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Artículo

CAMERA TRAP PHOTOGRAPHIC RATES ON ROADS VS. OFF ROADS: LOCATION DOES MATTER

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ABSTRACT. We present the results of a camera trap survey conducted in 2008 in the Atlantic Forest of Iguazú National Park, Misiones, Argentina, testing whether placing camera traps on dirt roads/trails or in off-road locations produce important biases in the recorded species. Seven pairs of camera trap stations were active for 26.6 ± 8.9 days; for each pair, one station was located on a narrow unpaved road and the other about 50 m from the road. We used the first order Jackknife estimator to compare species richness between on-road vs. off-road locations. We used records from another camera trap survey conducted at Iguazú National Park in 2006-2007 to assess whether species with a high Road-use Index (ratio of photographs of animals walking along roads to photographs of animals crossing the roads) had a higher ratio of records on roads/off road stations in the 2008 survey. Multivariate ANOVA based on dissimilarities (ADONIS) was used to compare mammal assemblages recorded at stations located on roads vs. off roads. We obtained 228 independent records of 15 species of medium-large sized terrestrial mammals. Stations located on roads had a higher recording rate (1.06, SD = 0.57 vs. 0.24, SD = 0.13 records per day) and recorded more species than off-road stations (15 vs. 10 recorded species; 19.3, SE = 2.8 vs. 14.3, SE = 2.8 species estimated with the 1st order Jackknife model). Species differ in their relative probabilities of being recorded on roads vs. off roads, something that can be predicted with the Road-use Index. The ADONIS indicated that the mammal assemblage surveyed on roads was statistically dissimilar to that surveyed off roads, a result that can be explained by the differential tendency of the species to use roads and trails.

RESUMEN. Tasa de registros fotográficos con cámaras trampa en caminos vs. fuera de ellos: la ubicación es importante. Presentamos los resultados de muestreos con cámaras trampa que realizamos en el Parque Nacional Iguazú, Misiones, Argentina, en 2008 para evaluar si ubicar las cámaras trampa en caminos o senderos o fuera de ellos afecta el ensamble de mamíferos muestreado. Siete pares de estaciones estuvieron activas durante 26.6 ± 8.9 días. Una estación de cada par estuvo ubicada en un camino de tierra angosto y no transitado; la otra a 50 m de distancia perpendicular del camino dentro del bosque. Usamos los registros de otro muestreo con cámaras trampa realizado en el parque nacional Iguazú en 2006-2007 para evaluar si las especies con una mayor proporción de fotos caminando sobre los senderos en lugar de cruzándolos transversal o tangencialmente (índice de uso de senderos) fueron relativamente más registradas en las estaciones ubicadas en senderos en 2008. Usamos el estimador Jackknife de primer orden para comparar la riqueza de especies en estaciones de senderos y fuera de ellos. Un ANOVA multivariado basado en disimilitudes (ADONIS) fue usado para comparar los ensambles de mamíferos registrados en caminos y fuera de ellos. Obtuvimos 228 registros independientes de 15 especies de mamíferos terrestres medianos-grandes. Las estaciones ubicadas en caminos tuvieron una mayor tasa de registros (1.06 ± 0.57 vs. 0.24 ± 0.13 registros/día) y una mayor riqueza que las estaciones fuera de ellos (15 vs. 10 especies observadas; 19.3, SE = 2.8 vs. 14.3, SE = 2.8 especies estimadas con el modelo Jackknife de 1er orden). Las especies difirieron en sus probabilidades relativas de ser registradas en caminos vs fuera de

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ellos, algo que puede predecirse a partir del índice de uso de senderos. El ADONIS indicó que el ensamble de mamíferos muestreado en caminos fue estadísticamente distinto al muestreado fuera de ellos, un resultado que puede ser explicado por la tendencia diferencial de las especies a usar los caminos.

Key words: Detection probability. Mammal assemblage. Random sampling. Recording rate. Relative abundance.

Palabras clave: Abundancia relativa. Ensamble de mamíferos. Muestreo aleatorio. Probabilidad de detección. Tasa de registros.

INTRODUCTION

Camera traps have become a standard methodology to study mammal populations and assemblages (Rowcliffe and Carbone, 2008; O'Connell et al., 2011). They have been used to monitor species distributions (González-Esteban et al., 2004), to make species inventories (Silveira et al., 2003; Srbek-Araujo and Chiarello, 2005; Trolle and Kéry, 2005), to compare the relative abundance of a species under different ecological conditions (Di Bitetti et al., 2008a, 2008b), to compare the relative abundance of different species (Kelly and Holub, 2008), to describe and compare daily or seasonal patterns of activity (van Schaik and Griffiths, 1996; Di Bitetti et al. 2006, 2008b; Bridges and Noss, 2011), and to estimate the absolute abundance of mammal species for which individual identification is possible (Karanth, 1995; Karanth and Nichols, 1998; Silver et al., 2004; Kelly et al., 2008) or for species for which it is not (Rowcliffe et al., 2008, 2011).

Very often the frequency of records of a species (or its recording rate) is used as an index of relative abundance. However, the use of relative abundance indices to compare populations across space and time has been a contentious issue in ecological and wildlife research (Nichols and Karanth, 2002; O'Brien, 2011; Sollmann et al., 2013). The detection probability (p) of a species is dependent on many different factors, among which the location of the cameras can have a strong influence (Weckel et al., 2006). Camera trap studies that use the frequency of records or the recording rate to compare the relative abundance of a species among sites (e.g., site 1 vs. site 2) have made the assumption that p is the same among sites: $p_1 = p_2 = p$. However, if the assumption does not hold true, and $p_1 \neq p_2$, then the frequency of records of a species will be a biased estimator of relative abundance when detection probability is not the same among places. The expected value of p could be influenced by several factors that may vary from site to site and this may preclude the use of the frequency of camera trap records (or recording rate) as an index of relative abundance (Tobler et al., 2008; Sollmann et al., 2013).

Potential biases in detection probability can also be important when using camera traps for density estimation. For example, Rowcliffe et al. (2008) proposed a random encounter model (REM) that could be used to estimate animal densities without the need to identify individuals. This model requires, among other variables, an unbiased estimate of the recording rate of the species. This model also requires both a completely randomized survey design and animals not biasing their movements in relation to camera trap locations. If these assumptions are not met, density estimates could be biased.

Several mammal species use specified pathways to move across their habitat, usually using animal-made trails or human-made dirt roads or paths (Weckel et al., 2006). Even in species that do not use trails, random walk models rarely depict their daily movements (Hirsch et al., 2013). Thus, studies aimed at quantifying mammal abundance or at getting descriptions of mammal assemblages should be very careful of where to place surveying stations in order to avoid important biases. However, in most camera trap studies stations are not placed randomly in the forest, but rather along dirt roads, human-made trails or animals paths in order to increase the probability of recording animals (Carbone et al., 2001), which may preclude using data from these surveys to derive unbiased descriptions of the mammal assemblages.

A better understanding of the factors that affect the recording probability in camera trap studies will contribute to knowing whether important biases preclude the use of camera trap records as an index of relative abundance (Nichols and Karanth, 2002) or to estimate density following a REM (Rovero and Marshall, 2009). It will also help improve survey design to estimate density (Royle and Gardner, 2011), occupancy (MacKenzie et al., 2005; MacKenzie and Royle, 2005) or to describe mammal assemblages and their diversity (Tobler et al., 2008; Ahumada et al., 2011). A recent study suggests that placing camera-trap stations on trails vs. off trails does not produce important biases in the mammal assemblages recorded in a tropical forest of Ecuador (Blake and Mosquera, 2014). Our study evaluates whether this is more generally the case.

MATERIALS AND METHODS

This study was carried out at Iguazú National Park, Misiones province, Argentina (approximately 25° 66' S, 54° 30' W). Iguazú National Park is one of the best wildlife habitats of the Upper Paraná Atlantic Forest ecoregion (Di Bitetti et al., 2003). The study site has a humid subtropical climate with a mean annual precipitation of 1900-2000 mm and no marked dry season. The Iguazú National Park contains the complete assemblage of native mammals of this ecoregion (Crespo, 1982).

To assess whether different mammal assemblages are recorded by camera trap stations located on dirt roads and by those located off roads we conducted a relatively short (39 days) camera-trap survey at Iguazú National Park between June 18 and July 26, 2008. We placed seven pairs of camera-trap stations along two rarely used (< 1 vehicle per day), relatively narrow (about 5-m wide) and not-open-to-the-public dirt roads (from now on "roads"). Each pair of stations was separated by a distance of > 1 km from the next nearest pair. All camera traps were the same model (Leaf River® Trail Scan Model C-1). One of the camera traps of the pair was placed on one side of the road (pointing to the middle of the road) and the other one was placed inside the forest at a perpendicular distance of about 50 m from the other camera trap. The area right in front of the camera located inside the forest was cleared with a machete, but we took special care to not open a path that leads to this camera (to avoid facilitating animal movement to the camera-trap location).

Not all the cameras were active for the same amount of time, because of battery failure, but mean effort (± SE) between treatments were not statistically significant (road: 25.43 ± 3.45 days; off road: 27.71 ± 3.45 days, $F_{1,12} = 0.219$, $P = 0.648$). In this study successive pictures of a species were considered independent records only if one hour or more had passed between them.

For each species we estimated the frequency of stations on roads with presence of the species (+1) to the frequency of stations off roads with its presence (+1). For example, if a species was recorded at three on-road stations and at no off-road station, its "On-road/off-road Index" will be = 3+1/0+1 = 4. Increasing values of this "On-road/off-road Index" indicate an increasing tendency for a species to be more frequently recorded at stations located on roads than at those off roads.

From the photographic records obtained during an intensive camera-trap survey (48 stations, 2268 camera trap days) we conducted at Iguazú National Park of Argentina during 2006-2007 (see Di Bitetti et al., 2008a, 2008b; Paviolo et al., 2008, 2009 for details) we developed a simple index that describes the tendency of a species to walk along dirt roads and trails ("Road-use Index"). To develop this index we assessed for each independent photograph whether the animal was recorded walking along the road and thus following a line parallel to the road or trail (we recorded this instance as 1) or moving perpendicularly or diagonally to the road/trail (0). From these records we estimated, for each species, in what proportion of the pictures the individuals were walking along the road or trail instead of crossing it. At one extreme, species with a Road-use Index close to 1 would tend to move almost exclusively along trails or roads, and species with values close to 0 are those that would avoid walking along trails or whose movements are independent of the presence of human-made trails or roads.

To test the hypothesis that the Road-use Index measures the tendency of a species to walk along dirt roads or trails we correlated (Pearson correlation) the natural logarithm of the On-road/off-road

Index with the Road-use Index. Harmsen et al. (2010) described the tendency of the species to follow trails as opposed to cross them using footprints recorded along trails in a tropical forest of Belize. Since most species in Harmsen et al.'s (2010) study are shared with our study, we also correlated our Road-use Index with the percentage of footprints that followed trails in Belize for the shared species for which they recorded > 6 footprint sets. For these one-tailed statistical tests we set an alpha probability level of 0.05 to commit a type I error.

We used the Wilcoxon rank sums test to compare the species richness recorded at on-road vs. off-road camera-trap stations. Since species richness may be affected by sampling rate (detectability), we further used program SPADE (Chao and Shen, 2010) to estimate the species richness recorded on roads vs. off roads using incidence counts for multiple samples and thus controlling for the potential effect of detectability. Estimates based on these non-parametric methods, especially those obtained with the Jackknife model, perform better than those based on species accumulation curves (Tobler et al., 2008). We provide estimates obtained with the first order Jackknife model (Burnham and Overton, 1978).

Estimates of species richness provide no information on species identity and relative abundance. Thus, to compare the mammal assemblages recorded at stations located on roads vs. those located off roads we conducted a multivariate ANOVA based on dissimilarities (ADONIS; Oksanen, 2013) and an analysis of similarity (ANOSIM; Quinn and Keough, 2002) to test whether stations located on roads differ from those located off roads based on their species composition. For these analyses we used the frequency of records of the eight species of mammals recorded at ≥ 4 camera-trap stations and the Bray-Curtis dissimilarity index. The ADONIS F statistic, the ANOSIM R statistic, and their probability values were estimated based on 99 999 permutations. These analyses were conducted with R (R Development Core Team, 2012) using package vegan (Oksanen et al., 2012; Oksanen, 2013). For these two-tailed statistical tests we also set an alpha probability level of 0.05 to commit a type I error.

RESULTS

During the survey we obtained 228 independent records of 15 species of medium-large sized terrestrial mammals (**Table 1**). The camera trap recording rate of mammals was four times higher on stations located on roads (1.06 records per day, SD = 0.57) than on those located off roads (0.24 records per day, SD = 0.13, Wilcoxon rank sums test, $\chi^2 = 8.265$, DF = 1, P = 0.004). Recording rates of camera trap pair presented no statistically significant correlations (r = 0.585, N = 7, P = 0.084).

Fifteen species were recorded on roads but only ten of these were recorded off roads. Most mammal species were recorded at more stations and had a higher frequency of records at camera-trap stations located on roads than at those located off them (**Table 1**). Species richness between pairs of camera traps presented no statistically significant correlations (r = 0.406, N = 7, P = 0.183). Camera traps located on roads tended to record a higher richness of mammal species (mean = 6.43 species, SD = 2.99, range: 2-10 species) than those located off roads (mean = 3.14 species, SD = 1.86, range: 1-7 species, Wilcoxon rank sums test, $\chi^2 = 3.607$, DF = 1, P = 0.058). Estimates of species richness (1st order Jackknife) for locations on roads tended to be higher than for off-road ones (19.3 species, SE = 2.8 vs. 14.3 species, SE = 2.8), but 95% confidence intervals overlap considerably (on roads: 16.3-28.9 species, off roads: 11.3-23.9 species).

Species with higher tendencies to move along roads or trails in 2006-2007 (with a high Road-use Index) also have high On-road/off-road Index values in 2008 (**Fig. 1**, r = 0.671, N = 15, P = 0.003). The species with a higher tendency to follow trails in Belize also had a higher Road-use Index in Misiones (**Fig. 2**, r = 0.912, N = 8, P < 0.001). Felids have, in general (the margay seems to be an exception), a higher Road-use Index (mean = 0.74, SD = 0.19, N = 6) than other species (mean = 0.58, SD = 0.17, N = 16, species with < 10 records were excluded, Wilcoxon rank sums test, $\chi^2 = 4.571$, DF = 1, P = 0.033), suggesting a higher tendency to follow dirt roads and trails. Most herbivores (e.g., brocket deer, agouti, paca) and omnivores (e.g. coati, tayra, armadillo) do not seem to have a high tendency to follow trails.

The ADONIS indicates that the mammal assemblage recorded at camera-trap stations located on roads was statistically dissimilar to that surveyed at stations located off roads ($F_{1,12} = 3.7121$, P = 0.00368). A similar result

Table 1

Number of stations where each species was recorded and total frequency of records obtained at seven pairs of camera-trap stations located in Iguazú National Park, Argentina, in 2008. At each of the 7 pairs of stations, the on-road camera trap was located on a narrow dirt road and the off-road camera was located 50 m inside the forest. Species are ordered by decreasing Road-use Index[4].

Common name	Scientific name	N stat.[1] on roads	N stat.[1] off roads	Freq.[2] on roads	Freq.[2] off roads	On-road/off-road Index[3]	Road-use Index[4]
Puma	*Puma concolor*	3	1	6	1	2.00	0.88
Ocelot	*Leopardus pardalis*	7	1	31	1	4.00	0.84
Oncilla	*Leopardus tigrinus*	1	0	1	0	2.00	0.84
Jaguar	*Panthera onca*	5	0	9	0	6.00	0.79
Crab-eating fox	*Cerdocyon thous*	2	0	2	0	3.00	0.72
Jaguarundi	*Puma yagouaroundi*	2	0	2	0	3.00	0.69
Tapir	*Tapirus terrestris*	4	3	20	5	1.25	0.68
Brazilian rabbit	*Sylvilagus brasiliensis*	4	2	29	2	1.67	0.65
Red brocket	*Mazama americana*	5	4	21	13	1.20	0.65
Dwarf brocket	*Mazama nana*	1	1	1	1	1.00	0.53
Agouti	*Dasyprocta azarae*	6	6	55	16	1.00	0.52
Armadillo	*Dasypus novemcinctus*	1	1	4	1	1.00	0.51
Collared peccary	*Tayassu tajacu*	1	0	1	0	2.00	0.48
Paca	*Cuniculus paca*	1	1	1	1	1.00	0.36
Coati	*Nasua nasua*	2	2	2	2	1.00	0.16

[1] Number of stations where the species was recorded; [2] Absolute frequency of independent records of the species; [3] On-road/off-road Index, this index is estimated as the frequency of camera trap stations located on roads with presence of the species + 1 / the frequency of stations located off roads with presence of the species + 1; [4] Road-use Index, this index was measured as the frequency of pictures obtained from the flank of the animal (the animal was following the road, at a 90° angle to the aim of the camera trap) to those obtained in other positions (crossing the road) during a camera-trap survey conducted in 2006-2007 at Iguazú National Park. During this survey two camera traps were placed at each station facing each other at both sides of trails or unpaved roads.

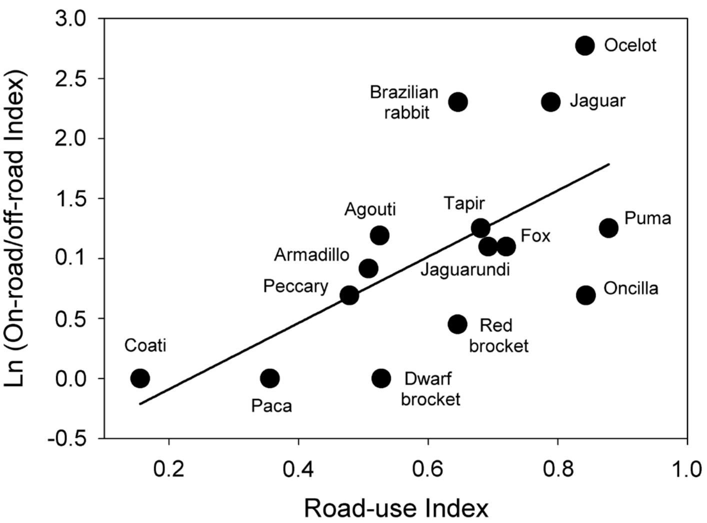

Fig. 1. Relationship between the Road-use Index and the Ln of the On-road/off-road Index (see **Table 1** and text for definition). The line represents the least squares regression line. Data are from **Table 1**.

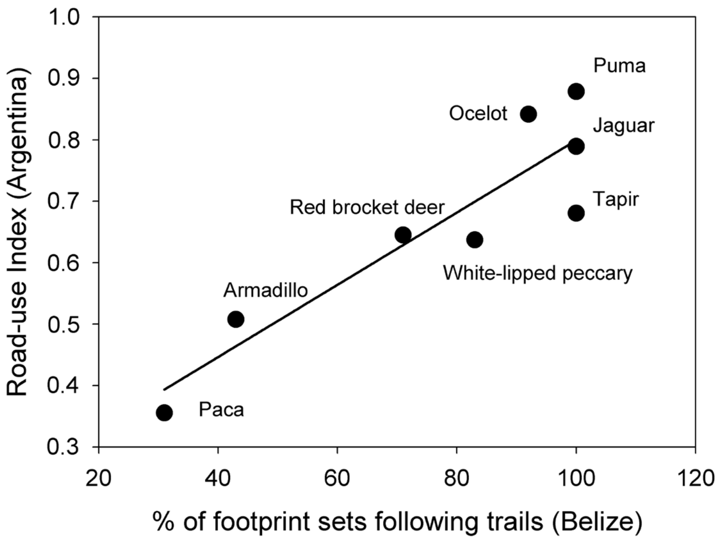

Fig. 2. Relationship between the percentage of sets of tracks following trails in a tropical forest of Belize and the Road-use Index (see **Table 1** and text for definition) in the Atlantic Forest of Argentina. Data from Belize are from Harmsen et al. (2010) and we only included species with a relatively large sample size of records (N > 6). The line represents the least squares regression line.

was obtained with the ANOSIM (R = 0.4266, P = 0.00459), further suggesting that the difference between the mammal assemblages recorded at camera-trap stations placed on roads and at those located off them was much higher than the mean dissimilarities observed among camera-trap stations within each of these two treatments.

DISCUSSION

In the Atlantic Forest of Iguazú National Park, camera-trap stations located on dirt roads had a much higher recording rate of terrestrial mammals and they recorded more species than stations located off roads. The mammal species recorded have different relative probabilities of being recorded on roads vs. off road, something that is easily captured by a simple index that describes the proportion of stations on roads that recorded a certain species to the proportion of stations off roads that recorded the same species. We further showed that this simple index is correlated with the independently-obtained Road-use Index that depicts the tendency of the species to walk along dirt roads or trails instead of crossing them. The latter index can be easily estimated from camera trap studies where stations are located on roads or trails, which is usually the case (Blake and Mosquera, 2014). We also showed that the tendency of the Neotropical mammal species to follow dirt roads or trails is maintained across their distributional range, since similar patterns are observed in the Atlantic Forest of South America and the tropical forests of Belize. As a consequence of the differential tendency of the Neotropical mammals to walk along trails or narrow roads instead of wandering through the forest, the mammal assemblage recorded at stations located on roads differed from that recorded at stations located off roads.

Camera-trap recording rates of some mammal species (e.g., tigers, Carbone et al., 2001) are much higher than those expected under a random sampling protocol, because researchers try to optimize this variable by placing camera traps in locations with a higher recording probability (e.g., along trails). Several species, in particular of large mammals, will use pathways and funnels that facilitate their movement, especially if the forest understory is very dense, as is the case in most secondary forests (several species, Harmsen et al., 2010) or dense bamboo forests (Cruz, 2012). In Belize, jaguars and tapirs (*Tapirus bairdii*) were exclusively photographed on human-made trails or tapir-made trails but never on small mammal trails or in the forest. Pacas (*Cuniculus paca*), nine-banded armadillos (*Dasypus novemcinctus*) and opossums (*Didelphis marsupialis*) showed the exact opposite pattern and their photographic recording rates increased with the distance to human-made trails and roads (Weckel et al., 2006). In Barro Colorado Island, Panamá (BCI), ocelots were much more frequently recorded at camera trap stations located on trails than at those located in random locations, while collared peccaries and brocket deer showed the opposite pattern (Kays et al., 2011). In the Atlantic Forest of Misiones, Argentina, jaguars, pumas, ocelots and jaguarundis (*Puma yagouaroundi*) have higher photographic recording probability at stations located on infrequently used unpaved roads than on narrow trails recently opened with machete (Di Bitetti et al., 2010); tapirs showed the opposite pattern (Cruz, 2012). In Belize, even though the camera trap photographic rates of jaguars, pumas and ocelots increased with trail width, pumas and jaguars differ in their relative tendencies to use these trails (Harmsen et al., 2010). With some possible exceptions (e.g., the margay), forest cats have a generalized tendency to follow small roads or trails (Karanth and Nichols, 1998, 2002; Weckel et al., 2006; Harmsen et al., 2010; Blake and Mosquera, 2014).

The difference between the mammal assemblages recorded on roads and off roads observed at Iguazú is easily explained by the strong difference in the tendencies of the species to follow small roads or trails. Contrasting with our results, a recent camera-trap study found that in a tropical rain forest of eastern Ecuador the recording rate, the species richness and the species composition recorded on trails did not differ markedly from those recorded on locations off trails. Only a few species of mammals, especially the large cats, were more frequently recorded on trails, but these differences were not large enough to generate differences in the assemblages recorded on trails vs. off trails (Blake and Mosquera, 2014). This contrasting result between study sites may derive from several factors, perhaps most importantly the fact that the paths used in these studies were structurally different. Whereas we placed the camera trap stations along old and rarely used vehicle roads, the trails used in Ecuador where narrower and opened by machete, with much heavier human transit than those at our study site.

A particular species' tendency to use roads and trails may also vary according to the ease of walking in the forest, which may depend in turn on habitat type (e.g., the density of the under-story vegetation), or on the density of potential predators and human hunting pressure (Griffiths and van Schaik, 1993). For example, BCI has a very clean understory, while the Atlantic Forest of Misiones, Argentina, a very dense one. As a consequence, even though ocelots favor roads/trails over off-road locations both in BCI and in Misiones (Kays et al., 2009, 2011; this study), this bias was much higher in Argentina (about 5 times higher than in BCI). The tendency of ocelots to follow trails may even change with the lunar cycle (Emmons, 1989; Di Bitetti et al., 2006). Red brocket deer showed a much lower camera trap rate on trails than at random locations in the forest at BCI (Kays et al., 2009, 2011) but not in Misiones (**Table 1**). Habitat type, forest structure, hunting pressure and several other factors may thus interact in unknown ways with the presence and density of roads to affect the relative probability of recording species on roads vs. off roads.

Despite the local or habitat-specific differences in the propensity of a species to use human-made paths, this tendency can be ascertained with a simple Road-use Index (**Fig. 1**). The general tendency of a mammal species to follow small roads, paths or trails seems to be an inherent and relatively constant characteristic, as suggested by the striking similarities found in two widely separated mammal assemblages (**Fig. 2**). The Road-use Index provides information on the tendency of a species to follow roads or trails in their daily movement, and on their relative probability of being recorded at camera trap stations located on roads or trails vs. in random locations. This index may help assess whether placing cameras on roads or trails will bias the recording rate of a species positively or negatively, and therefore how to interpret (and correct) camera trap data on the relative abundance of species, or how to improve survey design.

In conclusion, at most Neotropical locations, placing camera traps on roads/trails or off roads/trails will give different pictures of a mammal assemblage, with Blake and Mosquera's (2014) study site probably a rare exception. This in turn may preclude making unbiased comparisons of mammal assemblages (e.g., Ahumada et al, 2011). The differential tendency of many species to walk along trails means the probability of detecting a species on trails can be several times higher or lower than the probability of detecting a species off trails. Thus, in most comparative studies the frequency of records or the camera trap recording rate cannot be used as indices of relative abundance (see Sollmann et al., 2013 for an in-depth discussion on this issue). Our results also put into question whether density estimates based on random encounter models (e.g., Rowcliffe et al., 2008, 2011) can be generally used in camera-trap studies (but see Rovero and Marshall, 2009). Not only it may be unfeasible for logistic reasons, but we would argue that a completely randomized survey design to describe mammal assemblages may not provide an unbiased description of the mammal assemblage if a dense system of roads and trails is present. The density and characteristics of human-made or animal-made paths available at a certain location will interact with the tendency of the animals to move along them (or to avoid them) and will necessarily affect the relative proportion of records of the different species obtained at random locations (assuming that, by chance alone, in a pure and completely randomized surveying scheme >99% of camera traps will not be placed facing a road or a trail). We concur with Blake and Mosquera (2014) that surveys should use a combination of trail and off-trail camera-trap stations to provide a better description of the species composition and relative abundance of the mammal assemblage of a given location.

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