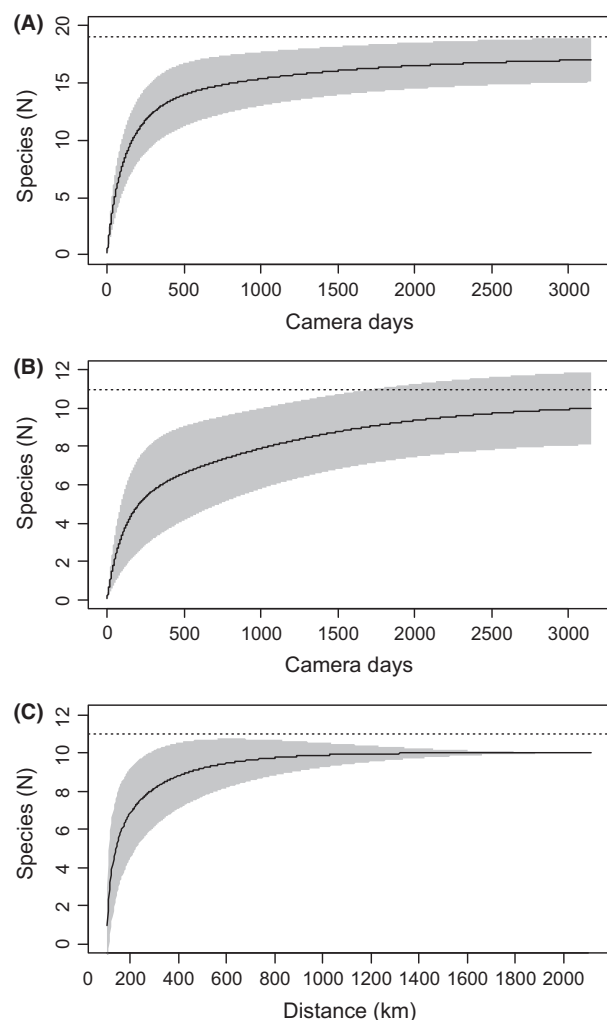


Figure 4. Species accumulation curves on the Rio Sucusari, Peru with 95% confidence interval for (A) all medium to large arboreal mammals (>0.5 kg) recorded on camera traps, (B) only diurnal species recorded on camera traps and (C) only diurnal species recorded on line transects. The dashed line indicates the total number of species detected with both methods combined.

only significant for one species (Western woolly opossum: mean: 0.254, CI: 0.011–0.614) and almost significant for three more (Southern two-toed sloth: mean: 0.263, CI: –0.015–0.758; Brazilian porcupine: mean: 0.237, CI: –0.030–0.624; Kinkajou: mean: 0.183, CI: –0.034–0.422).

Discussion

Efficiency of arboreal camera trapping for inventorying mammals

Reduced survey effort and increased detection for cryptic species are commonly cited advantages of camera traps

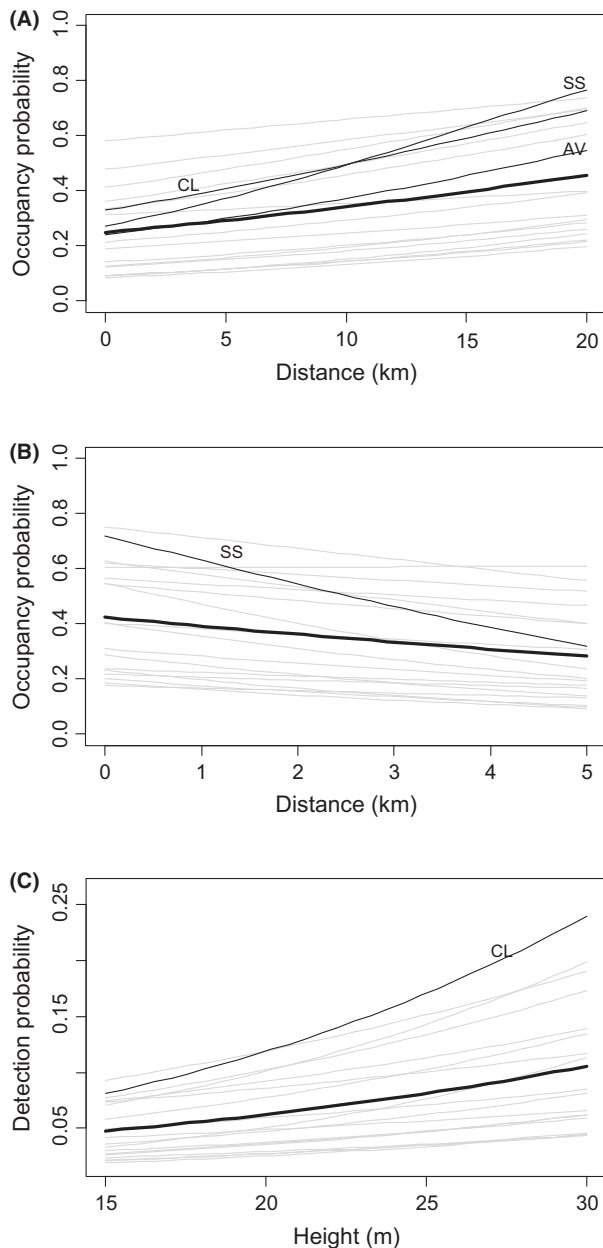


Figure 5. Relationship between; occupancy and the distance from (A) the indigenous community and (B) the main river channel, and (C) detection probability and the height of the camera trap placement in the tree for 18 species detected in an arboreal camera trap survey on the Rio Sucusari, Peru. Grey lines: non-significant relationship, black lines: significant relationship (SS, *Saimiri macrodon*; CL, *Caluromys lanatus*; AV, *Aotus vociferans*) and thick black line: mean across all species.

over line transects (Tobler et al. 2008). While these survey methods are often used to measure markedly different factors, (e.g. density or abundance for line transects and occupancy for camera surveys), both are used in

inventories, and to estimate species richness, so comparison of the effort required to obtain adequate data is useful. Our arboreal camera traps detected all species expected in the study area except for two habitat specialists, one of which may not have been present, within a time period typical of inventories in tropical forests. Both camera and transect methods each missed a different single diurnal species, both of which appear to be highly patchy in their distributions. Cameras were also effective for nocturnal species, detecting even a highly cryptic dwarf porcupine, while transect methods would have required separate night-time transects with a spotlight, which is rarely done in tropical forests and would at least double the required survey effort (Duckworth 1998; Nekaris et al. 2008).

The 1000 camera days required to detect 83% of all species equates to 26 days with our 38 camera design, but accumulation is expected to be even faster in non-hunted areas with larger population sizes. This is comparable to, if not more efficient than, terrestrial camera trapping in the same kind of habitat (Tobler et al. 2015, 2008). However, the limiting factor is actually the effort required to set up and take down the cameras. Our camera traps took one climber around 3 weeks to set up and two to take down, but in practice, the installation time is limited more by site access and trail cutting than climbing effort. An experienced climber might realistically expect to install an arboreal camera trap in around two hours, although the time spent getting an access line into a tree is highly variable. Conversely, line transects require researchers walking transects, often through difficult terrain, in addition to the initial time cutting trails. The 600 km required to match the camera inventory for only diurnal species is a considerable effort.

While as little as 85 km cumulative effort, achievable in perhaps 9 or 10 person-days after trail cutting, has been considered sufficient to extrapolate species richness from a single line (de Thoisy et al. 2008), the utility of such limited surveys is questionable, since cryptic and nocturnal species are typically overlooked and little inference can be made at a landscape level. Multiple trails covering an area similar to those covered by camera-trapping surveys are required to allow inference on the landscape scale. Our 22-trail line transect survey covered a slightly larger area than our arboreal camera-trapping survey, but took 4–8 cutters and four navigators 2 months to cut. Line transects take longer to cut than access trails because they need to be straighter, cross all habitats and obstacles and allow easier passage through the forest. It follows that camera-trapping surveys can cover a wider area much more efficiently, and are therefore generally better suited to large-scale studies that look at the distribution of species in relation to habitat or anthropogenic factors.

Although results are only presented for medium and large-bodied mammals, camera traps also recorded smaller mammals, including a number of rodents and opossums. While most are nocturnal and difficult to identify beyond genus level from infrared videos, this method also has the potential for inventorying smaller mammals, especially if cameras with a white flash are used. Although the camera traps only recorded limited numbers of birds, the method may be useful in surveying certain bird species, such as the harpy eagle and crested eagle, which are often missed by ornithological surveys (Thiollay 1989).

The additional processing time involved in processing camera trap images will also be a consideration in designing surveys. The number of 'false triggers' that contain no sign of any animals is higher in arboreal surveys than in terrestrial surveys, but is highly variable and depends on camera trap model and positioning (Gregory et al. 2014). Many of our false triggers came from cameras that were moved or damaged by animals, which means that false triggers are often clustered together and quicker to review or delete. Although hard to quantify, these false triggers are responsible for a large proportion of the processing time, and working to reduce these, following the guidelines proposed by (Gregory et al. 2014) will increase efficiency in future studies.

Viability of using arboreal camera traps for occupancy modelling

Occupancy of arboreal animals at Sucusari was generally low when compared to estimates for terrestrial species using a similar methodology (Tobler et al. 2015). These results may reflect true occupancy levels, given that the study site is hunted, but lower observed levels may also result from the effects of camera positioning. Although no significant relationships were found between detection frequencies and camera height for any species, all species had positive trends and camera traps were placed within a relatively narrow range in the canopy. Similarly, while occupancy was lower at sites closer to the village for all species, significant correlations were only observed for three species. We used the distance from the village and the river as proxies for hunting pressure, since hunters travel out from the village by river to hunt, and hunting has been repeatedly shown to greatly reduce the populations of arboreal mammals, particularly primates (e.g. Peres and Dolman 2000; Fa and Peres 2001; Linder and Oates 2011; Kumara and Singh 2004) using small camps on the riverbank. Only community members have access to the basin for hunting, since the community restricts entry by outsiders (Gilmore et al. 2010). Occupancy for the most-hunted primates, the red howler and woolly monkeys, was extremely low in comparison with other

primate species, probably reflecting the rarity of these species and their complete absence from areas closer to the community. Low numbers of detections for these species surely reduced the statistical significance of these relationships. The medium-bodied primates, the Marañon white-fronted capuchin and the hairy saki, are also hunted on the Sucusari, but by direct comparison, occupancy was higher for these species and the positive relationships between their occupancy and the distance from the village was stronger. Squirrel monkey occupancy was significantly correlated with distance from the village but habitat differences may explain this, as smaller primates are rarely hunted on the Sucusari since logging operations ceased a decade ago, and the large teams of bushmeat-dependent workers left the area (Gilmore et al. 2010). Indeed, occupancy for squirrel monkeys was negatively correlated with distance from the river, an expected result given their preference for riverine habitats (Campbell et al. 2011). Occupancy for the nocturnal western woolly opossum and Spix's night monkey were positively correlated with the distance from the village, but since these species are rarely hunted, we expect other factors beyond hunting prevalence to be influencing their distributions. Given that we were able to find patterns in the distribution of animals at this hunted site, and with relatively few cameras, we believe that as detection is improved, arboreal camera trapping will be a viable method for monitoring wildlife populations using occupancy modelling.

Survey design and camera placement

Our methods are similar to those of terrestrial camera trap surveys (Meek et al. 2014), but with some additional considerations. Positioning canopy camera traps is first limited by the presence of tall, climbable trees at survey points. Secondly, our limited range of camera heights may obscure relationships between height and detection probability. Limiting the range of heights may not only reduce heterogeneity in detection probability but will also reduce detection probabilities for species with preferences outside this range. In terrestrial surveys, variability in camera angle and vegetation can affect detection probabilities (Meek et al. 2014), and in trees, these issues are compounded. The canopy is structurally diverse, boughs vary in size, curvature and angle, and can be either clean or covered in epiphytes and vines. Optimal positions will vary between species. Gregory et al. (2014) provide useful guidelines on the placement of cameras to reduce false triggers, and applying these guidelines can also serve to standardize camera positioning. Positioning close to the trunk along a horizontal bough as they recommend appeared to result in good numbers of detections, but is not ideal for all species. Sloths, for example, tend not to

travel on the tops of large boughs. Future work might seek to define and standardize deployment configurations, such as camera height and bough width, which should be reported in detail, as with terrestrial surveys (Meek et al. 2014), and included in the models, to ensure that as much variability in detection as possible can be accounted for by covariates. Above all, given the high variability in possible camera set ups, even within a standardized survey, using multiple camera traps at each survey location is highly desirable. Camera traps installed at different heights and targeting different structural elements, can be integrated into a single occupancy model.

Conclusions

There are some clear advantages of camera-trapping techniques over line transects, especially in terms of being able to efficiently cover large areas from which landscape-level inferences can be made. The cameras were also particularly efficient for registering nocturnal taxa and other cryptic species that are typically missed by observers.

This first attempt at using multi-species occupancy modelling for a canopy mammal community has shown that viable occupancy data can be collected with arboreal camera traps. While occupancy is not necessarily a good indicator for population size or density (Efford and Dawson 2012), these models are well suited for comparisons of species diversity at different sites (Tobler et al. 2015) and for understanding species distributions in relation to varying levels of anthropogenic pressures.

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Supporting Information

Additional supporting information may be found online in the supporting information tab for this article.

Table S1. Regression coefficients for distance from village and estimated height of camera traps using a Royle–Nichols multi-species occupancy model for camera trap data from the Rio Sucusari, Peru. * significant values, † approaching significance.

Table S2. Activity patterns from camera trap data from the Rio Sucusari, Peru. Crepuscular activity was defined as 30 min before and after dawn or dusk.

Data S1. JAGS model code for multi-species occupancy model.