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Performance of camera trapping and track counts for surveying large mammals in rainforest remnants

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Abstract Getting information on terrestrial large mammals is particularly difficult in tropical rainforests and in altered landscapes, since the traditionally used method (line-transect census) presents low efficiency in dense vegetation, and is difficult to standardize among heterogeneous, fragmented areas where the small size of patches restricts the length of transects. Aiming to generate information to guide the choice of field protocols for surveying terrestrial large mammals in heterogeneous rainforest remnants, we compared the performance and the correlation between the results of two alternative techniques (track counts and camera trapping), and of two types of bait, in 24 forest remnants in a fragmented Atlantic forest landscape. Techniques resulted in similar observed and estimated richness and species composition at the study landscape, including medium-sized and nocturnal species usually poorly represented in line-transect censuses. Although camera trapping resulted in a higher recording rate of the most common species (*Didelphis aurita*) and track counts in higher recording rates of some less common species (e.g. *Dasypus novemcinctus*), observed richness and recording rates of most species were correlated across the 24 sites between techniques. Conversely, the use of different baits strongly influenced results, indicating the importance of standardizing baits in comparative studies. Our results suggest that the two alternative techniques present similar performance and are suitable for studying the factors affecting the distribution of large mammals in altered rainforest landscapes. The choice of field protocols should then focus on the available resources and infrastructure, and on particularities of the study area.

Keywords Animal signs · Baits · Biodiversity surveys · Biodiversity monitoring · Field protocols · Non-invasive techniques · Sampling efficiency · Sampling methods · Scent lures · Tropical forest

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Introduction

Large mammals are frequently labeled as flagship or keystone species given their charisma, degree of threat or important ecological roles (Terborgh 1988; Wright et al. 1994; Simberloff 1998). Due mainly to habitat loss and fragmentation and the persistent persecution and hunting, few areas in the world still maintain the full original assemblage of large mammals (Morrison et al. 2007). These local extinctions are expected to have important cascading effects given the roles large mammals play in the top-down control of mesopredators (Prugh et al. 2009) and herbivores (Terborgh et al. 2001), and as dispersers and predators of seeds (Wright et al. 2007). Although information on distribution, habitat use and response to threatening processes are needed to guide conservation actions, standardized field-surveys of large mammals are notoriously difficult to carry out. This is particularly the case in tropical, moist forests (de Thoisy et al. 2008; Tobler et al. 2008), where abundance and biomass of large mammals are lower in relation to wetter savannas and dry forests (Robinson and Bennett 2004), many species are nocturnal and solitary, and vegetation structure is complex and heterogeneous.

The efficiency of line-transect censuses, the method traditionally used to survey large mammals, is highly dependent on visibility, which is limited in dense tropical rainforests, especially in second-growth forests, and during the night when several large mammals are active. As a consequence, this technique requires the use of long sampling transects and frequently results in a low number of encounters (Haugaasen and Peres 2005; de Thoisy et al. 2008; Trolle et al. 2008). Standardized protocols using this method are thus further compromised in heterogeneous, altered landscapes due to the small size of forest patches and lower abundance of most species.

Alternative methods such as camera trapping (Trolle 2003; Srbek-Araujo and Chiarello 2005; Michalski and Peres 2007; Di Bitetti et al. 2008; Tobler et al. 2008; Harmsen et al. 2010) and track counts (Dirzo and Miranda 1990; Carrillo et al. 2000; Naughton-Treves et al. 2003; Harvey et al. 2006; Bali et al. 2007; Parry et al. 2007; Norris et al. 2008) are being increasingly used to survey rainforest mammals. Although only in specific circumstances they allow the identification of individuals and the estimation of abundance (e.g. Grigione et al. 1999; Trolle et al. 2008), if standardized they can provide data on site occupancy (Royle and Nichols 2003, Stanley and Royle 2005, O'Brien et al. 2010). Compared to line-transect census, they record a wider range of mammals in terms of body size and habits, are less dependent on visibility, and are easier to standardize among heterogeneous remnants in altered landscapes (Cutler and Swann 1999; Wilson and Delahay 2001; Pardini et al. 2003).

However, these two alternative methods differ in many aspects. Track counts depend on the presence of adequate substrate for footprint impression that may not always be available in tropical rainforests (Dirzo and Miranda 1990; Norris et al. 2008) and on weather conditions. They also require frequent checking by a trained professional, and the number of records is limited to the number of visits to sampling units (Silveira et al. 2003; Norris et al. 2008). Camera traps, on the other hand, are less dependent on weather conditions, require only sporadic visits to check equipment, and the number of records is not limited by the number of visits. They also register the exact time of records, but initial costs are higher (Cutler and Swann 1999; Wilson and Delahay 2001; Srbek-Araujo and Chiarello 2005; Tobler et al. 2008).

The choice between camera trapping and track counts for surveying rainforest mammals should be based on the performance of these field techniques. However, the direct comparison of the efficiency between these two alternative methods has been carried out mainly for medium-sized carnivores in temperate forests (Bull et al. 1992; Foresman and Pearson 1998; Gompper et al. 2006; Barea-Azcón et al. 2007) and for terrestrial large mammals along roads in tropical savannas (Silveira et al. 2003; Lyra-Jorge et al. 2008), primarily in pristine, homogeneous areas. Therefore, there is scarce information to guide the choice of survey methods and the design of field protocols to study the distribution of large mammals among heterogeneous rainforest remnants.

Regardless of the method, given the low densities and large home ranges, bait is frequently used to increase the chance of capturing or recording large mammals in tropical forests (e.g. Trolle 2003; Michalski et al. 2007; Norris et al. 2008). The use of bait also allows flexibility in the arrangement of sampling units, facilitating the standardization of sampling protocols among heterogeneous areas (Tomas and Miranda 2003). There is a wide range of products used as bait, such as scent lures and food from vegetal or animal origin (dead or alive), and several studies compared the performance of different baits (e.g. Andelt and Woolley 1996; McDaniel et al. 2000; Pardini et al. 2003; Michalski et al. 2007; Burki et al. 2010). Among the studies carried out in Neotropical forests (Pardini et al. 2003; Michalski et al. 2007), none tested the performance of local synthetic products that can act as scent lures.

The goal of this study is to provide information useful for guiding the choice of field methods to survey terrestrial large mammals in rainforest remnants and heterogeneous landscapes. Using standardized, paired sampling units in 24 forest remnants, we compared the performance and the correlation between the results obtained with camera trapping and track counts in sand plots, and between two types of baits, in a fragmented Atlantic forest landscape. To achieve this we established sampling units comparable between methods in terms of the area covered, which were sampled simultaneously using both techniques.

Methods

Study area and sites

The study was carried out in a 10,000-ha fragmented landscape in the municipalities of Tapiraí and Piedade, São Paulo State, Brazil (Fig. 1). Mean annual temperature is 18.9°C (mean minimum and maximum temperatures, 12.9 and 24.9°C, respectively), mean annual precipitation is 1,800 mm and altitude varies from 800 to 880 m. The study landscape was originally covered by forest classified as “Lower Montane Atlantic Rainforest” (Oliveira-Filho and Fontes 2000) reduced today to 49% of the landscape (secondary forest in intermediate to advanced stages of regeneration, Fig. 1). Remnants are surrounded by pastures (24% of the landscape), agriculture (13%), homogeneous plantation of *Pinus* spp. and *Eucalyptus* spp. (5%), and native vegetation in initial stages of regeneration (3%). The remaining forest is concentrated within the southeast of the landscape (Fig. 1), and is connected with the Serra do Mar, the largest continuous Atlantic forest area in Brazil (Ribeiro et al. 2009). We sampled 24 sites located in remnants of secondary forest, which were selected to encompass a large variation in forest cover and maintain a minimum distance of 900 m between sites (Fig. 1).

Data collection

We surveyed large terrestrial mammals ($\geq$1 kg) between October 2006 and July 2007, when all 24 sites (remnants) were sampled with camera traps and sand plots, using the

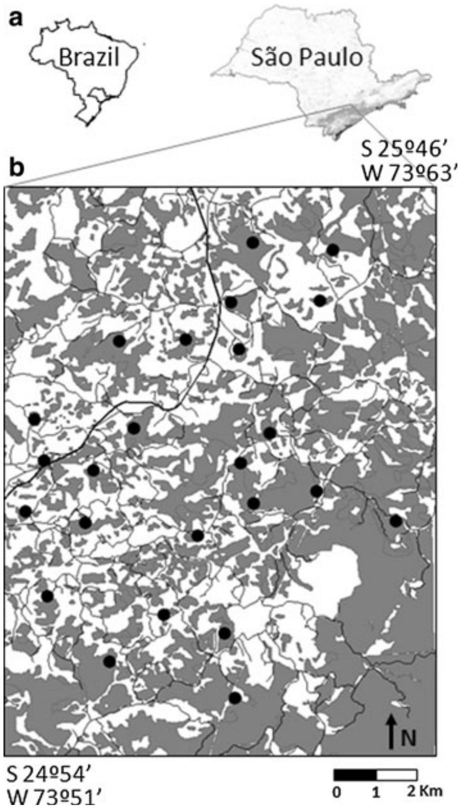

Fig. 1 **a** Map of the State of São Paulo, Brazil, showing the current distribution of Atlantic forest remnants (*gray*) and the location of Tapiraí/Piedade region. **b** Location of the 24 sampling sites (*black circles*) in forest remnants (*gray*), and distribution of roads (*darker* paved; *lighter* unpaved) in the study landscape

same standardized protocol. In each site we set three sampling units 100-m apart (largest possible distance given the size of the smallest remnant), each consisting of one camera trap (Trapa-camera, Marco Antonio Marques de Souza—ME, São Paulo, Brazil), and four sand plots (0.5 × 0.5 m each) set at 5 m from the camera (in front, in the back and on the sides), totaling three cameras and three groups of four sand plots per site. Sampling units were thus paired and similar-sized between methods. Because some Neotropical mammals prefer while others avoid using trails and streams or rivers (Weckel et al. 2006; Harmsen et al. 2010), all sampling units were set inside the forest away from trails and water bodies to prevent differences in detection probability among them. Additionally we set all cameras in places where the vegetation 5 m in front of them was sparse with no obstruction from trees and scrubs (reach of the sensor of the camera is between 6 and 8 m according to the manufacturer, but was in fact less than 5 m in the field), and set baits 1–2 m from the cameras.

Each site (remnant) was sampled during 40 days divided into three surveys (10 or 15 days each), during which 12 of the 24 remnants were sampled simultaneously, and both cameras and plots were baited and checked daily. Final sampling effort among the 24 sites varied from 90 to 118 camera-days due to problems with the cameras, and from 17 to 21 days of sampling with sand plots (from 51 to 63 sets of plot-days) due to rain.

We selected two broad types of baits. One was chosen among the products available on the Brazilian market, looking for liquid baits easy to transport and use in the field, which could act as scent lures, especially for carnivores (e.g. Bull et al. 1992; Crooks 2002;

Barea-Azcón et al. 2007). “Pip Dog” (Coveli Indústria e Comércio Ltda., Rio de Janeiro, Brazil) is based on ammonia carbonate and urea and is used to discipline domestic dogs to urinate in a specific area, whereas “Catnip Brasileiro” (Catnip Brasileiro, São Paulo, Brazil) is used to entertain cats and is made from an herb known as catmint (*Nepeta cataria*). The other type included banana, a cheap and abundant item that has been shown to be efficient as bait (Pardini et al. 2003; Norris et al. 2008), alone (in sand plots, given their small size), or together with corn and salt, which are commonly used by hunters in the study region (in cameras). In each site (remnant), in the first survey the central sampling unit (one camera and correspondent set of sand plots) received baits that included banana and the two lateral sampling units received scent lures, while in the last two surveys the central sampling unit received scent lures and the two lateral sampling units received baits that included banana.

To take into account the fact that animals stay in front of the camera for a while, we considered only those records of the same species in the same camera taken $\geq$1 h apart (Di Bitetti et al. 2008; Tobler et al. 2008). Similarly, we considered the presence of footprints of the same species at the same set of four sand plots (each sampling unit) on the same day as one record. We analyzed the recording rate (number of records divided by sampling effort) in total, i.e. considering all species together, and for groups of species with different diets (carnivores, omnivores and herbivores/frugivores; based on Cheida et al. 2006 for tayra—*Eira barbara*, and on Fonseca et al. 1996 for remaining species). To be able to identify which species were responsible for changes in recording rate in total and for groups of species, we also analyzed recording rates for individual species with sufficient records (those recorded at least three times and in at least two sites with each method). Two pairs of species were analyzed together due to difficulties in distinguishing them in the photos as well as from the tracks: the small cats, *Leopardus tigrinus* and *Leopardus wiedii*, and the brocket deer, *Mazama americana* and *Mazama gouazoubira*.

Data analysis

We built rarefied accumulation curves of the observed number of species with increasing sampling effort (number of sampling days) to compare the effort needed to record the same number of species in the study landscape between methods. We also estimated the expected number of species at the study landscape using the non-parametric estimator Jackknife 1. For both accumulation curves and estimated richness, we used EstimateS 7.52 (Colwell 2009) considering the results of the set of 24 sites together and the maximum number of sampling days common to all sites (30 for camera traps and 17 for sand plots).

To compare the observed richness and the recording rate between methods and baits, and test for the interaction between these factors, we used linear mixed-effects models and a z test (Pinheiro and Bates 2000) in the R environment version 2.8.1 (R Development Core Team, 2008). Methods and baits were considered fixed effects, while sites (the 24 remnants), sampling units (the three sets of one camera plus four sand plots in each site) and surveys (three per site) were considered random effect variables. We modeled both the observed richness and the recording rates as Poisson variables and used log as the link function (Crawley 2007). To model recording rate as the number of records divided by sampling effort (given that the sampling effort varied because of malfunctioning of the cameras and bad weather conditions in sand plots) we included the logarithm of the sampling effort (number of days of sampling) in the models as an offset variable so that the number of records was divided by this term (Crawley 2007; McCullagh and Nelder 1989).

Finally, we used Spearman rank correlations to test for the correlation of the results on observed richness and recording rates between methods as well as between baits across the 24 sites. Irrespective of the potential effects of methods and baits on the results obtained in each survey and sampling unit (tested by the mixed-effects models), a significant correlation indicates that differences in the results across sites are similar between methods or between baits, i.e. that distinct methods or baits result in a similar spatial pattern in the variation of recording rates and richness across sites.

Results

At the landscape scale, considering the two sampling methods together, we recorded 15 species of terrestrial large mammals—12 with camera trapping and 13 with track counts—14 of which were medium-sized native species, and one an invasive species, the domestic dog (*Canis lupus familiaris*) (Table 1). Eleven of the 15 species were recorded by both methods, which resulted in the same rank among the eight most recorded species, and a much higher number of records of the opossum (*Didelphis aurita*) compared to all other species (Table 1). Estimated richness for the study landscape with each method was close to that observed in total with both methods together (Table 1). Although both methods recorded, at the end of the sampling period, a similar number of species in the study landscape, the species accumulation curves indicate that track counts in sand plots assessed the assemblage faster than camera trapping, resulting in a higher number of species per unit of effort (Fig. 2).

At the level of the individual sampling units, however, the observed richness did not differ significantly between the two methods (Table 2). On the other hand, the recording rate of the most common species in the study landscape—the omnivorous opossum (*Didelphis aurita*)—was significantly higher in camera trapping compared to track counts (Table 2). As a consequence, both recording rates in total and for omnivores were significantly higher in camera trapping (Table 2). Alternatively the recording rates for less common species (the omnivorous nine-banded armadillo, *Dasypus novemcinctus*, and the group of herbivores/frugivores) were (or tended to be) significantly higher in track counts (Table 2).

Observed richness, recording rates for most species individually (*Didelphis aurita*, *Canis lupus familiaris*, *Cerdocyon thous*, *Nasua nasua* and *Eira barbara*), and, as a consequence, recording rates in total and for omnivores were higher in sampling units including banana as bait (banana, or banana, corn and salt) than in sampling units baited with scent lures (Table 2). However, there was an interaction between methods and baits, so that for half of these variables (recording rates for *Didelphis aurita* and *Cerdocyon thous,* for omnivores, and in total) the positive effect of baits containing banana was higher in camera trapping, where banana was used together with corn and salt (Table 2).

We observed significant positive correlations between the results obtained with camera trapping and track counts across the 24 sites for observed richness as well as for recording rates of the seven most common of the nine species analyzed individually, and thus for recording rates in total, for omnivores and herbivores/frugivores (Table 3). Alternatively, correlations among the results obtained in sampling units with different baits were not significant for observed richness (Table 3), and were significant for the recording rates of comparatively fewer species and group of species (Table 3).

Table 1 Number of records and observed and estimated richness of terrestrial large mammals obtained in the study landscape with each field-technique and bait

	Diet	Camera trapping			Track counts			Total
		Total	Banana	Scent lures	Total	Banana	Scent lures	
Didelphimorphia								
Didelphis aurita	O	1,283	1,202	81	659	499	160	1,942
Cingulata								
Dasypus novemcinctus	O	76	41	35	124	82	42	200
Euphractus sexcinctus	O				4	3	1	4
Pilosa								
Tamandua tetradactyla	O	1		1				1
Carnivora								
Canis lupus familiaris	O	61	51	10	31	25	6	92
Cerdocyon thous	O	132	126	6	90	76	14	222
Nasua nasua	O	39	32	7	19	12	7	58
Procyon cancrivorus	O	4	4		1		1	5
Eira barbara	O	68	66	2	55	49	6	123
Galictis cuja	C				2	2		2
Leopardus spp.	C	10	7	3	3	3		13
Artiodactyla								
Mazama spp.	HF	14	8	6	11	10	1	25
Rodentia								
Hydrochoeris hydrochaeris	HF	1	1					1
Dasyprocta azarae	HF	13	13		10	10		23
Lagomorpha								
Silvilagus brasiliensis	HF				1	1		1
Omnivores		1,664	1,522	142	983	746	237	2,647
Carnivores		10	7	3	5	5		15
Herbivores/frugivores		28	22	6	22	21	1	50
Total		1,702	1,551	151	1,010	772	238	2,712
Observed richness		12	11	9	13	12	9	15
Estimated richness		13.95			15.82			

O omnivore, *C* carnivore, *HF* herbivore/frugivore

Discussion

The two techniques—camera trapping and track counts—resulted in similar species richness and composition, and the set of recorded species suggests that the study landscape harbors a simplified assemblage of terrestrial large mammals, dominated by medium-sized species (between 1 and 5 kg). Most large frugivores, such as tapirs (*Tapirus terrestris*), paca (*Cuniculus paca*), and peccaries (*Pecari tajacu* and *Tayassu pecari*), as well as the large felids (*Panthera onca* and *Puma concolor*), were not recorded, although these species have been recorded elsewhere with the techniques used here (Pardini et al. 2003; Silveira et al. 2003; Trolle 2003; Srbek-Araujo and Chiarello 2005; Norris et al. 2008; Tobler et al.

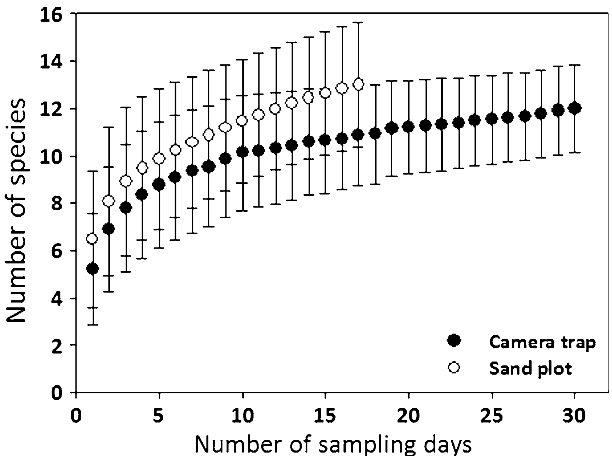

Fig. 2 Mean accumulation curves (with 95% confidence intervals) of the observed number of species of terrestrial large mammals with increasing number of sampling days obtained with two different field-techniques in the study landscape

2008) and present high recording rates in well-preserved mature forests (Tobler et al. 2008). Interviews with local residents, as well as occasional sightings and signs of mammals recorded during field work, reinforce the very low abundance of these large species in the study landscape. In fact, these species are known to be negatively affected by hunting and fragmentation in the Atlantic forest (Chiarello 1999; Cullen et al. 2000).

Thus both methods seem to be adequate to survey terrestrial mammals that occur in altered rainforest landscapes, including medium-sized and nocturnal species that are difficult to record with line-transect censuses (Silveira et al. 2003; Srbek-Araujo and Chiarello 2005). However, given the simplification of the observed assemblage in the study landscape, we highlight that the comparisons between methods and baits presented here cannot be generalized to all terrestrial large mammals originally found in the Atlantic forest.

Comparing methods

The differences we observed in the performance of the two methods are due to the fact that (1) the most common, smallest species frequently had more than one record per day in the same camera, and (2) the chance of recording less common or larger species were higher in track counts, probably because we used four sand plots per camera as a sampling unit. Despite the fact that camera trapping allows distinguishing records of the same species made at different times, eventually totaling more than one record per day, our data show that this is important for increasing recording rates only for very common and small species, the opossum *Didelphis aurita*. For the rest of the species, although sometimes we obtained more than one record per day (i.e. excluding the sequential photos of the same individual that stayed in front of the camera for a while), these were relatively rare occasions that did not lead to an average increase in recording rates per sampling unit in camera traps compared to sand plots. This may occur because of the large home ranges and high vagility of larger mammals. On the other hand, even not distinguishing among records of the same day, sand plots resulted in higher recording rates for less common species, such as the nine-banded armadillo (*Dasypus novemcinctus*) and herbivores/frugivores. This is

Table 2 Results of the mixed-effects models on the effects of the methods (track counts and camera trapping), the baits (scent lures and banana/banana corn and salt) and the interaction between them on the observed richness and recording rates of terrestrial large mammals

	Methods			Baits			Interaction		
	Estimate (error)	*z*	*P*	Estimate (error)	*z*	*P*	Estimate (error)	*z*	*P*
Observed richness	0.063 (0.087)	0.719	0.472	−0.839 (0.125)	−6.701	<0.001	0.254 (0.169)	1.506	0.132
Recording rates									
Total	−0.128 (0.044)	−2.878	0.004	−2.084 (0.089)	−2.344	<0.001	1.326 (0.114)	11.680	<0.001
Omnivores	−0.145 (0.045)	−3.216	0.001	−2.131 (0.091)	−23.289	<0.001	1.397 (0.116)	12.072	<0.001
Carnivores	0.280 (0.654)	0.428	0.669	−0.612 (0.794)	−0.771	0.441	−16.120 (2721.495)	−0.006	0.995
Herbivores/frugivores	0.610 (0.317)	1.927	0.054	−0.938 (0.504)	−1.861	0.063	−1.553 (1.192)	−1.303	0.193
Didelphis aurita	−0.317 (0.054)	−5.916	<0.001	−2.494 (0.121)	−20.672	<0.001	1.719 (0.147)	11.679	<0.001
Dasypus novemcinctus	1.263 (0.193)	6.543	<0.001	0.122 (0.239)	0.508	0.611	−0.294 (0.301)	−0.975	0.330
Canis lupus familiaris	−0.099 (0.250)	−0.397	0.691	−1.497 (0.363)	−4.123	<0.001	0.388 (0.585)	0.663	0.507
Cerdocyon thous	0.042 (0.147)	0.287	0.774	−2.703 (0.435)	−6.217	<0.001	1.568 (0.519)	3.021	0.003
Nasua nasua	−0.343 (0.348)	−0.986	0.324	−1.559 (0.466)	−3.345	<0.001	1.011 (0.649)	1.558	0.119
Eira barbara	0.320 (0.191)	1.674	0.094	−3.108 (0.736)	−4.220	<0.001	1.559 (0.853)	1.828	0.068
Leopardus spp.	−0.210 (0.760)	−0.276	0.783	−0.608 (0.801)	−0.759	0.448	−15.610 (2720.305)	−0.006	0.995
Mazama spp.	0.772 (0.523)	1.476	0.140	0.143 (0.628)	0.227	0.820	−1.680 (1.372)	−1.224	0.221
Dasyprocta azarae	0.548 (0.437)	1.253	0.210	−17.724 (2480.592)	−0.007	0.994	0.301 (3515.393)	<0.001	1.000

Estimates (with their standard errors in parenthesis) represent the estimated effect of each factor, and are presented in the log scale, since the models were constructed using log as the link function. Methods: positive estimates indicate higher values for track counts and negative estimates higher values for camera trapping; Baits: positive estimates indicate higher values for scent lures and negative estimates higher values for banana/banana corn and salt; Interaction: positive estimates indicate that the effects of the bait that included banana compared to scent lures was higher for camera trapping than for track counts

Table 3 Spearman rank correlations between the results obtained with the different field-techniques and baits across the 24 surveyed sites

	Methods		Baits in camera traps		Baits in sand plots	
	r	*P*	*r*	*P*	*r*	*P*
Observed richness	0.63	0.001	0.21	0.333	0.30	0.156
Recording rates						
Total	0.56	0.005	0.49	0.015	0.65	0.001
Omnivores	0.53	0.008	0.53	0.008	0.63	0.001
Herbivores/frugivores	0.41	0.045	0.18	0.391	−0.16	0.467
Carnivores	−0.01	0.973	−0.17	0.423		
Didelphis aurita	0.56	0.005	0.56	0.005	0.83	<0.001
Dasypus novemcinctus	0.54	0.006	0.26	0.215	0.09	0.671
Canis lupus familiaris	0.67	<0.001	0.31	0.147	0.50	0.012
Cerdocyon thous	0.78	<0.001	0.56	0.004	0.62	0.001
Nasua nasua	0.64	0.001	0.51	0.010	0.20	0.351
Eira barbara	0.76	<0.001	0.40	0.051	0.51	0.012
Leopardus spp.	0.19	0.372	−0.17	0.423		
Mazama spp.	0.36	0.084	0.10	0.645	−0.12	0.580
Dasyprocta azarae	0.50	0.013				

probably a result of using four sand plots per camera trap, covering an area at the laterals and back of the cameras, and suggests that increasing the number of sand plots is efficient to increase capture probability even when the plots are disposed close together. Indeed considering only records taken in different days, recording rates of the opossum was also significantly higher in sand plots (results not shown), demonstrating that the higher recording rates of this common, small species in camera traps resulted from records made in the same day.

Despite these differences in recording rates, however, both techniques resulted in similar values of species richness per sampling unit. At the landscape scale, although track counts in sand plots recorded the species present within fewer days of sampling, this technique did not require a shorter time in the field, since we needed 40 days to obtain around 20 days without rain when sampling with sand plots were possible.

It is difficult to use the data available in the literature to evaluate if these results are congruent with the findings obtained for other species or regions due to the heterogeneity in sampling design among previous studies, especially in terms of the analyzed variables (i.e. the way records were computed), and the number, size and/or location of sampling units used for track counts compared to camera traps (Bull et al. 1992; Foresman and Pearson 1998; Silveira et al. 2003; Gompper et al. 2006; Barea-Azcón et al. 2007; Lyra-Jorge et al. 2008). Despite these limitations, previous studies indicate a similar performance between methods and a tendency for track counts to record species richness faster.

Only one of the available studies compared recording rates between methods (Silveira et al. 2003), and two statistically compared the time elapsed till initial detection (latency) (Gompper et al. 2006; Barea-Azcón et al. 2007). Recording rates were higher in total and for most species individually using track counts along a road in a Neotropical savanna, but this was due to the much larger sampling units used for track counts (1.5 km of dirt road) than for camera trapping (one camera) (Silveira et al. 2003). No significant differences in latency were found between methods for temperate small carnivores (Gompper et al. 2006; Barea-Azcón et al. 2007). Three studies sampled more than three species and compared species richness between these two alternative methods (Silveira et al. 2003; Barea-Azcón et al. 2007; Lyra-Jorge et al. 2008). The total number of recorded species was similar between methods in both studies carried out along dirt roads in Neotropical savannas (Silveira et al. 2003; Lyra-Jorge et al. 2008). Track counts recorded species richness at the study area faster in the only work that compared accumulation curves between methods (Silveira et al. 2003). However, this result is again influenced by the difference in the area covered by sampling units between techniques. Species richness of small carnivores per sampling site in a temperate forest was also higher in track counts on scent stations than in camera traps (Barea-Azcón et al. 2007).

We also observed a high congruence between methods in relation to assemblage composition and structure, as found in both studies along dirt roads in Neotropical savannas (Silveira et al. 2003; Lyra-Jorge et al. 2008). The only study that previously tested for the spatial correlation between the recording rates obtained with track counts and camera trapping found that congruency increased with the size of the species (Silveira et al. 2003). However, track counts for smaller species were probably underestimated in this study since track censuses were done by car in a dirt road, and some medium-sized mammals, contrary to the observed for larger species, avoid wider trails and roads (Weckel et al. 2006; Harmsen et al. 2010). Indeed our study revealed that, once sampling units are spatially and temporally comparable among methods and standardized among sites, the data from camera trapping and track counts result in a spatially similar variation in observed richness and recording rates among sites.

Given the differences on how records are obtained between methods (an animal stepping on a small area of different substrate, or an animal passing by a larger area in front of a camera that triggers a flash) and thus on which factors should affect detection probability, the spatial congruence between the results of the different techniques suggests that the number of records reflects mainly patterns of species occupancy, activity, and frequency of use across sites. Most criticism to the use of recording rates in ecological studies are based on differences in behavior and ecology among species, which would make recording rates species-specific (Jennelle et al. 2002, Tobler et al. 2008), and a poor estimate of relative abundance among species in a particular site. However, recording rates should be better as an estimate of the relative frequency of use or activity (rather than abundance) of one species across sites (rather than among species in one site) if field protocols are standardized and simultaneously applied among sites as we have done in this study. This is important because recording rates are commonly used to evaluate differences within species among sites in the Neotropics (line transect census, Chiarello 1999; Cullen et al. 2000; Michalski and Peres 2007; Parry et al. 2007; Bali et al. 2007; track counts, Dirzo and Miranda 1990; Carrillo et al. 2000; Naughton-Treves et al. 2003; Harvey et al. 2006; Parry et al. 2007; Bali et al. 2007; Norris et al. 2008; camera trapping, Michalski and Peres 2007; Di Bitetti et al. 2008; Weckel et al. 2006; Harmsen et al. 2010).

Therefore our results indicate that these two methods could be used interchangeably, presenting similar performance and spatial congruence. The choice between methods can thus focus on other technical and cost differences. Camera trapping depends on higher investment to purchase, maintain and use the equipment (camera traps, films and batteries), while track counts depend on investments in personnel to establish sand plots and frequently check sampling units as well as on weather condition (Silveira et al. 2003; Barea-Azcón et al. 2007; Lyra-Jorge et al. 2008). However, as we checked cameras daily we observed that functioning of this specific equipment we used is frequently interrupted because of the high humidity in rainforests. Similarly, some studies also revealed problems with some types of cameras due to environmental conditions such as low temperatures (about −30°C) (Bull et al. 1992; Foresman and Pearson 1998). Moreover, when baited, cameras may also require a frequent checking to change the film since some individuals stay in front of the camera for a while, a problem that is solved with the use of modern digital cameras. The use of expensive apparatus as camera traps also increases the chance of losing equipment and data because of stealing (nine of the 36 cameras we used were stolen). Thus it may not always be possible to reduce the investment in frequent checking when working with camera traps in wet forests and/or in areas subject to high risk of stealing.

Comparing baits

Studies focusing on the efficiency of baits are difficult to compare, given the variety of types of baits, species and field methods that are considered (e.g. Andelt and Woolley 1996; McDaniel et al. 2000; Burki et al. 2010), with few studies carried out in the Neotropics using camera traps or sand plots (Pardini et al. 2003). Most of the available studies were performed with the aim of increasing the efficiency of protocols of vaccination or control of mammals in towns or rural areas in temperate regions (e.g. Andelt and Woolley 1996; Short et al. 2002; Campbell and Long 2008; Ballesteros et al. 2009), and few included a control, i.e. sampling unities without bait (Pardini et al. 2003; Campbell and Long 2008; Ballesteros et al. 2009; Thorn et al. 2009; Gardner et al. 2010).

In our study the use of food baits (banana, corn and salt, or only banana) showed to be more adequate to attract terrestrial mammals compared to the scent lures, resulting in higher species richness, recording rates for five species individually (*Didelphis aurita*, *Canis lupus familiaris*, *Cerdocyon thous*, *Nasua nasua*, and *Eira barbara*), and thus recording rates in total and for omnivores. Scent lures, on the other hand, did not result in higher recording rates for either canids or felids, for which they were designed, or any other species. Thus these scent lures for domestic cats and dogs available on the Brazilian market do not seem to be as effective as scent lures specifically designed for wild mammals in other regions (e.g. Bull et al. 1992; Crooks 2002; Barea-Azcón et al. 2007).

However, as most of the studies comparing the efficiency of baits, ours did not include sampling units without bait, and we cannot evaluate if using baits increases the absolute efficiency of recording species in camera traps and sand plots. Nonetheless, a study carried out in the Atlantic forest, comparing sand plots baited with banana, salt, bacon or without bait, also found that the use of banana resulted in the highest number of species, total records, and records of opossum and agoutis (Pardini et al. 2003), suggesting that banana is in fact an efficient bait for medium-sized omnivorous or frugivorous mammals in the Neotropics. The majority of the studies that did include controls have also shown that baits can increase detection probability (fish and other baits for hyenas in camera traps, Thorn et al. 2009; food baits for black bears in hair snares, Gardner et al. 2010) or recording rates (several baits for feral pigs and raccoons in camera traps, Campbell and Long 2008). Moreover, our results indicate that the quantity or the variety of food types increase the efficiency of food baits, since for recording rates of two species (*Didelphis aurita*, and *Cerdocyon thous*), and thus for the recording rate in total and for omnivores, the positive effects of food baits in comparison to scent lures was higher when using banana together with corn and salt, than only banana. It is important to mention, however, that food baits can act as a source of variation in detection probability, as animals may be more likely to investigate food-based baits when they are hungry or depending on seasonal variations in food resources. Indeed the efficiency of baits in attracting a particular species has been shown to vary according to factors such as individual behavior and age, time of the year, and population size (Short et al. 2002)

Studies that include more than one species have also consistently shown that the efficiency of baits varies strongly among species (Andelt and Woolley 1996; Wayne et al. 2005; Michalski et al. 2007; Campbell and Long 2008). In our study, although the baits containing banana were consistently better than scent lures for five species, at least one species for which we had a large number of records—the nine-banded armadillo (*Dasypus novemcinctus*)—did not show preference for banana. These differences among species should result in a lack of correlation between results with different baits as we observed in our study for species richness and recording rates of some species, highlighting the importance of including complementary baits and standardizing baits among areas in comparative studies.

Concluding, our results suggest that both methods can be equally efficient to survey terrestrial rainforest mammals and are adequate to study the factors that affect the distribution of these species in fragmented landscapes, since (1) they record medium-sized and nocturnal species, (2) can be standardized among heterogeneous areas, (3) show similar efficiency in recording the majority of species and species richness, and (4) resulted in similar patterns of distribution of species records among remnants. The relative cost efficiency between these techniques in heterogeneous rainforest remnants depends on the quality of the cameras (especially on resistance to humidity) and the chance of stealing. Alternatively the performance varied strongly between baits, and results with different baits were not always correlated, suggesting the importance of (1) standardizing the use of baits, and (2) including complementary baits or choosing baits that attract a large range of animals.

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