

Differential Use of Trails by Forest Mammals and the Implications for Camera-Trap Studies: A Case Study from Belize

Bart J. Harmsen^{1,2,4}, Rebecca J. Foster², Scott Silver³, Linde Ostro³, and C. Patrick Doncaster²

¹ Panthera Foundation, 8 West 40th Street, 18th Floor, New York, NY 10018, U.S.A.

² School of Biological Sciences, University of Southampton, Boldrewood Campus, Southampton SO16 7PX, UK

³ Wildlife Conservation Society, Wildlife, 2300 Southern Boulevard, Bronx, NY 10460, U.S.A.

ABSTRACT

Relative abundance indices are often used to compare species abundance between sites. The indices assume that species have similar detection probabilities, or that differences between detection probabilities are known and can be corrected for. Indices often consist of encounter frequencies of footprints, burrows, markings or photo captures along trails or transect lines, but the assumption of equal detection probabilities is rarely validated. This study analyzes detection probabilities of a range of Neotropical mammals on trails in dense secondary forests, using camera-trap and track data. Photo captures of the two large cats, jaguars (*Panthera onca*) and pumas (*Puma concolor*), were correlated solely with trail variables, while photo captures of their potential prey species had no correlation or negative correlation with trail variables. The Neotropical mammals varied greatly in their tendency to follow or cross trails based on footprints surveys. This indicates that camera locations on trails will have varying detection probability for these Neotropical mammals. Even the two similar-sized jaguars and pumas, occupying relatively similar niches, differed subtly in their use of trails. Pumas followed trails more completely while jaguars were more likely to deviate from trails. The ecological significance of these findings is that jaguars seem to be more willing to use the forest matrix away from trails than do pumas. We conclude that trail-based indices, such as photographic captures or tracks along trails, are not appropriate for comparison between Neotropical species, and not even between relatively similar species like jaguars and pumas.

Key words: bias; camera trapping; detection probability; jaguars; pumas; relative abundance; trail use.

ASSESSMENT OF HABITAT OR SITE PREFERENCE between sympatric species is often investigated through comparison of abundance, level of occupancy or density between sites. Absolute abundance measures are often more difficult and costly to obtain than relative values. Researchers may resort to comparisons of relative abundance derived from signs such as footprints, marking sites, burrows, feeding remains, or fecal material, and, more recently, camera-trap photographs. A fundamental assumption of comparisons of relative abundance of signs or camera-trap data is that the detection probabilities of the target species are similar when present (*e.g.*, all species have the same capacity to leave footprints in the substrate). Differences in detection probabilities must be assessed, and if they exist they must be corrected for (Buckland *et al.* 2001). Detection probabilities of sign indices are often assumed to be equal in comparisons of relative abundances of species but this assumption is rarely validated (*e.g.*, Emmons 1987, Hart *et al.* 1996, Boddicker *et al.* 2002, Miller & Miller 2005, Azlan & Engkamat 2006, Lynam *et al.* 2006, Stephens *et al.* 2006, Weckel *et al.* 2006, Joseph *et al.* 2007, Kasper *et al.* 2007, Kauffman *et al.* 2007, Blaum *et al.* 2008, Datta *et al.* 2008, Dinata *et al.* 2008). In this study, we test the assumption of equal detection probabilities of two cats with similar ecological niches, jaguars and pumas, and their potential prey species, inhabiting a broadleaf lowland rain forest in Belize.

Interspecific variation in behavior may result in differential detection probabilities when sampling multiple species. For example, sampling along forest trails or transects may be biased toward species that are the more willing to use exposed areas. Although

variation in the willingness to use trails could bias multispecies surveys, transects and existing trails are often used as the only means of surveying wildlife in dense secondary forests because the dense vegetation restricts movement by researchers off trail. It is important to know whether limiting surveys of multiple species to trail systems biases the results toward certain species. Studies sampling multiple species indicate that results are biased toward different species when using different sampling methods (Gompper *et al.* 2006) or different sampling designs (*e.g.*, linear vs. grid; Mahon *et al.* 1998). Single methods carried out in different habitat types give varying results within species (Fuller 1992, Marchandeanu *et al.* 2006) and even interaction effects between habitat and social status within species (Larruca *et al.* 2007). Camera trapping was shown to be biased toward different species depending on the microhabitat (Weckel *et al.* 2006, Larruca *et al.* 2007, Rowcliffe *et al.* 2008). All these examples demonstrate the importance of understanding differential detection rates of different species in different microhabitat. For example, Weckel *et al.* (2006) elegantly demonstrated that paca (*Agouti paca*) and armadillo (*Dasypus novimcinctus*) had a higher chance of photographic capture away from trails, but subsequently used a total dataset of captures on camera (independent of location) as a measure of relative abundance of prey species of jaguars.

An increasing number of studies use camera-trap capture rates to compare relative abundance based on capture rates of multiple species without assessing or correcting for differential detection probabilities (*e.g.*, Azlan & Engkamat 2006, Lynam *et al.* 2006, Weckel *et al.* 2006, Kasper *et al.* 2007, Kauffman *et al.* 2007, Datta *et al.* 2008, Dinata *et al.* 2008). The majority of survey locations within these studies are man-made trails or game trails across which people can traverse. Camera trapping depends on the use of a

Received 23 December 2008; revision accepted 29 April 2009.

⁴Corresponding author; e-mail: bharmsen@panthera.org

funnel, usually a trail, through which animals must walk to pass the camera. Different species will have different microhabitat preferences; therefore there is no reason to expect the different species to have similar capture probability along the different trails. For example, small Neotropical mammals show a preference for using the dense undergrowth (e.g., armadillo and paca; Weckel *et al.* 2006), while larger species such as jaguars and pumas prefer the open trails (Harmsen 2006). The differences in trail use or willingness to pass funnels stems from size variation, physical differences in permeability of the forest matrix and behavioral differences, for example tendency to display avoidance behavior of predators or conspecifics in exposed areas. It is therefore expected that the Neotropical medium to larger mammal assemblage shows variation in capture rate on cameras located on a high variety of trails.

We do, however, expect that similar-sized species with similar habitat requirements have similar capture rates at varying locations. In this study we analyze trail use by sympatric jaguars and pumas. Both species are known to travel along trails within forests (Rabinowitz & Nottingham 1986, Maffei *et al.* 2004, Harmsen 2006). These similar-sized cats potentially have high dietary overlap (Taber *et al.* 1997, Núñez *et al.* 2000, Crawshaw & Quigley 2002, Scognamillo *et al.* 2003) and both species have similar activity patterns and habitat use where they are sympatric (Scognamillo *et al.* 2003, Harmsen *et al.* 2009). Thus jaguars and pumas represent suitable model species to test whether species with similar ecological niches have similar detection probabilities within the same habitat. We hypothesized that jaguars and pumas have equal detectability on forest trails. If true, capture rates could be used as a valid index to compare abundance of these two cats. Any evidence that detection probabilities differ between the two cats may highlight a need to reassess previous studies that do not evaluate detection probabilities in multispecies camera-trap surveys. We do expect differential detectability of the larger Neotropical mammal assemblage, especially in comparison with the two large cats.

We used 110 camera-trap locations across a variety of locations on and off trail to assess how the Neotropical large to medium-size mammal assemblage differed in their use of trails. This study was carried out to assess if relative abundance indices can be used to compare abundances of the total mammal assemblages captured on cameras. Although concentrating mainly on detectability on camera traps, results are applicable to any survey method applying frequency data instead of methods that estimate numbers through individual recognition (mark-recapture).

METHODS

STUDY SITE AND CAMERA TRAPPING.—The study was conducted in the Cockscomb Basin Wildlife Sanctuary (CBWS) in Belize, Central America. CBWS is a broad-leaf tropical forest of regenerating secondary forest at several stages of succession (for details see Silver *et al.* 2004). The area was heavily logged until the 1980s, and in 1990 was declared a wildlife sanctuary of 425 km². The old logging roads and more recent tourist footpaths provide a system of established trails with additional connecting trails freshly cut for this study (Fig. S1). Long-term camera trapping by the authors has

demonstrated that CBWS supports populations of both jaguars and pumas (Harmsen 2006). Hunting of jaguars, pumas and prey species within the sanctuary is minimal (Harmsen 2006).

Camera stations were deployed in 110 different locations for periods of 2–20 mo over 2.5 yr, covering an effective sampling area of 198 km². At each location, a pair of passive cameras (Cam Trak South Ltd., Watkinsville, GA, U.S.A.) was set to photograph each side of the animal's body, with continuous 24-h operation and an enforced 3-min delay between consecutive photographs. Of the 110 camera stations, 42 were located along single man-made trails at ca 1 km intervals, 43 were located on game trails, and 25 were located off-trail, in natural open areas, along small streams or on river sand banks. The high camera numbers and density (up to six cameras per 10 km²) sampled a sufficiently wide range of microhabitats and trail types to allow us to study differences between species in trail use within different microhabitats. Camera-trap locations were restricted to sites with suitable funnels.

Jaguars were individually identified from their unique pelt patterns (Silver *et al.* 2004, Harmsen 2006). Although individual identification of the plain-colored puma is difficult, we were able to identify most puma individuals over the short term (up to 4 wk) from wounds, scars and skin parasites (Harmsen 2006, Kelly *et al.* 2008). In particular, botfly larvae (*Dermatobia hominis*) create visible lumps beneath the skin ca 25 mm diam for periods of 2–4 wk, providing a temporary but uniquely identifiable pattern.

THE DIFFERENTIAL DETECTION PROBABILITY OF NEOTROPICAL MAMMALS ON TRAILS.—Six habitat variables were recorded at each camera station: trail width, trail age, trail seasonality, altitude, slope and distance to flowing water. The average trail width associated with each station was calculated as the mean width at the station and 20 m in either direction along the trail (mean \pm SD = 1.7 \pm 1.4 m, range: 2.8–7.8 m). The age of the trail was ranked on a 3-point scale (0 = freshly cut, 1 = tourist trail established at least 1 yr before start of study, 2 = old logging road). Seasonality was scored on a 3-point scale (0 = maintained throughout year, 1 = maintained seasonally, 2 = freshly cut). Altitude (0–300 m), slope (ranking of sloping in surrounding area, min = 0 [flat], max = 5 [surrounded by many steep slopes]) and distance to water (0–420 m) were discerned from GIS data (Land and Information Centre, Government of Belize). Spearman's rank correlations were calculated between capture rate per location per species and each habitat variable. This analysis was carried out for all species captured at \geq 25 stations: jaguars, pumas, armadillo (*Dasyurus novemcinctus*), red brocket deer (*Mazama americana*), collared peccary (*Tayassu tajacu*), ocelot (*Leopardus pardalis*), common opossum (*Didelphis marsupialis*), paca (*A. paca*), tapir (*Tapirus bairdii*) and white-lipped peccary (*Dicotyles pecari*).

To test further whether the detection probability of each species varied with the only continuous trail variable (trail width), capture rates were linearly regressed against trail width per species. To test whether locations that optimize jaguar detection probability also optimize the detection probability of other species, Pearson's correlations were calculated between capture rates of these species and jaguar capture rate. A strong positive correlation for a given species would indicate that cameras deployed to survey jaguars are

also suitable to study that species. For analysis with trail width, all data were \log_{10} -transformed to approximate a normal distribution of the residuals and equal variances.

FOLLOWING AND CROSSING TRAILS.—Animals that have a tendency to follow trails have a higher chance of capture on trail cameras than animals that mainly cross trails. To examine which species had more of a tendency to cross or follow trails we surveyed trails for footprints and noted the direction of travel, either following the trail (consecutive footprints along the length of the trail for ≥ 25 m) or crossing the trail (consecutive footprints, crossing from one side to the other). Weekly footprint surveys were conducted during the wet season when the trails were muddy. Under these conditions tracks were easily visible without the need for special preparation of the trail substrate and we were able to follow them along the trails. Footprint surveys were not conducted during the dry season as the ground was too hard. The surveys were conducted along four established trails (length surveyed: 3.8, 3.9, 1.9, 4.4 km) and four freshly cut trails (length surveyed: 1.7, 2.6, 2.3, 4.1 km). The eight trails (Fig. S1) were surveyed sequentially during the 2003–2005 rainy seasons. Each trail was systematically scanned for footprints once per week for a period of 5–9 wk. Footprints were cleared after identification. One complete survey consisted of the entire footprint data collected along a single trail.

The trails were slowly walked by two surveyors who scanned for footprints. The assemblage of Central American mammals > 2 kg is relatively simple and footprints can be easily identified from their size and shape following Reid (1997). Surveyors identified tracks using Reid (1997) and experienced local guides. All surveyors could identify well-defined footprints to species level. Tracks lacking sufficient definition for identification to species level were discarded from the analyses.

Single sets of tracks from a single individual either following or crossing a trail were used as units of analysis (single footprints were not used). Frequency of use and direction of travel along trails were compared between species. The frequency of following vs. crossing would indicate to what extent a given species encountering a trail tend to cross it, avoiding the open space or follow it, profiting from its accessibility.

TRAIL USE BY JAGUARS AND PUMAS.—Trail use by jaguars and pumas was investigated using data from stations located along eight trails (Fig. S1) at *ca* 1 km intervals covering 4–8 km (see Fig S2A). Jaguars and pumas are known to move > 1 km when traveling (Núñez *et al.* 2002, Sunquist & Sunquist 2002, Cullen *et al.* 2005, Swenor *et al.* 2008); therefore, the camera spacing was suitable to detect trail traveling as multiple captures on consecutive cameras along the trail. Jaguars and pumas were present on all the trails. The hypothesis that both cats use the trails similarly was tested by comparing the number of ‘walks’ along a trail. The number of walks was used as an index of how frequently either species followed trails. A walk was defined as ≥ 2 captures of the same individual at different locations along a trail within a fixed time period, allowing up to 1 h between captures on consecutive cameras. Therefore, the maximum time allowed for a single walk depended

on which cameras were triggered. If two neighboring cameras were triggered they had to be triggered within 1 h to be classified as a walk. If only the first and final cameras on a trail were triggered then the time period over which the walk occurred was allowed to be longer: up to 4 h for trails with five cameras, and up to 8 h for trails with nine cameras. Calculation of the number of walks required individual recognition of both cat species. Walks for pumas were only assigned as walks if the puma at multiple cameras could be positively identified as the same individual. Consequently the number of puma walks is underestimated. Single captures on trails were also recorded. The proportion of single captures on the trails vs. the number of walks was compared between the species using a χ^2 test. Unidentified puma captures discarded from the walk analysis were not included as single captures.

The willingness to follow or leave a trail was compared between the two species (Fig. S2B and C). The number of consecutive cameras triggered during each walk was used as an index of trail-walking intensity, and the number of omissions of camera locations (Fig. S2D) during each walk was used as an index of the intensity of walking off-trail. A difference between the cats in number of cameras triggered during single walks would indicate difference in willingness between the species to stay on the trail, while a difference in omissions would indicate a difference in willingness to leave the trails and use the surrounding jungle matrix. The combination of all the three variables, difference in number of walks, number of cameras and omissions, will indicate if one of the species had more tendency to use the trails.

Camera failure was assumed to be comparable for both species since both species are a similar size class, and so have similar likelihood of triggering a camera sensor. Trail use (number of walks) and the intensity of walking on or off the trails were compared between jaguars and pumas using Student’s *t* tests, assuming unequal variance. Data on capture rates were \log_{10} -transformed to meet the assumptions of homogeneity of variances, normal residuals and linear trends. All analyses were carried out using Minitab version 14.

RESULTS

DIFFERENCES IN DETECTION PROBABILITIES OF NEOTROPICAL MAMMALS ON TRAILS.—Trail width, age and seasonality were the only habitat variables that correlated significantly with the capture rates of jaguars, pumas and ocelots (Table 1). Higher capture rates were strongly associated with wider, established trail systems. Capture rate of brocket deer was negatively correlated with trail width, while pacas and tapirs had higher capture rates on recently cut trails than old established trails (Table 1). Capture rates of the other mammals were not strongly correlated with trail variables. The capture rates of tapirs and opossums increased with proximity to rivers and streams (Table 1) and paca capture rate increased with proximity to rivers only ($r = -0.34$, $P < 0.05$). Trail width, age and seasonality were intercorrelated, as expected, with the older trails being wider and more permanent (Table 2). This is expected since used trails will get wider with age in a protected forest without mechanized clearing.

Capture rates of jaguars, pumas and ocelots increased with trail width (linear regression; Fig. 1), suggesting that these cat species

TABLE 1. Spearman's correlations ($P < 0.05$ in bold) for several Neotropical mammals (WL peccary = white lipped peccary) between capture rates per species per location and habitat and trail variables around the camera location ($N = 110$).

	Jaguar	Puma	Ocelot	Armadillo	Brocket deer	Collared peccary	Opossum	Paca	Tapir	WL peccary
Trail age	0.59	0.55	0.44	-0.12	-0.09	-0.08	0.12	-0.24	-0.24	0.01
Trail season	-0.61	-0.52	-0.34	0.13	0.14	-0.08	-0.09	0.12	0.28	0.11
Trail width	0.51	0.46	0.42	-0.06	-0.28	0.11	-0.09	-0.20	-0.12	-0.09
Altitude	-0.07	0.04	-0.08	0.04	0.16	-0.09	0.10	0.05	-0.09	0.06
Distance to water	-0.11	-0.10	-0.17	-0.06	-0.01	-0.03	-0.43	-0.10	-0.42	-0.04
Slope	-0.12	-0.10	-0.05	0.00	0.06	-0.06	0.20	-0.08	0.01	-0.05

prefer wider trails over narrow trails. The increase in capture rate with trail width was greatest for pumas and least for ocelots. For all other species there was no significant linear relation between trail width and capture rates, except for red brocket deer, whose capture rate decreased on wider trails.

Capture rates of pumas and ocelots were positively correlated with capture rates of jaguars (Table 3). However, with the exception of opossums, captures rates of the other mammals were not positively correlated with jaguar capture rates (Table 3). These data show that camera locations targeting jaguars were also well sited to detect pumas and ocelots, but may be poorly sited to detect their potential prey species.

The 25 off-trail stations did not capture pumas, ocelots or white-lipped peccary, and capture rates of jaguars, armadillos, collared peccary and opossums were low, ranging from 0.5 to 1.2 per 100 d. Off-trail cameras did not detect any jaguar individuals that were not detected on trail, and those detected off-trail were the same individuals as those with higher capture rates on trails. The capture rates of red brocket deer, pacas and tapirs were high in off-trail locations, ranging from 12 to 20 captures per 100 d, probably due to their higher association with streams and rivers than the other species.

FOLLOWING AND CROSSING TRAILS.—Forest mammals differed in their tendency to follow or cross trails (Table 4). All sets of jaguar and puma footprints traveled along the trails. Tracks of both of

these cat species could be followed for distances up to 3 km. The only other species to exhibit similar long-distance trail-following behavior were white-lipped peccaries, whose tracks could be followed for up to 4 km along trails. White-lipped peccary tracks were easier to follow than other species since large herds would churn up the ground, even on dry ground. Tapirs tracks were also only found following trails; however, half of the footprint sets reentered the forest within 1 km ($N = 12$), indicating that they left larger trails creating their own paths through the jungle. All other species followed trails for < 1 km, with pacas, opossums, armadillos and agoutis never following a trail for ≥ 100 m. These species indicated the highest frequency of trail crossing (Table 4). Although the number of sets of footprints of collared peccaries was low ($N = 5$), they were frequently encountered by surveyors walking off trail. When undisturbed by surveyors they were always observed off-trail or crossing a trail ($N = 20$).

These results indicate a variety of trail-use patterns among forest species and thus species-specific variation in their probability of detection on trail-based cameras. This is corroborated by anecdotal evidence from one camera station that was moved 25 m from its original location due to flooding. Capture rates of jaguars and pumas were similar in both locations (8–10 captures/100 d), while the paca capture rate increased from 0.4 to 8 captures/100 d when the camera was moved. The new location was at a crossing point (all photos were of the head or rear as the paca crossed the trail). There was no evidence of a game trail at the crossing point.

TRAIL USE BY JAGUARS AND PUMAS.—The difference between single captures and walks was well defined within the dataset when walks were based on ≤ 1 h between captures at consecutive stations along the trail. During walks, captures of jaguars and pumas at consecutive stations were separated by 15–30 min for both species and there was no significant difference between species (mean \pm SE: jaguars 24.5 ± 0.8 , pumas 23.0 ± 0.7 , $t_{70} = 1.38$, $P = 0.17$). The maximum time taken for a single walk was 2 h, which occurred between consecutive captures at stations that were 3 km apart (missing two cameras). The shortest time period between consecutive captures that were defined as two single captures, rather than as a walk, was 12 h between neighboring stations that were 1 km apart. All other single captures of individuals were separated by days rather than hours. Six potential puma walks comprising 15 captures were discarded as

TABLE 2. Spearman's correlations ($P < 0.05$ in bold) between the variables used for Table 1 per location.

	Trail age	Trail season	Trail width	Altitude	Distilled water	Slope
Trail age	–					
Trail season	0.80	–				
Trail width	0.66	-0.53	–			
Altitude	0.14	0.11	-0.21	–		
Distance to water	0.05	-0.09	0.03	0.09	–	
Slope	0.14	-0.10	0.01	0.54	-0.14	–

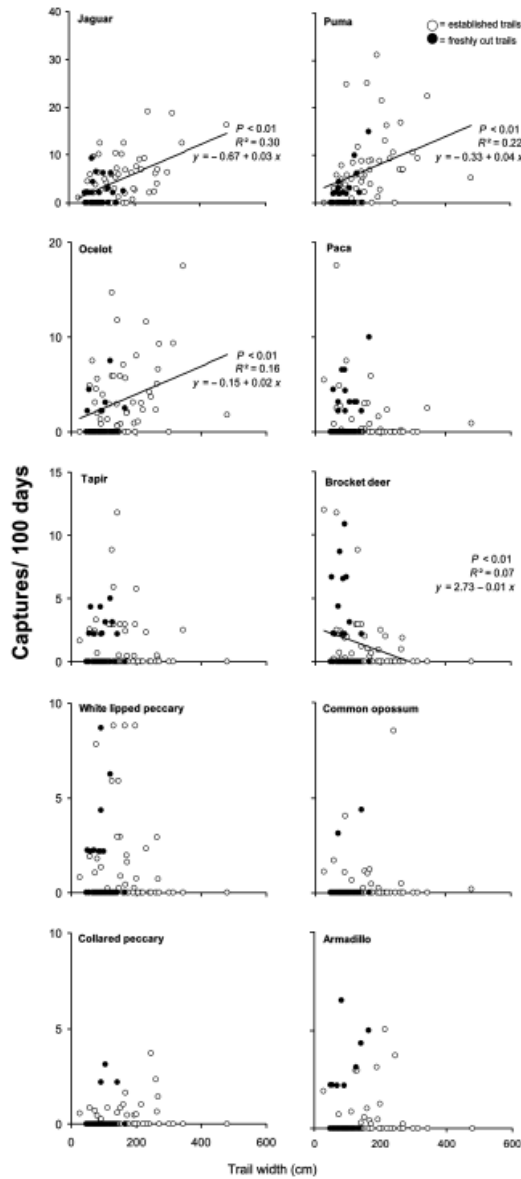


FIGURE 1. Variation in capture frequency of ten forest mammals with trail width. Filled dots show fresh trails, unfilled show established trails. Camera locations were separated between established trails and freshly cut trails. Significant linear regressions are shown for the total dataset. $N = 85$ camera locations.

identification was not reliable enough to ensure that it was the same individual.

Fifteen different jaguars and at least five different pumas were monitored walking on the eight survey trails, with an average of 5.3 (\pm SD 1.0) jaguars and ≥ 1 –2 pumas/trail. Pumas had a greater tendency to trigger multiple cameras along the trails than jaguars when comparing single captures with walks ($\chi^2_1 = 4.72$, $P < 0.05$; Table 5).

Jaguars triggered fewer consecutive cameras during walks along trails than pumas (back-transformed mean [confidence limits]: jaguars 3.23 [3.16–3.30], pumas 3.54 [3.43–3.66]; $t_{110} = -2.65$, $P < 0.01$). Conversely, the number of omissions of

TABLE 3. Pearson's correlations ($P < 0.05$ in bold) between the \log_{10} -transformed capture rates of jaguars and other forest mammals at $N = 110$ camera locations.

Species	Jaguar (<i>Panthera onca</i>)
Puma (<i>Puma concolor</i>)	0.65
Opossum (<i>Didelphis marsupialis</i>)	0.29
Ocelot (<i>Leopardus pardalis</i>)	0.23
Collared peccary (<i>Tayassu tajacu</i>)	0.17
Paca (<i>Agouti paca</i>)	0.16
Armadillo (<i>Dasybus novemcinctus</i>)	0.01
White lipped peccary (<i>Dicotyles pecari</i>)	-0.06
Tapir (<i>Tapirus bairdii</i>)	-0.14
Brocket deer (<i>Mazama americana</i>)	- 0.32

captures during walks along trails was significantly higher for jaguars than for pumas (back-transformed mean [confidence limits]: jaguars 1.20 [1.14–1.27], pumas 1.05 [1.03–1.07]; $t_{56} = 2.79$, $P < 0.01$). These results suggest that pumas tended to remain walking along the trail when active whilst jaguars were more likely to make excursions from the trail.

Cats were rarely detected by cameras located off-trail. Camera traps placed off-trail (on small streams, $N = 25$) recorded only eight captures of six different jaguar individuals. Pumas were not detected by any of the cameras that were not on the trail system.

DISCUSSION

The data reported here are consistent with a preference by jaguars and pumas for trails as travel routes, in accordance with observations on jaguars by Rabinowitz and Nottingham (1986) and Maffei *et al.* (2004). If optimal camera locations for both cat species are associated with trails, this study has further demonstrated that such trails are not well suited to the detection of other medium to large Neotropical mammal species. Species that have a greater tendency to cross rather than follow trails have a lower probability of detection on camera traps that are located on trails than the species that follow trails, unless the camera happens to be located at the crossing point, while trail followers have a high chance of capture when cameras or surveys are carried out on these trails. Weckel *et al.* (2006) demonstrated that photographic capture frequencies of armadillos and pacas in the forest increased with distance from wider trails. Our regular surveys of track direction on trails revealed that potential prey species have differential trail-use, with some species frequently following trails and others mostly crossing trails with consequently lower chance of capture by trail cameras. The average distance that a species generally follows trails should be taken into account apart from the simple dichotomy of trail following and trail crossing as was done in this study. The detailed study of jaguars and pumas indicate that there is high variation between trail followers, even for similar species such as jaguars and pumas. To correct for biases in comparisons between photographic capture frequencies of species, information is needed about the relation between capture

TABLE 4. Percentage of footprint sets that followed a trail for ≥ 25 m as opposed to crossing it, out of N sets of footprints collated from five surveys (five trails).

Species	% footprints		N
	sets that follow trail	Max distance along trail (km)	
Paca (<i>Agouti paca</i>)	31	< 0.1	13
Armadillo (<i>Dasybus novemcinctus</i>)	43	< 0.1	14
Opossum (<i>Didelphis marsupialis</i>)	50	< 0.1	2
Agouti (<i>Dasyprocta punctata</i>)	50	< 0.1	6
Collared peccary (<i>Tayassu tajacu</i>)	60	0.2	5
Brocket deer (<i>Mazama americana</i>)	71	0.2	24
White lipped peccary (<i>Dicotyles pecari</i>)	83	3.7	30
Ocelot (<i>Leopardus pardalis</i>)	92	0.5	25
Coati (<i>Nasua narica</i>)	100	< 0.1	2
Margay (<i>Leopardus wiedii</i>)	100	< 0.1	6
Tapir (<i>Tapirus bairdii</i>)	100	1.0	34
Jaguar (<i>Panthera onca</i>)	100	3.0	43
Puma (<i>Puma concolor</i>)	100	3.0	64

probability and macro- and micro-habitat variables surrounding a camera location. Correction factors might need to be site specific, and their enumeration will require large-scale systematic camera-trap surveys across a wide range of habitat variables. Such studies may be so time consuming and expensive as to warrant using alternative means of comparing abundance such as mark-recapture analysis by tagging individuals. Our study evaluated photographic captures as an index of relative abundance, but the concerns it raises are also true of other types of signs used for comparing species abundance in an area, such as track counts along transects (e.g., Buckland *et al.* 2001).

Detailed analysis of trail use by jaguars and pumas has indicated that although trails were more productive than off-trail as locations for detecting both species, cameras on trails were biased toward puma captures. Although both species can be considered trail walkers, as both the high capture rates on cameras and the track data demonstrate, jaguars were more likely to walk off-trail than pumas, thus reducing their probability of detection by on-trail cameras. These results suggest that capture rates may not be an appropriate index of relative abundance even for species with broadly similar ecological niches. Also, comparison within species between sites using camera traps has to take into account potential differ-

ences in detection probabilities between the sites. For example, trails in dense vegetation have a greater capacity to funnel animals past a camera than do trails through open areas where animals may have more opportunity to wander off the trail. The finding that both jaguars and pumas are best captured on trail systems has serious implications for camera studies. It means that semi-wilderness areas with established trail or logging road systems are more suitable for camera trapping than pure wilderness areas without such an infrastructure. The lack of infrastructure makes camera placement difficult and potentially suboptimal since traveling routes for cats are far less obvious, giving rise to potentially low capture rates. This in turn could give the erroneous impression that there are few cats present. Although less suitable for camera trapping, it is these undisturbed wilderness areas that are most in need of study.

Jaguars and pumas have remarkably similar ecologies for sympatric species. In their regions of coexistence, they have similar activity patterns and habitat use within overlapping ranges (Scognamillo *et al.* 2003, Harmsen *et al.* 2009). Several studies have shown high levels of dietary overlap (Taber *et al.* 1997, Núñez *et al.* 2000, Crawshaw & Quigley 2002, Scognamillo *et al.* 2003), indicating that both cats are capable of capturing the full array of prey species available to each. Other studies have shown wider dietary differences between the species, particularly in dense forest environments (Leite & Galvão 2002, Novack *et al.* 2005, Foster 2008). Local habitat differences might favor one cat focusing more on certain prey species. Differential use of open and closed habitat could facilitate coexistence of these similar-sized cats. The stockier, short-limbed jaguar may be better adapted for walking off trail than the long-limbed agile puma. Hunting by pumas might be more successful along wide trails where it can take better advantage of its capability for longer strides for a final pounce (final striking range) compared with the jaguar. This advantage will be lost in dense undergrowth.

This study shows that comparisons of relative abundance indices between species should be made with caution. We suggest that relative detection probabilities should be enumerated by a thoroughly stratified sampling design, including variables such as trail width, habitat types and habitat openness. Relatively subtle differences in behavior can cause differences in detectability between similar-sized species occupying similar niches. The current study indicates that researchers should put extra effort into assessing absolute abundance levels as a means of comparison between species.

ACKNOWLEDGMENTS

Funding for was provided by The Wildlife Conservation Society, which also gave logistical support and expertise, the UK Natural Environment Research Council, Liz Claiborne/Art Ortenberg Foundation, North of England Zoological Society, Brevard Zoo and Woodland Park Zoo. The Belize Audubon Society was a partner in the research and gave logistical support. We thank all of its park wardens in the CBWS for their cooperation, and E. Pop for field assistance and invaluable field expertise. Alan Rabinowitz for continued support.

TABLE 5. Numbers of walks and single capture events of jaguars and pumas along eight trails monitored over a 3-yr period, based on 15 different jaguars and at least five different pumas.

	Jaguar	Puma	Total
Walks	44	70	114
Single captures	343	349	692
Total	387	419	806

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Outline of the Cockscomb Basin Wildlife Sanctuary indicating the trails used for this study.

FIGURE S2. Conceptual representation of trail walking by jaguars and pumas, with camera traps shown by dots.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED

- AZLAN, M. J., AND L. ENKGAMAT. 2006. Camera trapping and conservation in Lambir Hills National Park, Sarawak. *Raffles Bull. Zool.* 54: 469–475.
- BLAUM, N., R. M. ENGEMAN, B. WASIOLKA, AND E. ROSSMANITH. 2008. Indexing small mammalian carnivores in the southern Kalahari, South Africa. *Wildl. Res.* 35: 72–79.
- BODDICKER, M., J. J. RODRIGUEZ, AND J. AMANZO. 2002. Indices for assessment and monitoring of large mammals within an adaptive management framework. *Environ. Monit. Assess.* 76: 105–123.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, UK.
- CRAWSHAW, P. G. JR., AND H. B. QUIGLEY. 2002. Hábitos alimentarios del jaguar y el puma en el pantanal, Brasil, con implicaciones para su manejo y conservación. In R. A. Medellín *et al.* (Eds.): *El Jaguar en el Nuevo Milenio. Una evaluación de su estado, detección de prioridades y recomendaciones para la conservación de los jaguars en America*. pp. 223–235. Universidad Nacional Autónoma de México/Wildlife Conservation Society, México.
- CULLEN, L. JR., K. C. ABREU, D. SANA, AND A. F. D. NAVA. 2005. Jaguars as landscape detectives for the upper Paraná River corridor, Brazil. *Nat. Conserv.* 3: 43–58.
- DATTA, A., M. O. ANAND, AND R. NANIWADEKAR. 2008. Empty forests: Large carnivore and prey abundance in Namdapha National Park, north-east India. *Biol. Conserv.* 141: 1429–1435.
- DINATA, Y., A. NUGROHO, I. A. HAIDIR, AND M. LINKIE. 2008. Camera trapping rare and threatened avifauna in West-Central Sumatra. *Bird Conserv. Int.* 18: 30–37.
- EMMONS, L. H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behav. Ecol. Sociobiol.* 20: 271–283.
- FOSTER, R. J. 2008. The ecology of jaguars in a human influenced landscape. PhD Dissertation, University of Southampton, Southampton, UK.
- FULLER, T. K. 1992. Do pellet counts index white-tailed deer numbers and population-change—a reply. *J. Wildl. Manage.* 56: 613–613.
- GOMPPER, M. E., R. W. KAYS, J. C. RAY, S. D. LAPOINT, D. A. BOGAN, AND J. R. CRYAN. 2006. A comparison of non-invasive techniques to survey carnivore communities in northeastern North America. *Wildl. Soc. Bull.* 34: 1142–1151.
- HARMSEN, B. J. 2006. The use of camera traps for estimating abundance and studying the ecology of jaguars (*Panthera onca*). PhD Dissertation, University of Southampton, Southampton, UK.
- HARMSEN, B. J., R. J. FOSTER, S. SILVER, L. OSTRO, AND C. P. DONCASTER. 2009. Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a Neotropical forest. *J. Mammal.* 90: 612–620.
- HART, J. A., M. KATEMBO, AND K. PUNGA. 1996. Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *Afr. J. Ecol.* 34: 364–379.
- JOSEPH, S., A. P. THOMAS, R. SATHEESH, AND R. SUGATHAN. 2007. Foraging ecology and relative abundance of large carnivores in Parambikulam Wildlife Sanctuary, southern India. *Zoos Print J.* 22: 2667–2670.
- KASPER, C. B., F. D. MAZIM, J. B. G. SOARES, T. G. DE OLIVEIRA, AND M. E. FABIAN. 2007. Composition and relative abundance of the medium-large sized mammals of Turvo State Park, Rio Grande do Sul, Brazil. *Rev. Bras. Zool.* 24: 107–1100.
- KAUFFMAN, M. J., M. SANJAYAN, J. LOWENSTEIN, A. NELSON, R. M. JEO, AND K. R. CROOKS. 2007. Remote camera-trap methods and analyses reveal impacts of rangeland management on Namibian carnivore communities. *Oryx* 41: 70–78.
- KELLY, M. J., A. J. NOSS, M. S. DI BITETTI, L. MAFFEI, R. A. ARISPE, A. PAVIOLO, C. D. DE ANGELO, AND Y. E. DI BLANCO. 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, Belize. *J. Mammal.* 89: 408–418.
- LARRUCEA, E. S., P. F. BRUSSARD, M. M. JAEGER, AND R. H. BARRETT. 2007. Cameras, coyotes, and the assumption of equal detectability. *J. Wildl. Manage.* 71: 1682–1689.
- LEITE, M. R. P., AND F. GALVÃO. 2002. El jaguar, el puma y el hombre en tres áreas protegidas del bosque atlántico costero de paraná, Brasil. In R. A. Medellín *et al.* (Eds.): *El Jaguar en el Nuevo Milenio. Una evaluación de su estado, detección de prioridades y recomendaciones para la conservación de los jaguars en America*. pp. 237–250. Universidad Nacional Autónoma de México/Wildlife Conservation Society, México.
- LYNAM, A. J., P. D. ROUND, AND W. Y. BROCKELMAN. 2006. Status of birds and large mammals in Thailand's Dong Phrayayen-Khao Yai forest complex. Biodiversity Research and Training Program, Wildlife Conservation Society, Thailand.
- MAFFEI, L., E. CUELLAR, AND A. NOSS. 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *J. Zool.* 262: 295–304.
- MAHON, P. S., P. B. BANKS, AND C. R. DICKMAN. 1998. Population indices for wild carnivores: A critical study in sand-dune habitat, south-western Queensland. *Wildl. Res.* 25: 11–22.
- MARCHANDEAU, S., J. AUBINEAU, F. BERGER, J. C. GAUDIN, A. ROOBROUCK, E. CORDA, AND F. REITZ. 2006. Abundance indices: Reliability testing is crucial—a field case of wild rabbit *Oryzodolagus cuniculus*. *Wildl. Biol.* 12: 19–27.
- MILLER, C. M., AND B. MILLER. 2005. Jaguar density in La Selva Maya. Report for Wildlife Conservation Society.
- NOVACK, A. J., M. B. MAIN, M. E. SUNQUIST, AND R. F. LABISKY. 2005. Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. *J. Zool.* 267: 167–178.
- NÚÑEZ, R., B. MILLER, AND F. LINDZEY. 2000. Food habits of jaguars and pumas in Jalisco, Mexico. *J. Zool.* 252: 373–379.
- NÚÑEZ, R., B. MILLER, AND F. LINDZEY. 2002. Ecología del jaguar en la reserva de la Biosfera Chamela-Cuixmala, Jalisco, México. In R. A. Medellín *et al.* (Eds.): *El Jaguar en el Nuevo Milenio. Una evaluación de su estado, detección de prioridades y recomendaciones para la conservación de los jaguars en America*. pp. 107–126. Universidad Nacional Autónoma de México/Wildlife Conservation Society, México.
- RABINOWITZ, A. R., AND B. G. NOTTINGHAM. 1986. Ecology and Behavior of the Jaguar (*Panthera onca*) in Belize, Central-America. *J. Zool.* 210: 149–159.
- REID, F. A. 1997. A field guide to the mammals of central and southeast Mexico. Oxford University Press, New York, New York.
- ROWCLIFFE, J. M., J. FIELD, S. T. TURVEY, AND C. CARBONE. 2008. Estimating animal density using camera traps without the need for individual recognition. *J. Appl. Ecol.* 45: 1228–1236.

- SCOGNAMILLO, D., I. E. MAXIT, M. SUNQUIST, AND J. POLISAR. 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *J. Zool.* 259: 269–279.
- SILVER, S. C., L. E. T. OSTRO, L. K. MARSH, L. MAFFEI, A. J. NOSS, M. J. KELLY, R. B. WALLACE, H. GOMEZ, AND G. AYALA. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* 38: 148–154.
- STEPHENS, P. A., O. Y. ZAUMYSLOVA, D. G. MIQUELLE, A. I. MYSLENKOV, AND G. D. HAYWARD. 2006. Estimating population density from indirect sign: Track counts and the Formozov-Malyshev-Pereleshin formula. *Anim. Conserv.* 9: 339–348.
- SUNQUIST, M., AND F. SUNQUIST. 2002. *Wild cats of the world*. The University of Chicago Press, Chicago, Illinois.
- SWEANOR, L. L., K. A. LOGAN, J. W. BAUER, B. MILLSAP, AND W. M. BOYCE. 2008. Puma and human spatial and temporal use of a popular California state park. *J. Wildl. Manage.* 72: 1076–1084.
- TABER, A. B., A. J. NOVARO, N. NERIS, AND F. H. COLMAN. 1997. The food habits of sympatric jaguar and puma in the Paraguayan Chaco. *Biotropica* 29: 204–213.
- WECKEL, M., W. GIULIANO, AND S. SILVER. 2006. Jaguar (*Panthera onca*) feeding ecology: Distribution of predator and prey through time and space. *J. Zool.* 270: 25–30.