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Artículo

CAMERA TRAPPING ON AND OFF TRAILS IN LOWLAND FOREST OF EASTERN ECUADOR: DOES LOCATION MATTER?

John G. Blake[1] and Diego Mosquera[2]

[1] Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, PO Box 110430, University of Florida, Gainesville, Florida, 32611, USA [correspondence: John G. Blake <john.blake@ufl.edu>].

[2] Estación de Biodiversidad Tiputini, Universidad San Francisco de Quito, P.O. Box 17-1200-841, Quito, Ecuador.

ABSTRACT. Camera traps are increasingly important in studies of mammals throughout the world. Typically, cameras are placed along trails or other travel routes. Yet, species composition and photographic rate may differ between cameras set along trails and those set off trails. We tested this idea in eastern Ecuador. Pairs of cameras were placed at 10 locations along narrow (< 1 m wide) trails in lowland forest and approximately 50 m away from trail sites in adjacent forest. Excluding people, there was little difference in total number of records between trail (333 photographs, 506 trap days) and off-trail sites (306 photographs, 509 trap days). Capture rates varied among locations (11 to 148/100 trap days on trails; 19 to 217/100 trap days off trails) and were not correlated between pairs of cameras on and off trails ($r = 0.37$, $P = 0.29$). People were only photographed along trails but capture rates of other species on trails were not correlated with numbers of people photographed at the same site ($r = -0.10$, $P > 0.75$). Twenty-three species were photographed, including 21 on trails and 22 off trails; *Panthera onca* was only photographed along trails whereas *Tinamus major* and *Priodontes maximus* were only photographed off trails. Species accumulation curves were similar for both sets of cameras; in both cases, curves approached an asymptote after about 200 records. Latency to first detection (LTD) varied from < 1 day (e.g., *Mazama americana* in trail and off-trail cameras) to 294 days (*Procyon cancrivorus* in on-trail cameras). Overall, LTD values were correlated between pairs of cameras on and off trails ($r_s = 0.66$, $P < 0.01$); means did not differ between cameras on and off trails. Species composition varied among trap locations but trail and off-trail cameras did not form distinct groups based on species composition.

RESUMEN. Trampeo con cámaras dentro y fuera de senderos en bosques bajos del este de Ecuador: ¿importa la ubicación? Las cámaras trampa son cada vez más importantes en el estudio de mamíferos alrededor del mundo. Comúnmente, se establecen a lo largo de senderos u otras rutas de viaje. Sin embargo, la composición de especies y tasas de captura fotográfica pueden diferir entre cámaras establecidas dentro y fuera de senderos. Probamos esta idea en el oriente de Ecuador. Pares de cámaras trampa fueron colocadas en 10 lugares a lo largo de senderos angostos (<1 m) en un bosque bajo y a aproximadamente 50 metros lejos de senderos en lugares adyacentes al bosque. Excluyendo personas, hubo poca diferencia en el número de registros entre cámaras en senderos (333 fotografías, 506 días-trampa) y fuera de ellos (306 fotografías, 509 días-trampa). Las tasas de captura variaron entre locaciones (11 a 148/100 días-trampa en senderos; 19 a 217/100 días-trampa fuera de ellos) y no existió correlación entre cámaras dentro y fuera de senderos ($r = 0.37$, $P = 0.29$). Las personas fueron fotografiadas únicamente en senderos pero las tasas de captura de otras especies en senderos no se correlacionaron con el número de personas fotografiadas en el mismo lugar ($r = -0.10$, $P > 0.75$). Veintitrés especies fueron fotografiadas, incluyendo 21 en senderos y 22 fuera de ellos. *Panthera onca* fue fotografiada solo en senderos mientras que *Tinamus major* y *Priodontes maximus* fueron fotografiados solo fuera de ellos. Las curvas de acumulación de especies fueron similares para ambos grupos de cámaras; en ambos casos, las curvas se acercaron a una asíntota después de cerca de 200 registros. La latencia de primera detección (LPD)

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varió desde < 1 día (e.g., *Mazama americana* en cámaras dentro y fuera de senderos) hasta 294 días (*Procyon cancrivorus* en cámaras en senderos). En general, los valores de LPD tuvieron correlación entre pares de cámaras dentro y fuera de senderos ($r_s = 0.66$, $P < 0.01$); las medias no difirieron entre cámaras dentro y fuera de senderos. La composición de especies varió en lugares de trampeo pero las cámaras dentro y fuera de senderos no formaron grupos diferenciados basados en la composición de especies.

Key words: Activity. Mammals. Photographic rate. Tropical forests. Yasuní.

Palabras clave: Actividad. Bosques tropicales. Mamíferos. Tasa de captura fotográfica. Yasuní.

INTRODUCTION

Camera traps have become a relatively common tool in many wildlife studies (O'Connell et al., 2011) and have been used, for example, to determine daily activity patterns (Lizcano and Cavelier, 2000; Gómez et al., 2005; Blake et al., 2011, 2012) and use of specific habitats, such as mineral licks (Matsubayashi et al., 2007; Tobler et al., 2009; Blake et al., 2010, 2011, 2013), as well as for more general community-level studies (Kasper et al. 2007; Tobler et al., 2008). Use of camera traps received an impetus from studies on tigers (*Panthera tigris*) that used individually recognizable coat patterns in capture-recapture analyses to estimate population densities (Karanth and Nichols, 1998; Karanth et al., 2004, 2006). Similar studies have been conducted on jaguars (*Panthera onca*; Kelly, 2003; Silveira et al., 2003; Wallace et al., 2003), ocelots (*Leopardus pardalis*; Trolle and Kéry, 2003, 2005; Di Bitetti et al., 2006; Maffei and Noss, 2007), and others (puma *Puma concolor*; Kelly et al., 2008; giant armadillo *Priodontes maximus* Noss et al., 2004; South American tapir *Tapirus terrestris*, Trolle et al., 2008; maned wolf *Chrysocyon brachyurus*, Trolle et al., 2007).

Most studies, particularly those that seek to estimate densities with capture-recapture analyses, place cameras along travel routes used by animals (e.g., roads, trails used by people, animal trails, or newly opened transects in forest; Kelly, 2003; Silveira et al., 2003; Wallace et al., 2003; Maffei et al., 2004; Karanth et al., 2006; Di Bitetti et al., 2006, 2008; Kelly et al., 2008; Blake et al., 2012) to increase the likelihood of capturing photographs of target species. Such a placement may be justified by the low densities typical of many species, such as jaguars (Maffei et al., 2011; Tobler et al., 2013), and the need to obtain sufficient number of captures and recaptures to estimate densities.

Despite the near universal recommendation that traps be placed in areas likely to be visited by animals, there have been few attempts to determine whether results from cameras placed along trails (hereafter, "trail" is used to indicate any kind of opened travel route, be it a dirt road, man-made trail, animal trail, or transect) differ from results obtained from cameras not placed along such travel routes (Harmsen et al., 2010; Sollmann et al., 2011). Yet, for studies that seek to understand community composition or daily and hourly activity patterns of animals, it is important to know whether results from trails are representative of areas away from trails as well. Species differ in their tendency to use trails as travel routes (Weckel et al., 2006; Harmsen et al., 2010) so that analyses based solely on trail-based cameras may provide an incomplete picture of community composition. Estimates of relative abundance may vary depending on camera location as well (Harmsen et al., 2010), particularly if animals actively avoid trails, perhaps to reduce probabilities of encounters with predators or humans (Weckel et al., 2006; Harmsen et al., 2010).

Our previous studies with camera traps in lowland wet forest of eastern Ecuador have been based on cameras placed along relatively narrow (~1 m) trails in forest (Blake et al., 2012) or at mineral licks (Blake et al., 2010, 2011, 2013). Here, we compare results from camera traps placed along trails to those placed away from trails in adjacent forest. We expected that some species, particularly cats, would be photographed more often along trails but that other species, such as peccaries (*Tayassu pecari*, *Pecari tajacu*) and deer (*Mazama americana*), that move widely through forest habitats (personal observations) as well as along trails, would not show a difference in number of photographs from cameras located on and away from trails. Animals might be more common on trails because they provide easier travel routes; alternatively, animals might avoid trails that experience high levels of human activity. Thus, we also expected fewer photographs at trail camera locations where humans were frequently photographed.

METHODS

Study site

We conducted our research at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador (~0º37’ S, 76º10’ W, 190-270 m asl). TBS was founded in 1994 by the Universidad San Francisco de Quito (USFQ) on a tract of undisturbed lowland rainforest within the ~2.7-million ha Yasuní Biosphere Reserve (Ministerio del Ambiente del Ecuador, 2010). The station and nearby areas contain a variety of habitats including terra firme and várzea forest, palm swamps and other wetlands, as well as areas of natural succession that follow tree falls, wind throws, or other natural disturbances. Understory vegetation is typically fairly thick (personal observations), so that trails provide travel routes for many species. The mean annual precipitation at Yasuní Research Station, approximately 30 km WSW of TBS, is about 3100 mm (Blake et al., 2012). Rainiest months are from April through June; January and August can be relatively dry.

Camera trapping

Pairs of cameras, triggered by an infrared heat-and-motion detector (Reconyx PC800 Hyperfire Professional IR™ and PC850 Hyperfire Pro White Flash™; Reconyx, Inc., Holmen, Wisconsin, USA), were deployed at 10 locations along preexisting trails (typically <1 m wide) and away from trails in adjacent forest (i.e., 20 cameras in total) for eight weeks (24 January - 21 March 2013) (**Fig. 1**); trails were initially established in the 1990’s and have been maintained since then. Pairs of trail and off-trail cameras were always the same model (2 pairs were IR; 8 pairs were white flash). Trap sites along trails were located approximately 500 to 800 m apart (straight line distance; 650 to 1050 m apart along trails); off-trail cameras were 40 to 60 m away from the trail. For the latter, we randomly selected a side of the trail and walked approximately 50 m into the forest. We did not place off-trail cameras in recent tree fall areas, along streams, in swampy areas, along obvious travel routes, or in other habitats that differed from that along the trail. For example, we did not place any cameras along trails on ridge-tops as off-trail cameras would have been located on much steeper slopes. Cameras were set approximately 0.75 m off the ground; cameras along trails were set back from the trail approximately 2 to 3 m. Vegetation was cleared for a few meters in front of each camera but was not otherwise disturbed. Thus, pairs of cameras were in the same type of habitat, had the same amount of vegetation cleared in front of each camera, and were set at the same height. Consequently, we made the assumption that detection probabilities would be the same if an individual of the same species crossed in front of a trail or an off-trail camera. We set cameras to take five photographs in succession, with a 1-sec delay between photographs,

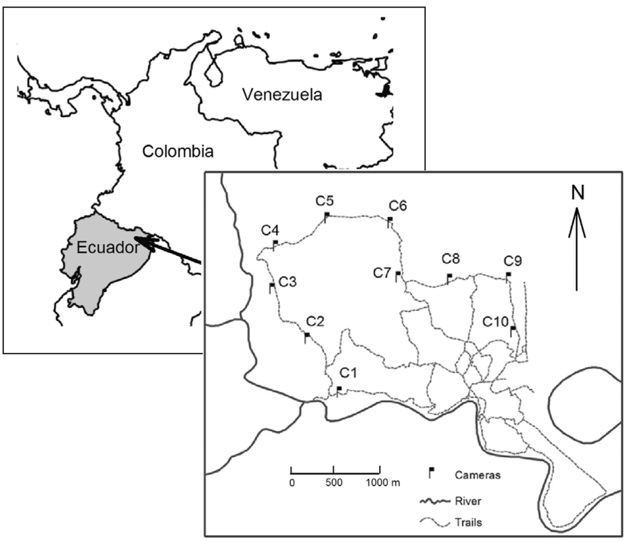

Fig. 1. Schematic of the trail systems and camera trap locations at Tiputini Biodiversity Station, Ecuador. Each camera location represents a pair of cameras, one on the trail and one approximately 50 m away from the trail.

and a minimum time between sets of photographs of 5 min. Date and time were automatically stamped on each photograph. All images were labeled with location, camera, date, time, and species.

Analyses

We summarized images by species, hour, and date. We classified photographs as belonging to independent records if more than 30 min had elapsed between consecutive photographs of the same species at a given location (see Blake et al., 2011). Activity was evaluated in terms of number of photographs, percentage of photographs or photographs/100 trap-days, depending on the analysis. We do not attempt to estimate densities but rather use photographs as an index of relative activity, acknowledging that photographic rates may be subject to a number of biases (Sollmann et al., 2013; but see Kays et al., 2011). We calculated the number of trap-days from the time the camera was placed in operation to the time it was taken down or until some problem occurred. One camera was opened by a white-lipped peccary (*Tayassu pecari*); one camera did not function for the first half of the study; and in one case the batteries died early. We classified records by two hour blocks, starting at midnight, to examine hourly patterns of activity. Photographs were categorized by trap site to allow comparison of spatial distribution patterns of species and capture rates.

When appropriate, we used a paired *t*-test to compare photographic rates between trail and off-trail cameras. We also used correlation analyses (Pearson's *r*) to examine relationships between capture rates of pairs of cameras and to determine if number of photographs from trail cameras was related to number of people photographed at the same site. We used Fisher Exact Tests to determine if the number of cameras at which a species was recorded differed between trail or off-trail locations. We determined latency to first detection (LTD; Foresman and Pearson, 1998; Barea-Azcón et al., 2007) for species recorded by trail and off-trail cameras and used a Wilcoxon Signed Ranks Test to determine if LTD differed consistently between sets of cameras. We used correlation analysis (Spearman's r_s) to examine the relationship between LTD values for the two sets of cameras. Further, we constructed species accumulation curves (number of species against number of records) for trail and off-trail cameras and used linear regression on ln-transformed data to compare the slopes. We used a chi-square contingency table test to compare hourly activity patterns between trail and off-trail cameras based on numbers of photographs by two hour blocks, all species combined. We used non metric multidimensional scaling (NMS) with the Bray-Curtis distance measure to graphically portray the composition of species photographed along trails versus off trails. Photographic rates were relativized (by species) prior to the analysis (McCune and Grace, 2002). NMS was followed by an analysis of similarity (ANOSIM; Bray-Curtis similarity, standardized photographic rate) to determine if species composition differed between on and off-trail cameras. NMS was performed with PC-ORD Version 6.12 (McCune and Mefford, 2011); ANOSIM was run with PRIMER Version 6.1.11 (PRIMER-E, 2008). Other analyses were run with STATISTIX Version 10 (Analytical Software, 2013). Nonparametric tests were used when data did not meet the assumptions of parametric tests but did meet those of nonparametric tests. In all cases, statistical tests were applied only when appropriate (i.e., when results were not obvious; Cherry 1998, Johnson, 1999).

RESULTS

Overall patterns

Excluding people, we obtained 639 independent records (photos of the same species separated by at least 30 min at the same site) representing 23 species (four bird species; 19 mammals) (**Table 1**); 333 were from cameras along trails (506 trap days) and 306 from cameras located away from trails (509 trap days). An additional 139 independent photos of people also were recorded, all from cameras along trails. Overall photographic rate (excluding people) did not differ between cameras located on trails (mean/100 trap days = 65.1 ± 12.75 se) and those away from trails (64.5 ± 18.02). Photographic rate varied among locations both on (11 to 148/100 trap days) and off (19 to 217/100 trap days) trails but capture rates between pairs of cameras on and off trails were not correlated ($r = 0.37$, $p = 0.29$). Capture rate for people was 26.4/100 trap days (range from 0 to 102/100 trap days) but capture rate of other species was not correlated with capture rate of people ($r = -0.10$, $p > 0.75$). Species accumulation curves were similar for trail and off-trail cameras (**Fig. 2**; linear regression on ln-transformed data: $R^2 = 0.96$, slope = 0.52 ± 0.02 se for on-trail cameras; $R^2 = 0.92$, slope = 0.54 ± 0.03 for

Table 1

Number of cameras at which a species was photographed and number of independent photographs (i.e., photographs at a given camera separated by at least 30 min) of that species from cameras located along trails (On) and away from trails (Off) at Tiputini Biodiversity Station, January - March 2013. Latency, or time to first photograph (in trap-days), is shown for each species. Nomenclature for mammals follows Wilson and Reeder (2005).

Scientific name	Common name	Locations		Photograph		Latency	
		On	Off	On	Off	On	Off
Birds							
Mitu salvini	Salvin's curassow	6	3	7	6	<1	1
Penelope jaquacu	Spix's guan	3	2	6	2	16	10
Psophia crepitans	gray-winged trumpeter	10	8	42	29	2	1
Tinamus major	great tinamou	0	2	0	5		8
Mammals							
Myrmecophaga tridactyla	giant anteater	1	2	1	2	10	3
Dasypus novemcinctus	nine-banded armadillo	3	5	28	10	4	15
Priodontes maximus	giant armadillo	0	2	0	2		15
Atelocynus microtis	short-eared dog	2	4	2	7	28	1
Procyon cancrivorus	crab-eating raccoon	1	1	1	1	294	33
Nasua nasua	South American coati	2	2	3	2	7	4
Eira barbara	tayra	3	1	9	1	24	24
Leopardus pardalis	ocelot	4	2	9	2	11	15
Puma concolor	puma	1	1	2	1	3	20
Panthera onca	jaguar	4	0	4	0	5	
Tapirus terrestris	South American tapir	3	4	6	11	1	2
Pecari tajacu	collared peccary	9	8	23	47	4	2
Tayassu pecari	white-lipped peccary	8	9	29	33	2	2
Mazama americana	red brocket deer	9	10	63	81	<1	<1
Mazama gouazoubira	grey brocket deer	1	1	1	1	6	35
Sciurus igniventris	northern Amazon red squirrel	4	5	9	5	7	23
Cuniculus paca	paca	3	5	12	14	6	7
Dasyprocta fuliginosa	black agouti	7	5	50	14	1	<1
Myoprocta pratti	green acouchy	5	7	25	28	<1	<1

off-trail cameras). In both cases, rate of species accumulation had started to level off by about 200 records. Hourly activity (number of photographs) was greater during the daylight hours for cameras on and off trails (**Fig. 3**) but activity was higher along trails during the mid-morning period and off trails during late afternoon and early evening ($\chi^2 = 21.3$, df = 11, $p < 0.05$).

Individual species

Photographs per species varied from 2 to 144 (**Table 1**); 13 species (2 birds, 11 mammals) were photographed at least 10 times. Twenty species were photographed both on and off trails; great tinamou (*Tinamus major*) and giant armadillo were only recorded off trails and jaguars were recorded only on trails. Four spe-

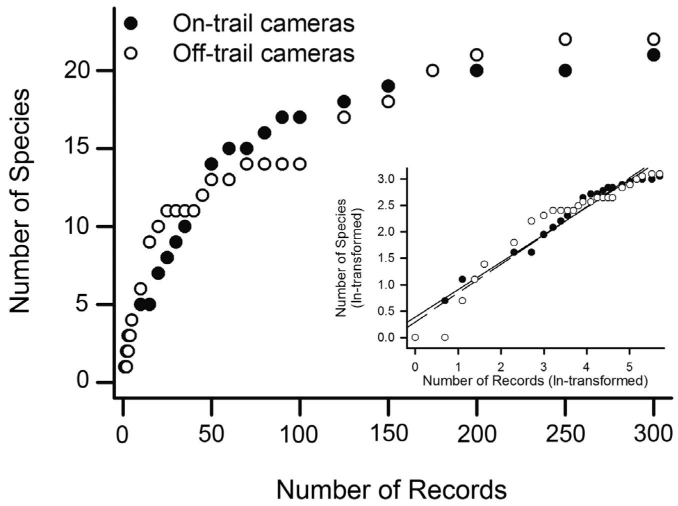

Fig. 2. Species accumulation curves based on number of independent records (see text) for cameras located on trails and off trails at Tiputini Biodiversity Station, Ecuador. In-set shows regression lines for ln-transformed data.

cies (gray-winged trumpeter *Psophia crepitans,* collared peccary *Pecari tajacu,* white-lipped peccary, red brocket deer *Mazama americana*) were recorded at 17 to 19 cameras (**Table 1**), indicating that they were widely distributed both on and off trails. No species showed a significant difference in distribution between number of trail versus off-trail cameras at which it was recorded (Fisher Exact Tests, $p > \sim 0.30$ except jaguar, $p < 0.09$; comparisons based on presence/absence at a camera location). Photographs per species ranged from two (*Priodontes maximus,* crab-eating raccoon *Procyon cancrivorus,* grey brocket deer *Mazama gouazoubira*) to 144 (red brocket deer).

Differences in number of photographs between trail and off-trail sites likely reflected behavior of specific individuals for some species. Nine-banded armadillos (*Dasypus novemcinctus*) were photographed 28 times along trails but 24 were from the same camera; it was recorded at five sites away from trails and three sites along trails. Photographic rate between trail and off-trail sites was correlated for red-brocket deer ($r = 0.90$, $p < 0.001$) and white-lipped peccary ($r = 0.69$, $p < 0.05$) but not for other species.

Latency to first detection (LTD) ranged from less than one day (i.e., recorded on the same day the camera was installed) for four species to 294 days for crab-eating raccoon on trails (**Table 1**). LTD was within the first week for

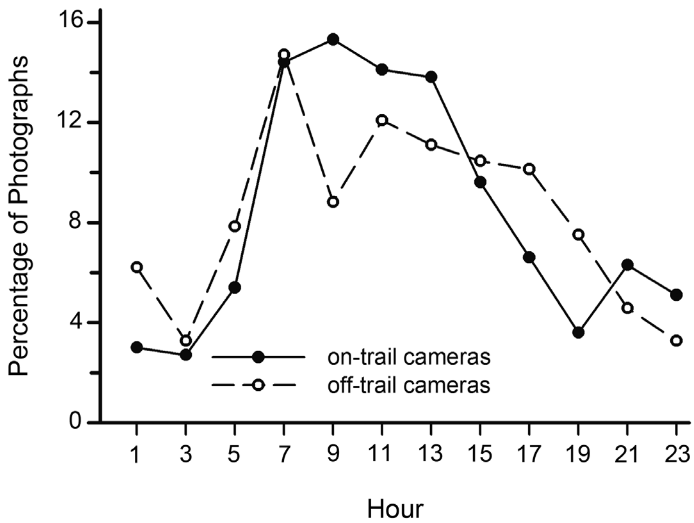

Fig. 3. Hourly activity as measured by percentage of photographs captured by cameras located on narrow (~ 1 m) trails and in adjacent forest at Tiputini Biodiversity Station, Ecuador, January – March 2013. Hours were combined into two hour blocks (e.g., 3 represents photographs taken from 0201 to 0400; 5 represents 0401 to 0600; and so forth).

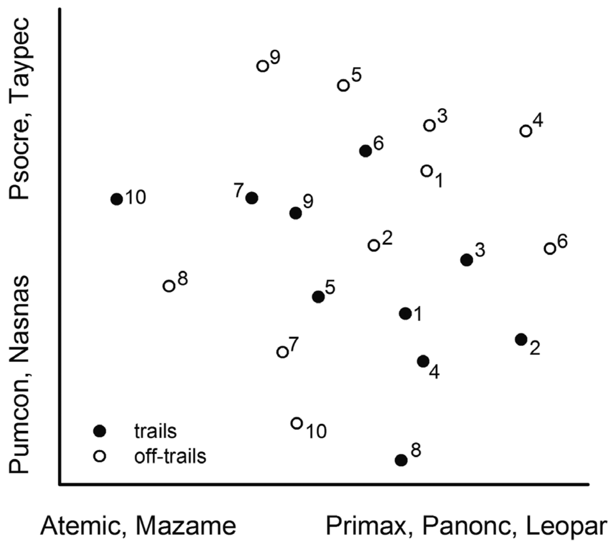

Fig. 4. NMS ordination of trail and off-trail cameras, based on numbers of photographs for individual species, operated at Tiputini Biodiversity Station, 24 January - 21 March 2013. Numbers correspond to the locations in **Fig. 1**. Species most highly correlated (positive or negative) with the first two axes are indicated: Atemic, *Atelocynus microtis*; Leopar, *Leopardus pardalis*; Mazame, *Mazama americana*; Nasnas, *Nasua nasua*; Panonc, *Panthera onca*; Primax, *Priodontes maximus*; Psocre, *Psophia crepitans*; Pumcon, *Puma concolor*; Taypec, *Tayassu pecari.*

15 species on trails and for 12 species off trails. In addition to the raccoon, LTD was >30 days only for grey brocket deer. LTD was less on trails for eight species, less off trails for eight species, and the same for four species (considering species recorded both on and off trails); there was no difference in overall LTD rates on trails compared to off trails (WSRT, W = -17, p = 0.64). LTD per species was correlated between on and off-trail cameras ($r_s = 0.66$, $p < 0.01$, N = 20). Species recorded at only one treatment were excluded from this analysis.

Species composition

Overall species composition did not separate trail from off-trail cameras (**Fig. 4**; ANOSIM, R = -0.035, p = 0.65). Further, pairs of cameras (trail and off-trail) were not more similar to each other than to other sites. Instead, similarities and differences among the 20 sites represented variation in relative abundances of different species that were related to locations of individual cameras, rather than to position relative to trails. For example, the first axis of a NMS ordination described a gradient of sites with greater representation of short-eared dog (*Atelocynus microtis*) and red brocket deer to those with greater representation of giant armadillo, jaguar, and ocelot.

DISCUSSION

Cameras located along trails and those located away from trails did not differ in overall capture rate or in overall species composition. Instead, individual cameras recorded different sets of species but those differences were not related to trails. Similarly, species accumulation rates were basically the same for each set of cameras. Although some species were more commonly photographed along trails and others off trails, the distribution of sites (cameras) at which species were recorded did not differ between cameras on or off trails. Lack of apparent significant difference between trail and off-trail cameras may, for some species, reflect relatively small number of records. Jaguars, for example, were only photographed four times but all were from trails. Similarly, there were six or seven individual ocelots photographed by trail cameras (not all images could be assigned to a specific individual) but only one or two in off-trail cameras. Thus, larger samples sizes might reveal more differences, at least for individually recognizable species. On the other hand, the latency to first detection did not differ consistently between cameras on or off trails; LTD was comparable for many species, and often fairly short (< one week) for both sets of cameras.

Most previous studies that have used camera traps in tropical forests have placed cameras along trails or transects, often because of the assumption that cats, the frequent object of study, are more likely to be encountered along trails. Results of this study support that conclusion; jaguars were only photographed along trails, ocelots were only rarely photographed away from trails, and pumas were photographed twice along trails and once away from trails. In total, cats were recorded 15 times in trail cameras and only three times by off-trail cameras. Other carnivores also may use trails as travel routes as well. For example, tayras (*Eira barbara*) were more commonly encountered along trails. In contrast, short-eared dogs, although often photographed along trails in previous studies at this site (Blake et al., 2012), were more commonly photographed away from trails in this study.

Use of trails (or lack thereof) may be geographically consistent for some but not all species. Cats, including jaguar, puma, and ocelot, were much less common off trails in this study and in Belize (Weckel et al., 2006; Harmsen et al., 2010). Similarly, Sollmann et al. (2011) reported that photographic rate of jaguars was ten times greater along roads than off roads in Cerrado grasslands. On the other hand, Baird's tapirs (*Tapirus bairdii*) were not photographed off trails in one Belize study (Weckel et al., 2006) but were more common off-trails in a second study (Harmsen et al., 2010); South American tapir (*Tapirus terrestris*) was photographed twice as often off trails in the current study. Nine-banded armadillos and pacas (*Cuniculus paca*) were not photographed along man-made trails in Belize (Weckel et al., 2006) but both species were recorded by trail cameras in the present study. Similarly, Weckel et al. (2006) reported that neither species of peccary showed a preference for trails or off-trail sites but Harmsen et al. (2010) did not record white-lipped peccaries off trails; both species were recorded both on and off trails in the current study although the collared peccary was somewhat more common off trails. Thus, whether or not a species differs in likelihood of being photographed along or away from trails may vary among locations, perhaps in relation to differences in habitat, presence of other species, or variation in resource distribution patterns.

Some of the differences in reported use of trails may be related to trail width. Harmsen et al. (2010), for example, found that capture rates of cats were positively correlated with the width of trails, which ranged from about 2 to 8 m in their study; in contrast, captures of red brocket deer were negatively correlated with trail width. In our study, trails were narrow and perhaps did not provide as strong a contrast with surrounding vegetation. Similarly, Tobler et al. (2013) suggested that age of trails also might influence their use by jaguars; presumably, older, more established trails would better facilitate movement. Differences in behavior also might influence patterns of habitat use. Jaguars, for example, are more nocturnal in Belize (Weckel et al., 2006) than in Ecuador (Blake et al., 2012). At our study site, males also were more diurnal than females (Blake et al., unpublished data). Such differences in activity might influence use of trails, particularly if activity patterns of prey differ as well.

Location of camera traps clearly can influence likelihood of capturing different species but that influence may vary among study areas. Thus, conclusions reached in one study might not apply equally well to another site. In this study, the specific location of the camera appeared to have more influence on the species recorded, whether or not that camera was located along a trail or away from the trail. On the other hand, many previous studies only have placed cameras along trails, under the assumption that photographic rates would be higher there than away from trails. Given that photographic rate and rate of species accumulation did not differ between cameras placed on trails or away from trails in this study, it is clear that the assumption of higher encounter rates along trails may not hold in all cases. Instead, it is likely that some combination of trail and off-trail cameras will provide a more complete picture of the species composition and relative abundance of different species in a given location. Determining the proper balance between locations will depend on objectives of the study (e.g., mark-recapture studies of felids likely should continue to rely on trail-based cameras for the most part) as well as specific study area.

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