



RESEARCH ARTICLE

An empirical evaluation of camera trap study design: How many, how long and when?

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Abstract

1. Camera traps deployed in grids or stratified random designs are a well-established survey tool for wildlife but there has been little evaluation of study design parameters.
2. We used an empirical subsampling approach involving 2,225 camera deployments run at 41 study areas around the world to evaluate three aspects of camera trap study design (number of sites, duration and season of sampling) and their influence on the estimation of three ecological metrics (species richness, occupancy and detection rate) for mammals.
3. We found that 25–35 camera sites were needed for precise estimates of species richness, depending on scale of the study. The precision of species-level estimates of occupancy (ψ) was highly sensitive to occupancy level, with <20 camera sites needed for precise estimates of common ($\psi > 0.75$) species, but more than 150 camera sites likely needed for rare ($\psi < 0.25$) species. Species detection rates were more difficult to estimate precisely at the grid level due to spatial heterogeneity,

presumably driven by unaccounted habitat variability factors within the study area. Running a camera at a site for 2 weeks was most efficient for detecting new species, but 3–4 weeks were needed for precise estimates of local detection rate, with no gains in precision observed after 1 month. Metrics for all mammal communities were sensitive to seasonality, with 37%–50% of the species at the sites we examined fluctuating significantly in their occupancy or detection rates over the year. This effect was more pronounced in temperate sites, where seasonally sensitive species varied in relative abundance by an average factor of 4–5, and some species were completely absent in one season due to hibernation or migration.

4. We recommend the following guidelines to efficiently obtain precise estimates of species richness, occupancy and detection rates with camera trap arrays: run each camera for 3–5 weeks across 40–60 sites per array. We recommend comparisons of detection rates be model based and include local covariates to help account for small-scale variation. Furthermore, comparisons across study areas or times must account for seasonality, which could have strong impacts on mammal communities in both tropical and temperate sites.

KEYWORDS

camera traps, community ecology, detectability, mammals, relative abundance, species richness, study design, wildlife surveys

1 | INTRODUCTION

Monitoring wildlife populations is more important than ever, given the imperiled status of many species around the world, and the rapid changes to the earth's climate and landcover (Dirzo et al., 2014). Camera traps are now a standard method for monitoring a variety of species over relatively large areas (Steenweg et al., 2017; Wearn & Glover-Kapfer, 2017), being used to quantify species diversity, and estimate occupancy and relative abundance. These estimates can be compared across space and time to monitor changes in populations and test hypotheses about the effects of landscape and human factors on species relative abundance, distribution and interspecific interactions.

The growth of camera trap surveys for monitoring biodiversity has led to substantial variation in study designs across projects, with sample size ranging from 1 to >1,000 camera sites (Burton et al., 2015). The foundational questions a researcher must address when designing a camera trap study include the following: how many camera traps to run, for how long and at what time of year? Although there have been strong theoretical assessments of camera trap survey design (Gálvez, Guillera-arroita, Morgan, & Davies, 2016; Guillera-Arroita, Ridout, & Morgan, 2010), unfortunately, empirical evaluations using real-world data have been fewer. For example, Si, Kays, and Ding (2014) found that adding camera trap sites was a higher priority than increasing survey length, and Shannon, Lewis, and Gerber (2014) found that precise estimates could be made with surveys of 30–50 sites for common animals, but those species with low probabilities of detection required extended survey lengths, and that adding camera sites was more effective than

lengthening survey duration to improve estimate precision. The influence of seasonality on camera trapping data has been largely neglected to date, probably because most tropical data come from cameras run during the dry season to reduce damage to cameras (TEAM Network, 2008), while most temperate zone data come from the growing season. A few studies have noted seasonal differences including migratory ungulates in the Serengeti (Palmer, Swanson, Kosmala, Arnold, & Packer, 2018) and a peak of coyote detections in California when individuals were dispersing (Larrucea, Brussard, Jaeger, & Barrett, 2007).

The surge in popularity of sampling with camera traps, combined with improvements in technology and data management, has facilitated the accumulation of large centralized datasets from around the world. These datasets can be examined to evaluate the consequences of survey study design across species and locations allowing for general recommendations to researchers and practitioners. We analysed 41 camera trap datasets including 1,771 sites to evaluate three aspects of camera trap study design: (a) how many camera traps should researchers run? (b) how long should they run each individual camera trap? and (c) does seasonality affect results? For each question, we subsampled large datasets to investigate how sample effort and design affect estimates of species richness, individual species detections and occupancy probabilities. To facilitate comparisons of sites from around the world, we used no habitat covariates in our occupancy or relative abundance models. These covariates would improve the precision of estimated parameters (occupancy and detection rate) by helping to explain variation caused by different environments. Therefore, our results on recommended sampling effort to reach a given level of

precision are conservative in comparison to the precision local studies might achieve when including habitat covariates. Our results allow us to offer general recommendations for camera trap survey design to achieve the most precise estimates of species richness, occupancy and relative abundance across a wide range of species around the world.

2 | MATERIALS AND METHODS

We analysed camera trap data from 41 studies from the eMammal (<http://www.eMammal.org>) and TEAM (<http://www.teamnetwork.org>) databases and co-authors (Figure 1; Table S1). Subsets of 28, 16 and 5 datasets were used to examine spatial, temporal and seasonal questions, respectively. We used 1 year of data from each TEAM site. All studies used similar camera trap protocols in that sites were un-baited and were set in grids or stratified-random design (i.e. not on well-established trails), making data directly comparable (Jansen, Ahumada, Fegraus, & O'Brien, 2014). Cameras were set at ~0.5 m above the ground on a tree, or high in the tree canopy (Peru), and set to trigger with passive infrared motion sensor at high sensitivity with no rest period between triggers. The camera brands used (Reconyx, Bushnell, ScoutGuard) had fast trigger times (<0.5 s) to minimize missing fast-moving species and used infrared flashes at night to avoid disturbing animals. Cameras were set to take multiple pictures at each trigger and continued to retrigger as long as animals were in sensor range. Triggers within 60 s of each other were considered one detection.

Our evaluation of study design focuses on the precision of three metrics frequently used by ecologists: species richness, occupancy

and detection rate. We compare species richness of subsampled data to the total number of species detected at a study area by the cameras, not the total number of species theoretically possible based on geographical range maps. Likewise, we compare estimates of occupancy and detection rate from subsamples of data to values calculated with the full dataset, although we have no way of knowing the 'true' value for a given species at a site. We make direct comparisons of occupancy estimates from camera arrays set at different spatial scales, but assume that the occupied site is the small detection zone directly in front of the camera and not some larger area defined by camera spacing (Efford & Dawson, 2012). To simplify our analyses, we consider number of samples and sampling effort separately, although there can be an interaction between these factors (Shannon et al., 2014). Although detection rate can be a misleading measure of relative abundance if field protocols are not standardized (Sollmann, Mohamed, Samejima, & Wilting, 2013), it has been tied mechanistically to abundance (Rowcliffe, Field, Turvey, & Carbone, 2008), and has been shown to reflect animal density in a number of studies using grids or stratified random sampling (e.g. Palmer et al., 2018; Parsons et al., 2017), and we therefore refer to it here as an index of relative abundance.

2.1 | Number of camera points

We subsampled from existing datasets (Table S1) using program R (version 3.3; R Core Development Team, 2018) to evaluate the number of sample points needed for precise estimates of species richness



FIGURE 1 Map showing locations of the 41 datasets used for analyses of the importance of survey duration, survey size and seasonality on estimates of biodiversity variables using camera traps

(using data from 28 study areas), occupancy and detection rate (using data from 20 study areas) within a given protected area. We estimated richness as the number of individual species detected in each study area across all cameras. We estimated detection rate as the total count of detections of each species divided by the number of camera nights (i.e. detections/day) at each study area. We ran occupancy models using the single species occupancy framework (MacKenzie et al., 2002) and estimated detection probability (p), defined as the probability of detecting an occurring species during a 7-day period at a camera site, and occupancy (ψ), defined as the expected probability that a given camera site is occupied, for each species. Although daily periods are sometimes used for occupancy analyses of camera trap data for common species, these weekly intervals allowed us to use the same protocol for all species. We recognize that occupancy estimates for wide-ranging animals detected with camera traps is more analogous to 'use' than true occupancy, though no less informative in terms of habitat use (Burton et al., 2015; Efford & Dawson, 2012). Although some of the cameras from our fine-scale grids might not be spatially independent for wide-ranging species, we note that the independence assumption is not necessary (though it is helpful) since the MLE of ψ is consistent even if occupancy statuses are not independent (Royle & Link, 2006). We constructed models using the package UNMARKED (Fiske & Chandler, 2011) in R. We estimated detection rate and occupancy for two species at each of 20 study areas, the most common species and the least common with at least 100 detections (and therefore enough to have a reasonable chance of models converging). The one exception was for the UCSC Grid study area, where only one species had >100 detections.

We subsampled sites by randomly selecting from one to the maximum number of cameras in the study, using the data collected at subsampled cameras to generate estimates. A minimum of five camera sites was used for occupancy analysis due to model convergence issues. For each of 50 subsamples (without replacement) at each camera sample size, we recorded the mean, standard deviation, standard error and 95% confidence interval for richness, detection rate and occupancy probability. We used the total sample for each camera, which was variable, but should not affect our results. For detection rate, we assume animal movement is constant over the study period so camera deployment length should not affect these estimates or recommendations (i.e. a camera running 5 days captures 10 deer and if it ran 10 days instead it would capture 20). For occupancy, we also did not standardize the number of trap days per camera; however, we tested whether there was a relationship between survey effort and the estimated occupancy probability but found no significant relationship ($T_{37} = 0.867, p = .39$).

To determine how many cameras were adequate to obtain precise estimates of occupancy and detection rate, we set two thresholds: (a) when the width of the 95% confidence interval changed <1% and remained <1% regardless of added cameras, representing the point of diminishing return on investment and (b) when the standard error was <10% of the mean and remained <10% regardless of added cameras, representing a precise measurement. For richness, we assessed how many cameras were necessary to

detect 95% of the total number of species detected with all cameras. We stratified the studies based on latitude (tropical and temperate) and scale of the study (small was ≤ 0.2 km camera spacing, large was ≥ 1.0 km spacing) when considering how many camera sites were needed to meet each threshold. We summarized the effect of camera number on richness in each stratification level by fitting an asymptotic curve to the resampled data points using a nonlinear least squares method.

2.2 | Sample duration

We subsampled long camera deployments (~60 sampling days) to evaluate the effect of sample duration on detection rate and species accumulation across each deployment day for selected species to determine how survey duration affected precision. We selected 24 representative species of large (>100 kg, $n = 6$), medium (5–100 kg, $n = 9$) and small (<5 kg, $n = 9$) mammals including three trophic levels (carnivores, omnivores and herbivores) from surveys with a minimum of 10 camera sites, excluding deployments with less than 20 sampling days (range = 10–77 deployments per study) across five continents (Table S2). These groupings represented potential differences in movements/home-ranges across the taxa but also accounted for some inevitable variation in detection probability associated with the sizes and trophic guilds of target species (Cove, Spínola, Jackson, Sàenz, & Chassot, 2013). We calculated the daily detection rate of each species across all sites with detections within a selected study area and examined how the cumulative daily detection rate changed with increasing camera deployment. We considered the detection rate at the end of the sampling period as the true result for a site and set a threshold of precision as the number of sampling days that were required to obtain an estimate within 10% of this value.

We used negative binomial generalized linear models to determine how this threshold duration varied with three species traits—species-specific trophic guild (e.g. carnivores, omnivores or herbivores), size (small, medium and large), climatic zone (tropical or temperate)—maximum number of days per deployment and final detection rate. To determine which species traits or survey effects most influenced the detection rate bias, we compared eight a priori hypotheses, including a null model, in an information-theoretic framework, based on their Akaike weights (Burnham & Anderson, 2002). These analyses allowed us to consider whether relationships were general to all mammals or specific to guilds or study regions. Furthermore, we plotted the mean per cent detection rate error across all species to visualize an inflection point in the per cent error patterns, such that increasing effort beyond a threshold point resulted in diminishing returns in terms of accuracy (sensu Lashley et al., 2018).

To assess species accumulations, we selected five tropical and five temperate study areas and randomly selected 30 camera sites to represent each study area. We determined the accumulations for each individual camera site in addition to the total accumulation for each study area. For both tropical and temperate regions, the totals of each study area were averaged together to represent how long it

can take to reach a high percentage of total species per region, as determined by the actual camera data.

2.3 | Seasonality

To evaluate the importance of seasonality in camera trap surveys, we calculated monthly and seasonal estimates of mammal detection rates, occupancy and species richness for five locations that experience seasonal differences in either temperature or precipitation and that had at least 1 year of continuous camera data (Table S1). For two temperate climates with seasons determined by changes in temperature (Montana and North Carolina), we defined seasons as summer (April–September) and winter (October–March). For three tropical or subtropical climates with seasons determined by changes in precipitation, we identified seasons as wet and dry, where the wet seasons used were May–October (China), November–April (Peru) and July–December (Panama).

To consider the effect of seasonality on estimated species richness at each site, we calculated the total number of species observed each month. We present observed species richness for sites with equal effort between months (Montana, North Carolina, China and Panama) and where sampling effort was unequal (Peru), we present estimated richness from the iNEXT package (Hsieh, Ma, & Chao, 2016). To facilitate visual assessment of seasonal trends in species richness and detection rates, we fit a nonparametric LOESS smoother line to the points.

We calculated the detection rate of each species for each study area. To identify whether season was a significant predictor of detection rate at a study site, we included season as a predictor and species-specific detection rate as the response in a quasi-Poisson generalized linear model, adjusted for overdispersion (Wedderburn, 1974). We considered season to have a significant effect on detection rate if the 95% confidence interval around the season coefficient did not overlap with zero.

We also quantified the effect of season on species occupancy and detection. We created species-specific detection histories by splitting continuous camera deployments into intervals representing seven camera trap nights. For the Panama dataset (BCI plots), cameras were not deployed continuously, rather they were moved every 7–12 days within each 1 of 10 1-ha survey blocks. In this case, each 7- to 12-day interval represents a separate deployment within the same survey block. For each species, we used season of deployment as a predictor, calculated the season coefficient in occupancy and detection models using package UNMARKED in R, and if the 95% confidence interval around the season coefficient did not overlap with zero we considered it a significant effect.

3 | RESULTS

We examined camera trap sampling design patterns for 106 mammal species and used common names when describing results in the text, but present taxonomy in Table S2. Animal detections not identified to the species level were not included.

3.1 | Number of cameras

On average, large-scale (≥ 1.0 km spacing), tropical study areas required more cameras ($M = 35 \pm 1$ SE) for species richness to reach an asymptote than did smaller-scale (≤ 0.2 km camera spacing) sites (Figure 2; Table S3). With much lower total species counts, small-scale sites detected 95% of total species with less effort, requiring 22 ± 3 sites in the more diverse tropics and 17 ± 4 in the temperate studies. The number of cameras necessary for richness to level off varied with camera spacing ($\beta = 70 \pm 23$, $t = 3$, $p = .0005$), with large-scale camera grids requiring more sites. Only two large-scale temperate study areas were available and levelled off at 17 or 18 species (Table S3) but were not included in the graph due to low sample size.

We plotted the improvement in precision of detection rate and occupancy estimates with increasing number of cameras for 39 species from 20 study areas (Figure 3; Table S1). The example plots in Figure 3 illustrate how we determined when an estimate was precise (10% or 20% SE from final value) and when adding additional cameras did not lead to significant improvements in the estimate (confidence intervals improve by $<1\%$). We found a strong negative relationship between the occupancy level of a species and the number of cameras needed to get a precise estimate (Figure 4c) and the point of diminishing returns (Figure 4d). Furthermore, occupancy could only be estimated with certainty for species with occupancy values >0.7 (Figure 4c; Table S4). The number of cameras needed to get precise occupancy estimates was marginally correlated with detection rate (linear regression: $\beta = -13.3 \pm 7.1$, $t = -1.89$, $p = .08$).

There was also no relationship between the detection rate of a species and the number of cameras needed for precise estimates

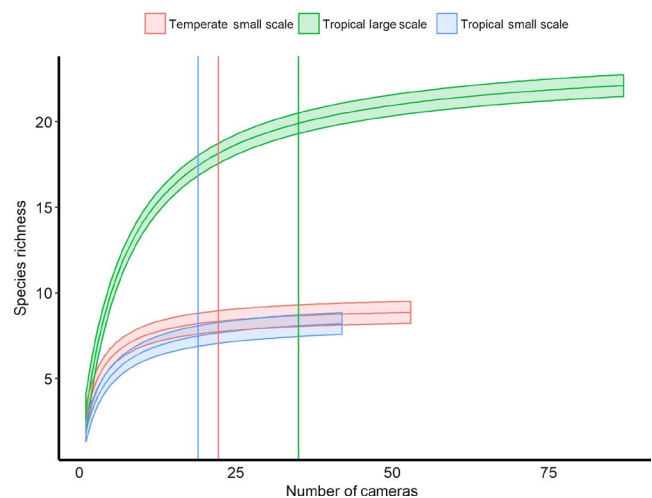


FIGURE 2 Species accumulation curves with increasing camera sites showing average (lines) and SE (shading) across 19 tropical and 9 temperate study areas. Vertical lines show where a class of sites reached 95% of all the total number of species recorded, which was least for small-scale (≤ 0.2 km camera spacing) tropical study areas (17 ± 4 SE sites), followed by small-scale temperate (22 ± 3 sites) and large-scale (≥ 1.0 km spacing) tropical studies (35 ± 1 sites). Results per site are in Table S3

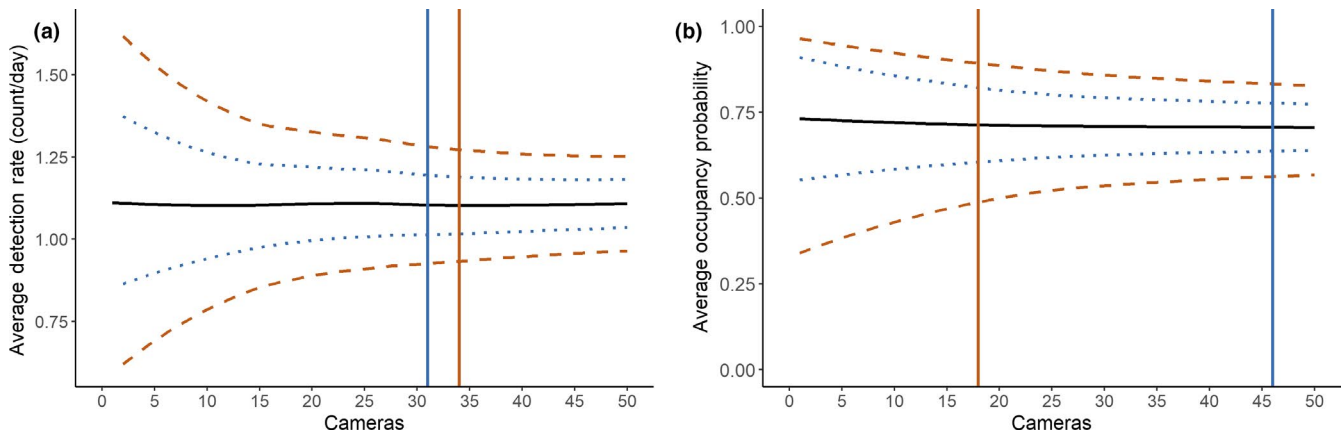
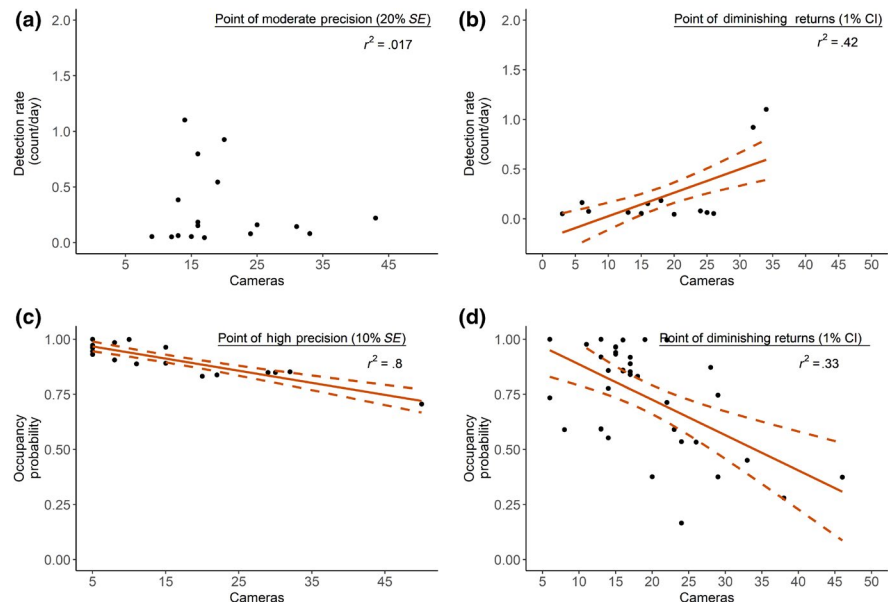


FIGURE 3 Examples of changes in detection rate (a) and occupancy (b) with increasing number of cameras at a site for two species: white-tailed deer (a) and red acouchi (b). The black line represents the average of 50 subsamples while the blue dashed line shows standard error and the red dashed line shows the 95% confidence intervals. For each species, we calculated the number of cameras needed to reach a precise estimate with standard error that was 10% of the estimate (solid blue line representing point of high precision) and the point of diminishing returns where the change in the confidence interval between timesteps was $<1\%$ (red solid line representing point of diminishing return)

FIGURE 4 Number of camera sites needed to estimate detection rate (a, b) and occupancy values (c, d) to a point of precision ($SE < 20\%$ A or $< 10\%$ C) or to the point of diminishing returns (confidence intervals improve by $< 1\%$ with additional cameras, b, d). Each dot on the graph represents a species, with example plots showing how these were derived in Figure 3. Only two species reached high ($< 10\%$ SE) confidence estimates for detection rate so we show the results for a lower (20%) confidence level in A. No trend line is provided in A due to the low coefficient of determination. Values and species names are reported in Tables S4 and S5



of detection rate, although only two species reached our 10% SE cut-off (Table S5), so we had to evaluate this relationship at 20% SE (Figure 4a). When considering the point of diminishing returns, there was a positive relationship, indicating that species with higher detection rates required more camera locations before the confidence intervals reached an asymptote.

3.2 | Sample duration

At a single camera site, species richness increased such that after the first 30 days, each camera detected $96.67\% \pm 0.01 SE$ or $85.62\% \pm 0.02 SE$ of the species it would detect over 60 days in temperate or tropical sites, respectively (Figure 5). However, when all cameras at a study area were considered together, species richness plateaued

rapidly, with $89.7\% \pm 5.60 SE$ of the species at temperate sites detected in 2 weeks and 100% in 30 days. For tropical sites, $84.9\% \pm 5.05 SE$ of species was detected in 2 weeks, $97.1\% \pm 1.82 SE$ in 30 days.

Since detections typically accumulate slower than days, the ratio of detections/day is erratic and highly erroneous at smaller (< 2 weeks) sampling intervals, but then rapidly improve. Across species, the mean time needed to obtain an estimate within 10% of the final estimate was $34.4 \pm 2.5 SE$ days (Figure 6). The variation in time needed to get a precise measure of detection rate was best explained by final detection rate (Akaike weight = 0.41, Table S7), with some additional model support suggesting a difference between temperate and tropical study areas (Akaike weight = 0.15, Table S7). We used those two covariates to make predictions of survey length requirements across detection rates that we observed in temperate and tropical study areas (Figure 7).

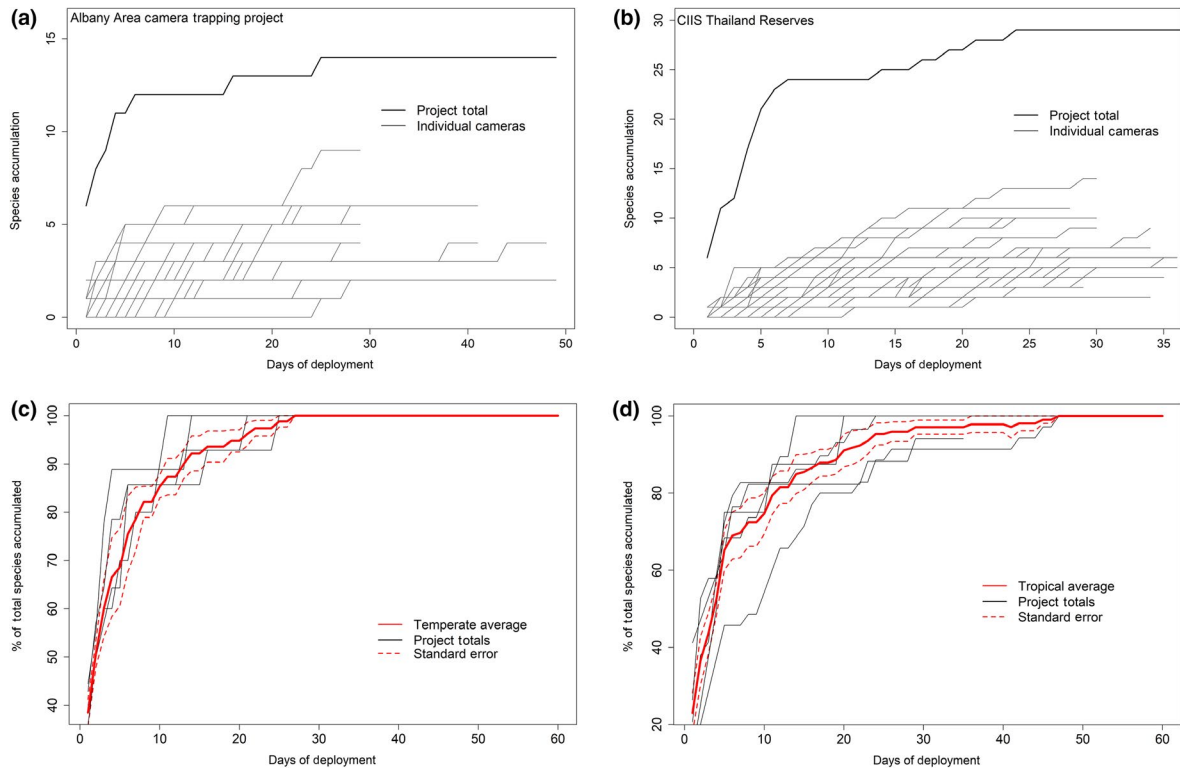


FIGURE 5 Example species accumulation curves at one temperate (a, Albany Area) and one tropical study site (b, Thailand Reserves) illustrating the rate of species detection by individual cameras (grey lines) and for the whole survey (black lines). Eight additional sites are graphed in Figure S1. For five temperate (c) and tropical (d) sites combined, curves are shown in proportion to the total number of species they detected at the end of the 60-day survey

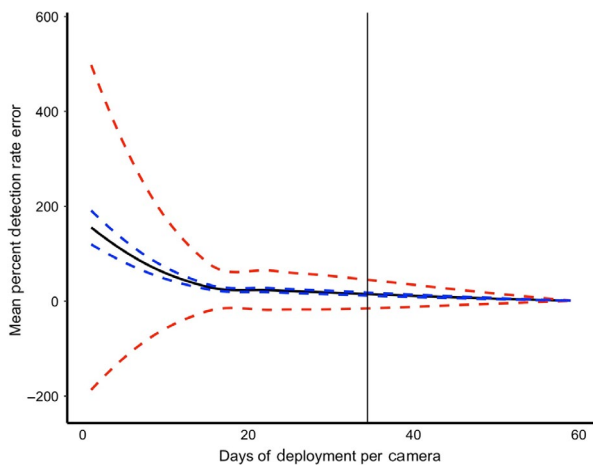


FIGURE 6 Change in the accuracy of detection rate estimates with increased sample duration showing mean per cent daily detection rate error, with 95% confidence intervals (red dashed lines) and standard error (blue dashed lines). These are estimated from 24 representative species at 11 study areas across five continents. The vertical line (34 days) represents the mean number of days at which the per cent error decreased below 10% for the remainder of the survey (Tables S6 and S7)

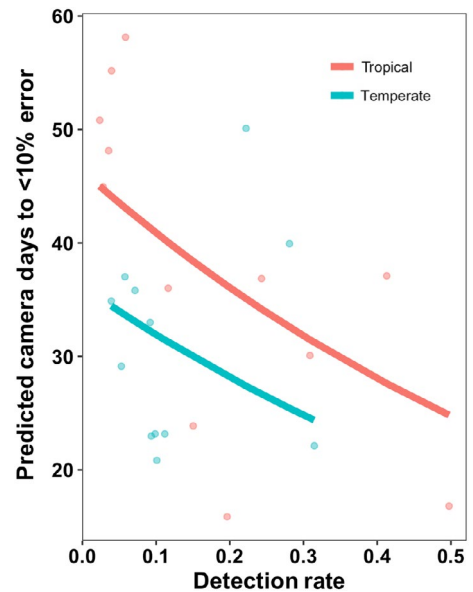


FIGURE 7 Model predictions of the number of days of camera trap sampling before the per cent error of the estimated detection rate decreases below 10% based on negative binomial regression models with the final species detection rate and tropical versus temperate zones as predictors

TABLE 1 Summary of significant seasonal variation in occupancy and detection rate models for 70 species across five sites. '0' indicates no variation, '+' and '-' indicate higher or lower values in the winter (Montana and North Carolina) or wet season (China, Panama and Peru). Models that did not converge have blank cells. Species indicated with * had so few detections in a season that statistical models did not converge, but clearly showed strong seasonal patterns such as complete absence due to hibernation. Model parameter values are available as supplemental material (Figure S2; Table S9)

	Model occupancy	Model detection	Detection rate	Notes
Montana				
Columbian Ground Squirrel			–*	Hibernates
Brown Bear			–	Hibernates
Moose			0	
Striped Skunk			0	
White-tailed Deer	0	–	–	Elevational migrant
White-tailed Jackrabbit			0	
Gray Wolf			0	
Elk	–	0	0	
American Badger			0	
North American Porcupine			0	
Bobcat	0	0	0	
Coyote	+	–	0	
Snowshoe Hare	0	0	0	
Puma	0	0	0	
Mountain Cottontail	0	0	0	
American Red Squirrel			0	
Mule Deer	+	+	0	Elevational migrant
Prairie Ridge, NC				
Woodchuck			–*	Hibernates
Coyote	0	–	0	
Virginia Opossum	+	–	0	
Northern Raccoon			0	
White-tailed Deer	0	0	0	
Eastern Cottontail	0	0	0	
Bobcat	0	0	0	
Eastern Gray Squirrel	0	–	0	Seasonal seed hoarder
Gray Fox	+	0	+	
Red Fox			0	
China				
Wild Boar			0	
Reeves's Muntjac	0	–	–	
Edwards's Long-tailed Giant Rat			0	
Hairy-fronted Muntjac	0	0	0	Elevational migrant
Pallas's Squirrel			0	
Hog Badger	0	0	0	
Chinese White-bellied Rat	+	+	+	Strong seasonal breeder
Masked Palm Civet	0	+	0	
Panama				
Collared Peccary	0	–	–	
Northern Tamandua			–	
Red Brocket Deer	0	–	–	

(Continues)

TABLE 1 (Continued)

	Model occupancy	Model detection	Detection rate	Notes
White-nosed Coati	0	0	–	
Common Opossum			0	
Agouti			0	
Tayra			0	
Paca	0	+	0	
Baird's Tapir			0	
Red-tailed Squirrel			0	
Ocelot	0	0	0	
White-faced Capuchin			0	
Nine-banded Armadillo	0	0	0	
Peru Canopy				
Tayra			+	*
Brazilian Porcupine	0	–	0	
Western Woolly Opossum	–	0	0	
Olingo	0	0	0	
Hairy Saki Monkey	–	0	0	
Tamandua	0	0	0	
<i>Microsciurus</i> sp.			0	
Dwarf Porcupine	+	–	0	
Black-mantled Tamarin	0	0	0	
White-fronted Capuchin	0	0	0	
Spix's Night Monkey	–	+	0	
Common Woolly Monkey	0	0	0	
Kinkajou			0	
<i>Scurius</i> sp.			0	
Common Squirrel Monkey	0	0	0	
Two-toed Sloth	0	+	0	
Yellow-handed Titi Monkey			0	
Red Howler Monkey	0	0		

3.3 | Seasonality

We examined the effects of seasonality on animal communities at five study areas with varying latitudes and species compositions (Table S8). All five sites showed seasonal effects for some but not all species (Table 1; Table S9; Figure S2). Although there was no clear seasonal trend in species richness for the site in China (Figure 8a), overall detection rates increased in the wet season (Figure 8b), and there was species-specific variation in the detection rates by season (Figure 8c,d). For example, we found much higher detection rates in masked palm civet, hog badger and Chinese white-bellied rat during the wet season, weaker pulses of Reeve's muntjac and wild boar during the dry season, and little seasonal variation in the detection rates for other species.

The proportion of species with significant seasonal changes in occupancy or detection probability was surprisingly consistent across four sites, being 37.5%, 37.5%, 37.5% and 38.4% in Montana, China,

Peru and Panama, respectively; while for North Carolina it was 50.0% (Table 1; Figure S2). However, when considering the magnitude of the effect in terms of the average size of the change in detection rate (higher season/lower season) for species where detection or occupancy models indicated a significant seasonal effect, the two temperate sites had relatively larger changes (Montana: 480% change, North Carolina: 390% change) than the two tropical sites (Peru: 230%, Panama: 180%), while the subtropical Chinese site average change was 470%.

4 | DISCUSSION

In the most comprehensive empirical study on camera trap survey design to date, we evaluated how the number of cameras deployed, the length of time they are run, and the seasonality of the site affect estimates of mammal species richness, occupancy

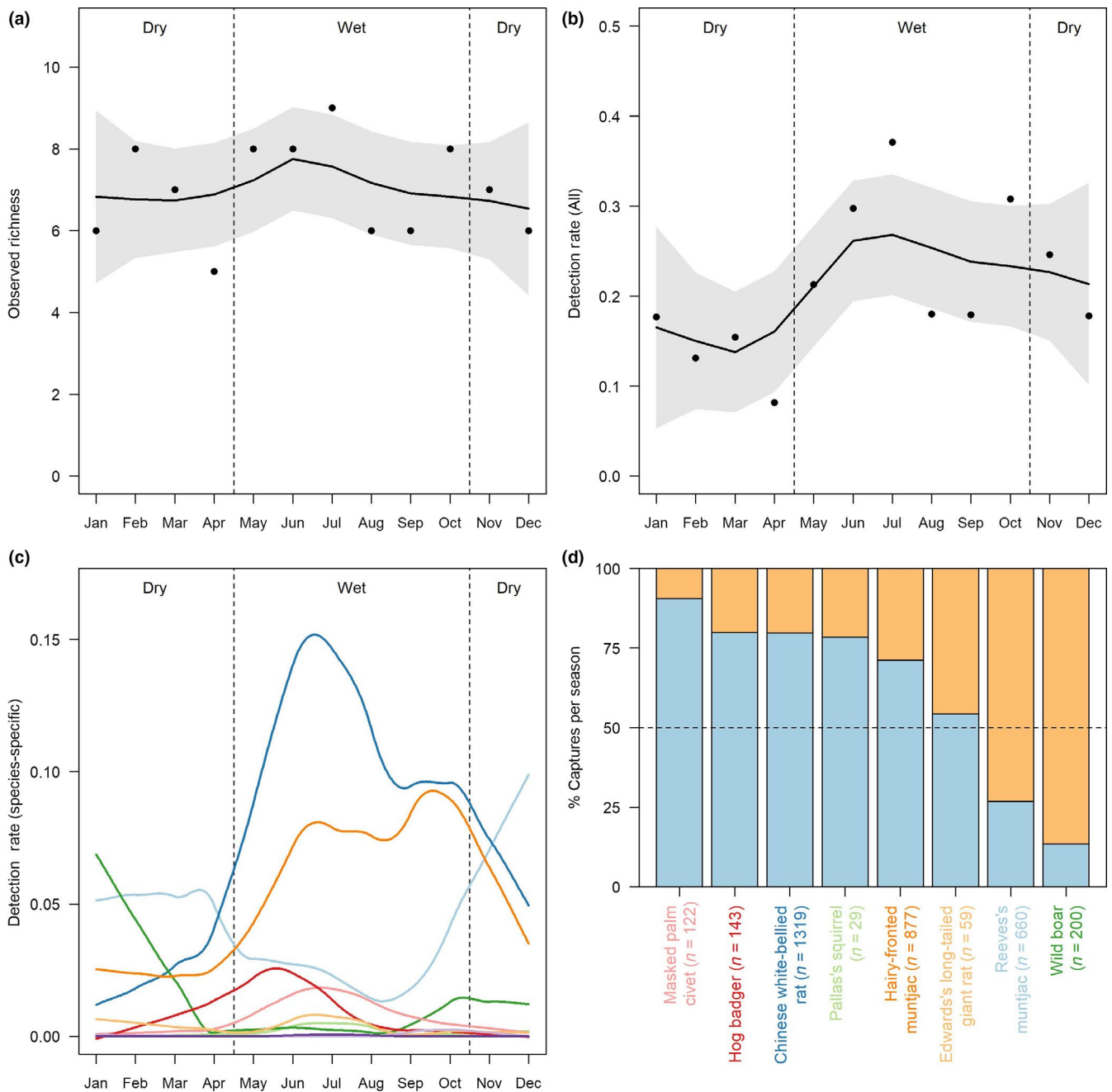


FIGURE 8 Seasonal variation shown as monthly averages for (a) estimated species richness, (b) total mammal detection rate, (c) species-specific detection rate (for species with >20 records) and (d) seasonal averages for mammals surveyed by camera traps (for species with >20 records, blue shows wet season) from 2009 to 2011 in Gutianshan Plot, China. Points are average monthly observed richness (a) and detection rates (b); lines are smoothed observed richness (a) and smoothed average detection rates (b, c); shaded areas are approximate 95% confidence intervals around smoothed averages. The species in plot (c) follow the colour coding in (d), and both only show species with >20 records. The raw data for all sites are presented in Table S9, seasonal graphs for sites in Montana, North Carolina, Panama and Peru are presented as Figure S2

and detection rates. Our samples include 41 study areas across 20 countries on five continents, making our results broadly relevant to others designing camera trap studies. All cameras were run in systematic or stratified random designs, off major trails and without bait, providing relatively unbiased measures of the animal community and offering comparable data across a variety of habitats.

4.1 | Number of cameras

We found that more camera sites (~35) were needed to detect a high percentage of species richness for larger-scale studies. A likely explanation is that larger-scale studies sample a greater diversity of habitats and have a larger component of β -diversity, which serves as a good reminder that species lists from small-scale surveys will

be incomplete representations of the larger area. Given higher species richness in tropical areas, it was surprising that both tropical and temperate small-scale sites required similar number of cameras (17–22) to detect 95% of the total species eventually detected with the full dataset. Given the variation across studies, we recommend that studies aiming to quantify the diversity of species in an area use at least 35 camera sites for large-scale surveys (≥ 1.0 km spacing), and 25 for small-scale (≤ 0.2 km camera spacing) tropical sites.

Occupancy and detection rate are two metrics often used as indices of abundance to compare across years or sites for monitoring population trends or testing ecological hypotheses, and are the most common metrics used to study species that cannot be uniquely identified (Kays et al., 2017). We found that more cameras were needed to get precise estimates of species with lower occupancy values (i.e. less common species) which is in agreement with recent studies (Beaudrot, Ahumada, O'Brien, & Jansen, 2019; Shannon et al., 2014). Among the 39 species considered, occupancy could only be estimated precisely ($SE < 10\%$ of occupancy estimate) for species with high (> 0.7) occupancy probabilities (Figure 4a; Table S4). Extrapolating this linear relationship suggests that 3–4 times more cameras (~150 camera sites) would be needed to produce precise estimates for species with an occupancy probability of 0.25. This is worrisome given that rare species are the most important to monitor, and that low occupancy probabilities are common in camera trapping studies. For example, almost half (48%) of the 158 carnivore populations evaluated in a recent global analysis had occupancy levels < 0.25 (Rich et al., 2017). Adding ecological covariates to occupancy models would help increase precision of occupancy estimates, and are therefore especially important for working with species with low occupancy probabilities. These models might allow more precise estimates with fewer camera sites than our results suggest, as we did not include any covariates to enable large-scale comparisons.

Community-level occupancy models (Dorazio, Kéry, Royle, & Plattner, 2010) might also help improve the precision of occupancy estimates for rare species by sharing information across species, but there are extensive assumptions about guild-specific detection probability relationships that need to be considered (Pacifi, Zipkin, Collazo, Irizarry, & DeWan, 2014). Detecting ecological relationships will always be difficult for species with few detections and we suggest that these situations might warrant the use of lures or baits, or adaptive sampling (Pacifi, Reich, Dorazio, & Conroy, 2016; Specht et al., 2017).

We expected that it would require fewer cameras to precisely estimate occupancy for species with higher detection rates, since data would presumably accumulate faster, but we found no relationship (Table S5). We suspect that this reflects patchy space use by animals, with higher detection rates being driven by repeated use of the same sites, rather than many sites across the camera array. Alternatively, this might be simply a principal of the data structure. One possibility is related to pseudo-Poisson patterns of count data, where variation and mean tend to be proportional and the lower bound becomes less constraining at higher densities (Guisan, Edwards, & Hastie, 2002). Another possibility could be that since the count cannot go

below zero, when you have rare species there are so many estimates right around that lower bound that precision is actually quite high, whereas with more abundant species we would have a lot more variation in the count and lower precision.

We were surprised to not find a relationship between detection rate and the number of cameras within a study area. Only two species reached our 10% SE precision cut-off for detection rate, and even when considering a lower point of precision (20% SE), there was no strong tendency for species with higher detection rates to be easier to survey with fewer sites (Figure 4a). In fact, we found that species with higher detection rates required more cameras to reach the point of diminishing returns. We suspect this difference between occupancy and detection rate stems from a higher spatial variation in detection rates within a study site. As a binary variable (each site is either 0 or 1), occupancy probabilities are capped at 1 and inherently less variable than detection rates, and thus appear to be easier to estimate precisely from camera traps. It is important to note that we used raw detection rate values and made no attempt to account for variation within sites with ecological models. Adding habitat covariates and using model estimates for detection rates would likely improve the precision of detection rate estimates, adding important ecological inference, and making comparisons between sites more valid.

4.2 | Sample duration

By subsampling long camera deployments, we were able to evaluate the relationship between sample duration and accuracy and offer recommendations for optimized study design. In general, the number of species detected by a camera rapidly accumulated during the first 2 weeks of deployment, after which few new species were detected. Only the more diverse tropical sites continued to accumulate species up to about 1 month (Figure 5).

We found that detection rates—the widely used measure of relative abundance—were highly variable for the first 2 weeks of camera deployments: the addition of a single detection could dramatically change the estimate. However, after 2–3 weeks, there was a sharp improvement in precision for all species, and from about 1 month onwards, estimates were within 10% of the estimate from the full 60-day samples (Figure 6). The exact sampling duration needed to reach this 10% precision level varied depending on the final detection rate of the target species, with precise estimates being reached sooner for species with higher detection rates, with slightly different relationships for tropical versus temperate areas. The higher error rates for apparently rare species (based on final detection rates) showcases that researchers should likely implement species-specific efforts when targeting rare species but might achieve accurate relative abundance information for common species within short sampling windows. Similar to our examinations of detection rate and the number of cameras, spatial heterogeneity among sites most likely influences these site-specific detection rates and capture rates might therefore be subject to more local variation in detectability

due to microhabitat variation, which should be accounted for in model-based approaches (Kolowski & Forrester, 2017).

In practice, species richness and relative abundance measures for a study area are not taken from single camera points but derived from an array. Thus, our analysis of the performance of single cameras is most relevant when considering the return on investment of time, rather than absolute error rates of each individual camera. In this case, the stabilization of detection rate between 2 and 3 weeks suggests that 3 weeks should be the minimum deployment length, while estimates will continue to improve up to about 1 month. These recommendations agree with earlier studies that point out that increasing the number of locations is generally better than sampling longer at the same site for detection rate (Si et al., 2014), but our results draw from a broader dataset of species and localities.

4.3 | Seasonality

All five sites we examined for seasonal dynamics had a mixture of species with and without seasonal variation in occupancy and/or relative abundance. Thus, sampling an area in only one season would not necessarily yield estimates of animal abundance and species richness that are representative. The number of species at each site showing some seasonal trends was high, ranging from 37% to 50% of the mammal community, without obvious latitudinal trends (Table 1). However, the magnitude of the effect was roughly two times stronger in the two temperate study areas we analysed, where species are known to migrate, hibernate or seasonally cache food. Hibernation and seasonal migration are not known for the mammal species that showed seasonal variation in Peru and Panama, and we suspect that these patterns could be caused by seasonal breeding or shifts in foraging strategies in response to changes in fruit availability. Species detectability is also known to change from wet to dry season in Panama (Rowcliffe, Carbone, Jansen, Kays, & Kranstauber, 2011), highlighting the importance of using an analytical framework that accounts for detectability. The subtropical montane Chinese study area had similar effect sizes to the temperate study areas. Some of the specific patterns for the Chinese species can be explained by known behaviours of reducing activity during the cold (Masked palm civet; Zhou et al., 2014), elevational migration (Hairy-fronted muntjac; Zheng, Bao, Ge, & Zheng, 2005) or seasonal breeding (Chinese white-bellied rat; Bao, 1993).

While it might not be surprising that all animal communities would have strong seasonal effects, our results illustrate the importance of taking season into account when planning field surveys or making comparisons between existing data. Although some of these changes were predictable based on animal biology, most were not, especially in tropical sites (Table 1). Furthermore, the simple two-season comparison we used for our analyses belies a more complicated temporal pattern seen for many species when looking at variation in abundance over a finer (i.e. monthly) scale. For example, at our Montana study area, Columbian ground squirrel detections

peaked in early summer, white-tailed deer peaked in late summer, and mule deer peaked at the transition between winter and summer (Figure S2c).

4.4 | Study design recommendations

Based on these analyses, we recommend that studies aimed at estimating species richness and relative abundance/occupancy of mammal species use arrays of at least 40–60 camera traps run for 3–5 weeks. Studies targeting rare species will need more camera locations but could also benefit from the use of target-specific attractants or more adaptive study designs (Pacifiçi et al., 2016). Studies aimed at estimating species diversity over small areas (i.e. <1 km²) may use fewer cameras (~20), but should note this will be an incomplete record of diversity over larger scales. Study area averages of detection rate required more effort to estimate precisely than occupancy, due to high variation within camera arrays, so we recommend comparisons of detection rates be model based and include local covariates to help explain small-scale variation, which should also provide additional ecological inference about the target species. Finally, comparisons across study areas or over time must account for seasonality, which had strong impacts on mammal communities in both tropical and temperate sites.

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AUTHORS' CONTRIBUTIONS

R.K., C.B., H.M.B., M.V.C., C.P.H., A.W.P., B.S.P., S.G.S., K.P. and M.S. conceived the ideas, designed the methodology and analysed the data; B.S.A., M.B.-W., M.B., S.F.B., P.D., S.E., A.L.S.G., P.A.J., T.W.K., M.G.M.L., F.S., F.R., D.S., X.S., W.R.S. and W.J.M. contributed data; R.K. led the writing of the manuscript. All authors

contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All camera trap detection data used in this paper are available at Dryad Digital Repository <https://doi.org/doi.org/10.5061/dryad.p8cz8w9m2> (Kays et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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