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Comparison of species richness and detection between line transects, ground camera traps, and arboreal camera traps

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Abstract

Monitoring trends in the occurrence of species over time is important for informing conservation plans and concurrent management actions. Understanding the effectiveness of field methodologies for collecting accurate and precise data is crucial for optimizing allocation of sampling effort and resources. In this study, we compared mammalian species richness and detection probabilities between three field methodologies: line transects, ground camera traps and arboreal camera traps in Nyungwe National Park, Rwanda. Arboreal camera traps may be suitable for monitoring mammal communities with arboreal species, but their relative effectiveness compared to the more common field methods, line transects and ground camera traps, is relatively unknown. Using single-season occupancy models with multi-species data and single-species multi-method occupancy models, we estimated mammalian species richness and detection probability for each method and combination of methods. In addition, we estimated single-species occupancy and detection probability by method for six diurnal primate species. And, we tested for the effect of height on a tree on estimated occupancy probability and detection probability for arboreal camera traps. Overall, for all species the combination of ground and arboreal cameras was the most effective methodology in terms of highest estimates of occupancy and detection coupled with highest precision. However, for the six primate species the most effective method differed between species. The height of the arboreal camera trap in the tree did not significantly affect estimates of occupancy or detection. We suggest using all three field methods concurrently to maximize detection of all species; however, if only two methods can be deployed combining arboreal and ground cameras provided the highest and most precise estimates of occupancy and detection. The addition of arboreal camera traps could improve detection of species and improve future species monitoring programs.

Introduction

Monitoring species occurrence and distribution over time is often important for setting conservation priorities and assessing management actions (Goldsmith, 2012; Stein *et al.*, 2013; Sutter *et al.*, 2015). For many species of conservation concern, monitoring plans are developed to track trends in species occurrence or abundance within a specified management unit (e.g. park or reserve). Effective management plans can be difficult to develop because the need for accurate and precise data estimates can be hampered by resource limitations. Identifying the most effective approaches for monitoring wildlife is therefore critical for successful conservation.

For tropical mammal species such as primates, field data on species occurrence and distribution have traditionally been gathered using line transect surveys (Voss & Emmons, 1996; Peres, 1999; Marshall, Lovett & White, 2008; Buckland *et al.*, 2010). During these surveys, human observers walk a predefined path and record observations of target species and their distance from the path. One significant limitation of line transects surveys is that they are typically conducted

during daylight hours, thus ignoring nocturnal species. Line transect surveys are occasionally conducted at night for nocturnal species, but this is not possible at many sites due to researcher safety or lack of permission or access to a site at night. Additionally, line transect surveys in general are not effective for detecting species that are rare or elusive, or species that use evasive behaviors when startled by humans conducting the surveys (Plumptre, 2000).

Over the past two decades, camera traps have become a widely used method for assessing the occurrence and distribution of mammal populations in many parts of the world because they are cost-effective and minimally invasive (e.g., Ahumada *et al.*, 2011; Tobler *et al.*, 2015). Cameras traps allow for continuous 24-h data collection with little human disturbance. Cameras are often oriented to focus at ground level, thus are more likely to photograph ground-dwelling species. Arboreal species that have limited contact with the ground, including many primate species, are thus less likely to be detected from cameras with a ground orientation. To address this, line transect surveys, which focus on both terrestrial and arboreal species, can be combined with ground camera trapping to create two lines of inference to inform species occurrence. Alternatively, camera traps have been deployed in tree canopies specifically to detect arboreal species as a single field method (Gregory *et al.*, 2014; Bowler *et al.*, 2017) or as an additional field method as part of multi-species monitoring programs (Whitworth *et al.*, 2016; Bowler *et al.*, 2017). The effectiveness of these arboreal cameras compared to line-transects or ground focused cameras is largely unknown.

A critical component of wildlife monitoring program design is to estimate imperfect detection (i.e. some species may be present even if they are not observed). Failing to account for imperfect detection can result in biased estimates of site occupancy, which can lead to incorrect management decisions based on inaccurate inferences (Kéry & Schmid, 2004). In their simplest form, field data from line transects and camera traps can be reduced to presence–absence information for each species of interest at each site. Site occupancy models can then be fit to species occurrence data to estimate species richness and detection probabilities (Burton *et al.*, 2012; MacKenzie *et al.*, 2017; Moore *et al.*, 2019). Rigorous comparisons of data collection methods using the same model to estimate species richness and detection probability are limited, but are needed because detection probability can vary between methods (Lyra-Jorge *et al.*, 2008; De Bondi *et al.*, 2010; Steinbeiser *et al.*, 2019). Specifically, data collection methods with low detection probabilities are more likely to underestimate species richness (Williams, Nichols & Conroy, 2002).

Here, we analyzed species occurrence data that were simultaneously collected along transects using three field methodologies: (1) line transect surveys, (2) ground camera traps, and (3) arboreal camera traps in Nyungwe National Park (NNP), Rwanda. We compared point estimates and parameter uncertainty for species richness and probability of detection using data combined from all three field methods, from each combination of two field fields, and from each field method individually. We used single-season occupancy models which accounted for imperfect detection, and multi-species data (MacKenzie *et al.*, 2002, 2017). Given that camera trap approaches are non-intrusive and have less observer influence on species' presence, we hypothesize that camera traps will produce a higher estimate of species richness and detection probability than line transect surveys, and that these estimates will be more precise. Secondly, we focused on primate species because NNP is considered a primate diversity hotspot (Plumptre *et al.*, 2007). We used single-season, single-species, multi-method occupancy models (Nichols *et al.*, 2008) to compare estimated detection probability for each of the six diurnal primate species between the three field methods. We hypothesize that arboreal camera traps will have the highest detection probability for the monkey species, while ground cameras traps will have a higher detection probability for chimpanzees due to the amount of time these species spend in each substrate (Wildlife Conservation Society, pers. obs.). Lastly, we tested whether the height at which arboreal camera traps are fixed to the tree affected the estimated species richness or detection probability. We hypothesize that the cameras placed higher in the trees will record higher species richness and detection probability based on the findings of a previous study (Bowler *et al.*, 2017).

Materials and methods

Study site

Our study was conducted in NNP, a montane tropical forest located in southwestern Rwanda (2°15′–2°55′S, 29°00′-29°30′E; Fig. 1). NNP covers a variety of habitat including rain forest, bamboo forest, savannah, and swamp. NNP is a top priority site for biodiversity conservation because it contains populations of several endemic and globally threatened species including the endangered eastern chimpanzee (Plumptre *et al.*, 2007, 2002). The park is 1019 km^2 in size and covers an elevational range from 1451 to 2950 m. NNP is contiguous with Kibira National Park in Burundi on the southern border and is surrounded by dense human population on all other sides (Plumptre *et al.*, 2002).

Field methodology

Data were collected at 18 sites within NNP in 2017 (Fig. 1). The majority of the sites were near the main road that bisects the park, with two additional sites in the north of the park, two sites along the road south to Burundi, and two sites south of the road near the eastern border of the park. These sites covered an elevational range of 1688–2952 m. The dominant habitat type of all sites was continuous rain forest; however, a few sites crossed over small patches of other habitat types (six crossed through swamp, two crossed open savannah, and one site crossed through shrub habitat). Shrubs grow in areas where fire had destroyed the native vegetation. Bamboo forest only covers a small portion of the park and was not covered during this survey due to safety

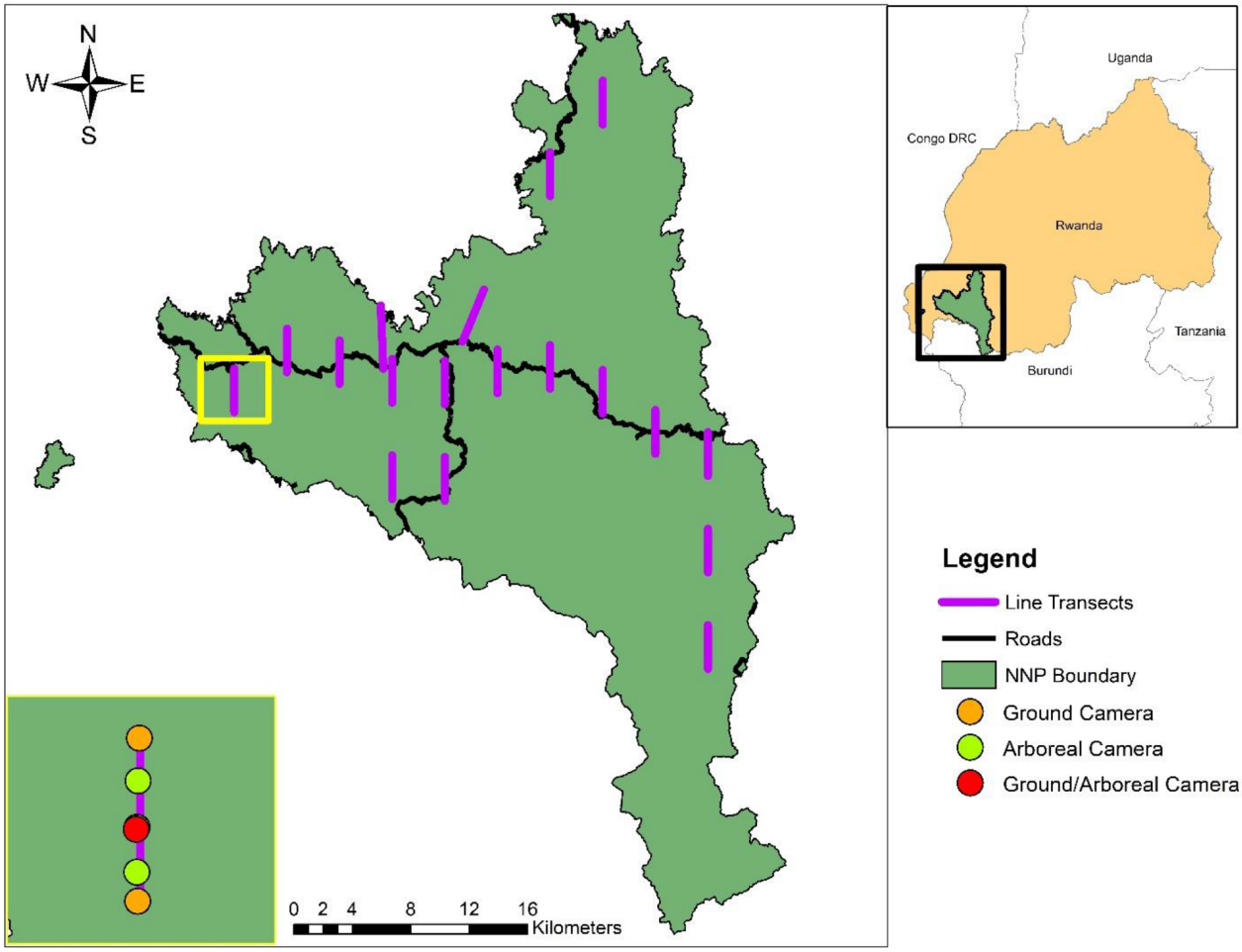

Figure 1 Overview map of Nyungwe National Park (NPP), Rwanda including the location of transects, and the configuration of cameras traps per transect. Ground/Arboreal Cameras denotes a location where both types of cameras were deployed.

concerns. Data were collected during this study using three field methodologies: line transects, ground camera traps, and arboreal camera traps. The field effort required to collect data using these methods was equivalent across the study, with two field days required for walking surveys, and/or deploying and retrieving cameras.

Line transects

Line transect surveys were conducted twice in 2017, between July and October, along a series of 18 pre-established straight-line transects (Fig. 1). Transects varied in length between 3000 and 4500 m (mean = 3284 m; total = 118.23 km). Transects were walked in teams of three researchers starting between 5:20 AM and 6:33 AM and ended between 9:40 AM and 1:20 PM. Each line transect survey took between 4 and 7 h to complete (mean = 5 h). When species were sighted during a transect walk, data were collected on the type of species, number of individuals, distance to transect, and GPS coordinates of the sighting. Only direct sightings of an animal were included in this study. In addition, because surveys were conducted during daylight hours, strictly nocturnal species were not available for detection using this method.

Camera traps

Camera trap models used included Reconyx PC800 Hyperfire (Holmen, WI, USA) infrared professional cameras, HC500 Hyperfire semi-covert infrared cameras, and HC600 Hyperfire infrared digital cameras. Camera models were randomly chosen for each location, with no systematic differences between the cameras used in the canopies versus at ground level. Camera traps were placed within 50 m of the transect at the designated location where there was an available tree for attaching a camera facing North or South to avoid direct sunlight. Each camera was set to take three photos each time that it was triggered with no photographic delay between photos and was set to high sensitivity to avoid missing animals. Sample photos were taken with all cameras during

deployment to ensure that they were capable of capturing all animal that moved in front of the cameras. No bait was used at camera stations. Cameras were in the field for 30 days total, which was divided into two 15-day sampling occasions, with cameras active 24-h per day. Camera trap photos were entered into the Wild.ID software (TEAM Network, 2018) for identification.

Ground cameras

Ground cameras were placed at the beginning, middle, and end of each of the 18 transects used for the line transect surveys (Fig. 1), which resulted in a total of 54 ground cameras deployed in this study. Ground cameras were placed between 0.6 and 1.5 m (mean = 1.01 m) off the ground. This variation in height was due to the slope of the land in which the trees were located. On steep slopes it was sometimes necessary to fix a camera at a slightly higher or lower height so that it could be angled appropriately. Of the 54 cameras, 52 recorded usable data, one camera had an unknown failure after deployment and one camera was stolen during the study period. Because cameras were placed near the ground, strictly arboreal species were not available for detection by this method.

Arboreal cameras

Arboreal cameras were placed halfway between the beginning and the middle of the transect, at the middle of the transect, and halfway between the middle and the end of the transect, for the 18 transects used in the line transect surveys (Fig. 1), which resulted in a total of 54 arboreal cameras deployed. The arboreal cameras were fixed to a tree between 4 and 17 m high (mean = 8.5 m), facing horizontally along a branch of the tree, such that all species that move along the branch will be captured on the camera. All cameras recorded usable data; however, three cameras stopped taking photos before they were collected due to battery depletion. Because cameras were placed within trees, strictly terrestrial species were not available for detection by this method.

Occupancy models

We developed competing models for three analyses aimed at understanding the efficiency of three field methods measured in terms of estimated species richness and detection probability and the precision of these estimates. Our first objective was to compare species richness, detection probability and the precision of these estimates using each combination of one, two, or three field methods (line transects, ground camera traps, or arboreal camera traps). Our second objective was to compare detection probability and its precision between field methods for six primate species of interest. Objective three was to test for the effect of height of camera in tree on occupancy and detection.

For our first analyses, we developed a model to estimate species richness and detection probability for all three field methods combined simultaneously using spatial and species covariates. We then used this same model (i.e. model with the same covariates) to compare estimates of species richness and detection probability using data collected from two field methods or one field method. This approach collapsed all data from each combination of methods allowing us to fit single-season occupancy models with multi-species data.

Our second analysis focused on the six primate species of management interest that are available for detection by all three field methods. We fit a single-species, single-season, multi-method model for each species, which adds an additional term from the basic single-season occupancy model to account for the method of data collection (i.e. field method). This model allows us to assess which field method had the highest and most precise estimate of detection probability for each species.

Finally, for our third objective, we assessed a basic methodological question as to whether the height of the arboreal camera in a tree influenced estimates of occupancy and probability of detection. We fit our data to a single-season occupancy model with multi-species data as in the first analysis, using only the species that are available for detection by an arboreal camera (i.e. species that spend at least part of their time in the trees).

Method comparison – all species field methods combined

We used single-season occupancy models with multi-species data to estimate species richness and probability of detection (MacKenzie *et al.*, 2002, 2017) for each of the three methods individually, as well as each combination of two methods, and for all three methods combined. This framework requires sites that are visited on multiple occasions, detection/non-detection data for each species at each site during each sampling occasion, as well as a full species list. In our study, a site referred to a transect; we combined the three ground or three arboreal cameras along each transect for analysis. There were two sampling occasions during 2017, which corresponded to a survey for line transects, or 15 days for camera traps. Each species was given a value of 1, if it was detected during the sampling occasion at a particular site, or a value of 0, if it was not detected during the sampling occasion at a particular site. If a species was not available for detection by a particular method based on known life-history attributes (i.e. arboreal species would not be detected on the ground), it was denoted by a missing value (–). The full species list contained all species which were detected by any one method during the study period. We did not include species which historically have occurred in the park but were not detected during this study in the analyses.

In the single-season occupancy modeling framework with multi-species data, each row of data referred to a particular site (i.e. transect) and species. We estimated two parameters: (1) ψ_t, probability of occupancy, defined as the proportion of species present at each transect, and (2) p_s, probability of detection, the probability that a species is detected given that it is present. Species richness can then be derived from the

probability of occupancy by using the following formula (MacKenzie *et al.*, 2017):

$$\mathrm{SR} = \sum_{s=1}^{S} \psi_{ts}$$

with S representing the total number of possible species, and ψ_{ts} is the unconditional occupancy for each transect t for each species s.

First, we fit a model using all available data (i.e. data collected using all three field methods). We considered spatial (i.e. transect) covariates on the probability of occupancy and species covariates on the probability of detection. Spatial covariates included the minimum elevation (mean = 2104 m, range = 1688–2402 m), maximum elevation (mean = 2411 m, range = 2020–2952 m), distance to nearest access point (i.e. park boundary or road; mean = 386 m, range = 0–2570 m), and distance to nearest tourist trail (mean = 2851 m, range = 0–11917 m). All spatial covariates were scaled to mean of zero and standard deviation of one before analysis. In this study, elevation is used as proxy for habitat, as the park is primarily tropical forest with differences in habitat composition related to elevation. Species covariates included average adult body mass (Jones *et al.*, 2009), whether or not the species is solitary/lives in pairs versus lives in a group, and an activity category, based on whether they are nocturnal or diurnal and whether they are arboreal or terrestrial. Species were organized into activity category based on findings from previous camera trap surveys within the park (Wildlife Conservation Society, unpubl. data). Average adult body mass was scaled to a mean of zero and standard deviation of one like the spatial covariates.

We used an information-theoretic approach with the Akaike information criterion (AIC) to select the most parsimonious model from the candidate model set using each combination of covariates (i.e. model with the lowest AIC score; Burnham & Anderson, 2007)). We only considered singular covariates on each parameter because of possible multicollinearity between covariates. Once we had the most parsimonious model, we then fit this same model (i.e. using the same covariates) using subsets of the available data [i.e. using each combination of methods (e.g. arboreal and ground cameras) and each individual method (e.g. just ground cameras)]. We compared the estimates of species richness and detection probability and the precision of these estimates between the models using different subsets of data.

Method comparison – primate species by field method

For the six diurnal primate species that were available for detection by all three field methods, we used single-species, single-season, multi-method occupancy models (Nichols *et al.*, 2008) to compare the probability of detection for each species for each field method. This model estimates three parameters: (1) ψ, the probability that a site (e.g. transect) is occupied, (2) θ_i, the probability the species is available to be detected by the field methods at each sampling occasion i, and (3) p_m, the probability of detection for method m. For this model, we still considered our 18 transects as the sites, our two sampling occasions corresponding to a transect walk or 15 days of camera trap sampling, and our three field methods. We fit a separate model for each of the six species and compared the probability of detection for each method. Since we were only interested in the comparison of detection probabilities between methods, we did not consider any covariates in these models.

Arboreal camera traps – effect of camera height in tree

We used a single-season occupancy model with multi-species data to test for the effect of camera height in tree on species richness and the probability of detection for the arboreal camera traps. We used the same framework as described above (Method comparison – all species field methods combined), but instead of our sites corresponding to transects and species our sites corresponded to each individual arboreal camera trap (54 cameras total) and species. We only included species in the model that were available for detection by arboreal cameras (i.e. species that spend at least some of their time in the canopy). We considered height of the camera on the tree as a covariate for both occupancy and the probability of detection.

Models for all analyses were fit using the RPresence package version 2.12.27 (MacKenzie & Hines, 2018) in the R computing environment version 3.5 (R Development Core Team, 2019)

Results

Descriptive results

Observers recorded a total of 99 direct mammal observations during line transect surveys. Using camera traps, 23 584 photos were obtained using ground cameras. Of these photos, 14 563 photos contained identifiable animals. For arboreal cameras, 47 066 photos were obtained, of which 12 687 contained identifiable animals. The rest of the photos were either collected during camera setup, blank, contained unidentifiable animals, or contained species that were not a part of this study such as birds or small rodents. All observations were identified to the species level with the exception of dormice, which were grouped into *Graphiurus* spp., and galagos and dwarf galagos, which were grouped into *Galago* spp. (Supporting Information, Appendix S1).

During the study, 35 different mammal species were detected using at least one of the three methods. We categorized each species based on their activity period (diurnal, nocturnal, both) and substrate use (terrestrial, arboreal, both) as observed during previous surveys within the park (Table 1; Supporting Information, Appendix S1). For line transect surveys, 11 of the 20 potential diurnal species (55%) or 31% of

Table 1. Mammal species detected during the survey period in Nyungwe National Park, Rwanda using ground cameras, arboreal cameras, or line transects. Substrate use (arboreal, terrestrial, or both) is demarcated by the bar on the left side of the table. An X indicates a species was not available for detection because of its activity pattern or substrate use. A blank square refers to a species that was available for detection but was not detected during the study period by that method

	Species	Common Name	Ground cameras	Arboreal cameras	Line transects
Arboreal	*Anomalurus derbianus*	Lord Derby's Anomalure	X	●	X
	Galago spp	Galago or Dwarf Galago species	X	●	X
	Graphiurus spp	African Dormouse species	X	●	X
	Perodicticus potto	Potto	X	●	X
	Poiana richardsonii	Central African Oyan	X	●	X
Both	*Cercopithecus lhoesti*	L'hoest's Monkey	○	○	○
	Cercopithecus mitis	Blue Monkey	○	○	○
	Cercopithecus mona	Mona Monkey			○
	Colobus angolensis	Angolan Colobus	○	○	○
	Dendrohyrax arboreus	Eastern Tree Hyrax	●	●	X
	Funisciurus carruthersi	Carruther's Mountain Tree Squirrel	○	○	○
	Fuisciurus pyrropus	Cuvier's Fire-footed Squirrel	○		○
	Genetta maculata	Large-spotted Genet	●		X
	Genetta servalina	Servaline Genet	●	●	X
	Heliosciurus rufobrachium	Red-legged Sun Squirrel		○	
	Heliosciurus ruwenzorii	Montane Sun Squirrel	○	○	○
	Lophocebus albigena	Grey-cheeked Mangabey			○
	Nandinia binotata	African Palm Civet	●	●	X
	Pan troglodytes	Eastern Chimpanzee	○	○	
	Paraxerus alexandri	Alexander's Squirrel			○
	Paraxerus boehmi	Boehm's Squirrel		○	○
	Protoxerus stangeri	African Giant Squirrel	○	○	
Terrestrial	*Aonyx congicus*	Congo Clawless Otter	○	X	
	Atherurus africanus	African Brush-tailed Porcupine	●	X	X
	Canis adustus	Side-striped Jackal	●	X	X
	Cephalophus nigrifrons	Black-fronted Duiker	◐	X	◐
	Cephalophus silvicultor	Yellow-backed Duiker	◐	X	
	Cephalophus weynsi lestradei	Lestrade's Duiker	◐	X	
	Civettictis civetta	African Civet	●	X	X
	Cricetomys gambianus	African Giant Pouched Rat	●	X	X
	Leptailurus serval	Serval	◐	X	
	Mellivora capensis	Honey Badger	●	X	X
	Potamochoerus larvatus	Bushpig	◐	X	
	Thryonomys swinderianus	Greater Cane Rat	●	X	X
	Tragelaphus scriptus	Bushbuck	◐	X	

○ Diurnal
◐ Both
● Nocturnal
X Species not available for detection

all species were detected, for ground camera traps 25 of the 30 potential terrestrial species (83%) or 71% of all species were detected, and for arboreal camera traps 17 of the 22 potential arboreal species (77%) or 49% of all species were detected. For ground and arboreal camera traps combined, 32 of the potential 35 species (91%) were detected (Table 1; Fig. 2). Of the total 35 species detected, three species were detected only by line transect surveys, six species only by arboreal cameras, and 13 species only by ground cameras. The other 13 species were detected by more than one method (Table 1; Fig. 2).

Method comparison – all species field methods combined

Using all available data from all three field methods, the most parsimonious model did not include any covariates on occupancy but did include the effect of both average adult body

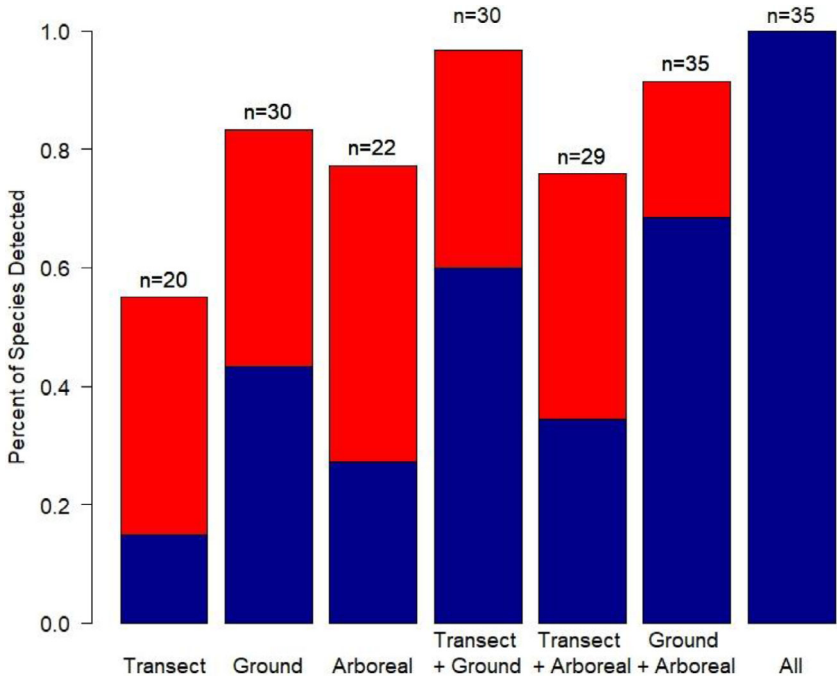

Figure 2 The per cent of possible species detected using each individual field method or combination of methods. The blue portion of each bar represents species that were unique to the particular method or combination of methods, and the red portion of each bar represents species that were also detected by another method. Per cent values are based on the naïve species richness (i.e. raw data) rather than estimated species richness. The total number of possible species for each method or combination of methods is included above the plot. Model, Akaike information criterion (AIC) score, number of parameters (n_{par}), ΔAIC (change in AIC between the given model and the top model), and model weight are given. Covariates on occupancy (psi) include maxelev (maximum elevation), access (distance to nearest access point), minelev (minimum elevation), and trail (distance to nearest tourist trail). Covariates on detection (*p*) include mass (average adult body mass), group (0 for group-living, 1 for solitary/lives in pairs), and cat (category based on activity period and location; NA (nocturnal and arboreal), NT (nocturnal and terrestrial), DT (diurnal and terrestrial), DA (diurnal and arboreal), DB (diurnal and both terrestrial and arboreal), NB (nocturnal and both terrestrial and arboreal). Models presented with ΔAIC < 2. Full model table is included in Supporting Information Appendix S2.

Table 2. Model selection table for single-season occupancy models with multi-species data using data from all three field methods combined

Model	AIC	n_{par}	ΔAIC	Weight
psi()*p*(mass + group)	1272.108	4	0	0.1383
psi()*p*(mass + cat)	1272.187	7	0.0795	0.1329
psi(maxelev)*p*(mass + group)	1272.654	5	0.5467	0.1052
psi(access)*p*(mass + group)	1272.723	5	0.6151	0.1017
psi(maxelev)*p*(mass + cat)	1272.757	8	0.6492	0.1000
psi(minelev)*p*(mass + group)	1272.76	5	0.6519	0.0998
psi(access)*p*(mass + cat)	1272.801	8	0.6934	0.0978
psi(minelev)*p*(mass + cat)	1272.852	8	0.7441	0.0953
psi(trail)*p*(mass + group)	1273.847	5	1.7396	0.0579
psi(trail)*p*(mass + cat)	1273.885	8	1.7770	0.0569

mass ($\beta = -0.766 \pm 0.128$) and whether or not the species is group-living or solitary/lives in pairs ($\beta = -1.007 \pm 0.342$) on detection probability (Table 2; Supporting Information, Appendix S2). However, there was little difference between the top 10 models based on ΔAIC scores.

Using the model with the lowest AIC score [i.e. *psi()p(mass + group)*] with detection histories based on data collected using all three methods, each combination of two methods, or each individual method, we calculated the estimated average occupancy probability at any one transect and estimated average detection probability for any one species. We found that using all data from all three field methods had the highest estimated average occupancy probability at 0.434 (SE 0.101), which corresponds to an average species richness of 15 species. This average occupancy dropped to only 0.254 (SE 0.086) for ground cameras only, which corresponds to a species richness of only eight species. However, though ground cameras alone have the lowest estimated average species richness their estimate was the most precise with a standard error term of only 0.086. Line transects had the lowest precision on their estimates with a standard error of 0.391. The highest detection probability was for the combination of ground and arboreal cameras at 0.706 (SE 0.239), while the lowest estimated average detection probability was for line transects only at 0.243 (SE 0.407). In terms of precision, the lowest precision was again for line transects only with a standard error term of 0.407, while the highest precision was for all methods combined with a standard error term of 0.238 or ground and arboreal cameras combined with a standard error term of 0.239 (Fig. 3). Estimates of richness and detection from all models in Table 2 that adequately converge only vary

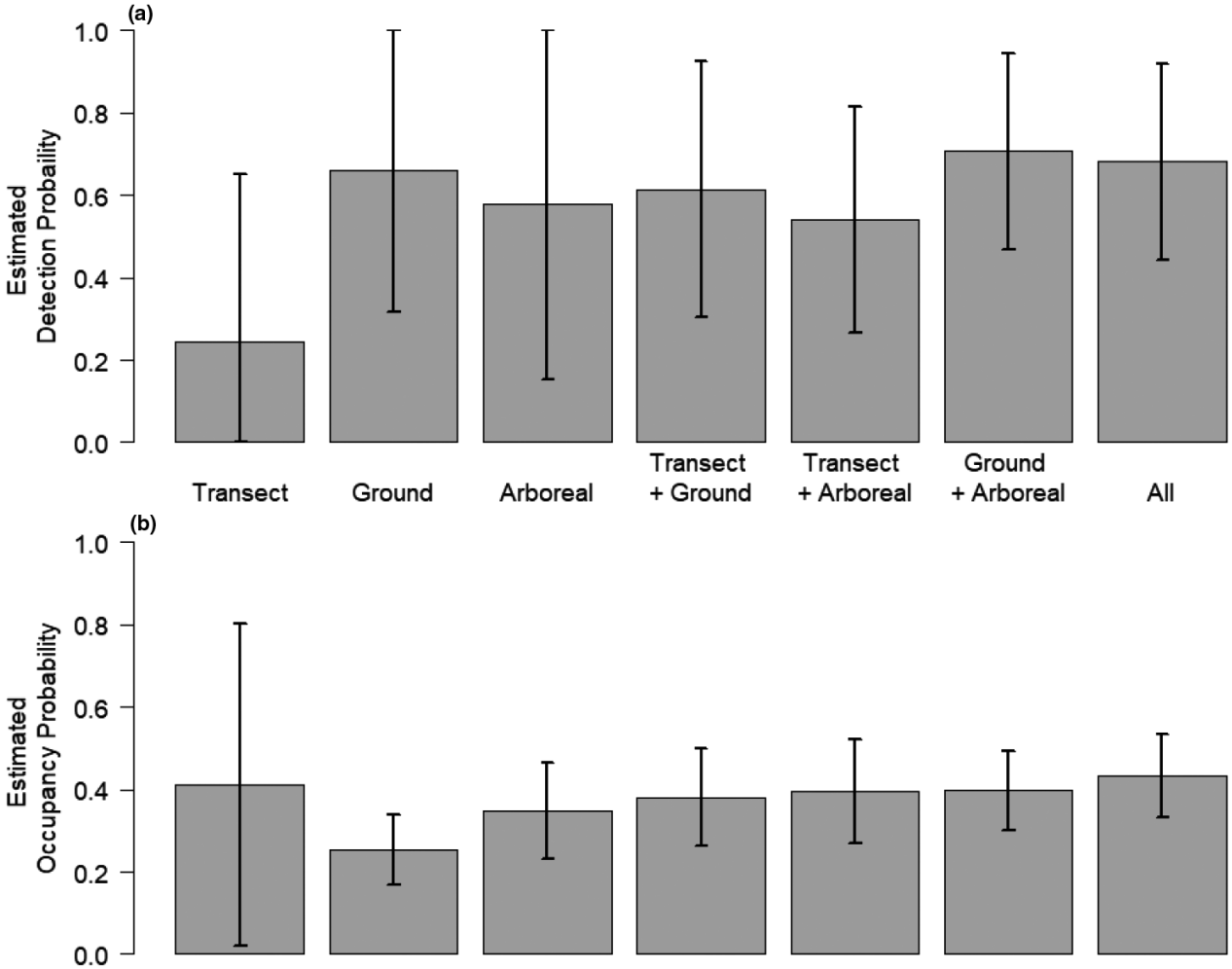

Figure 3 Estimated occupancy and detection probability for models fit using data collected through one field method, a combination of two field methods, or all three field methods. These values are the average estimated detection probability (a) for any one species or average estimated occupancy (b) for any one site (i.e. transect) with standard error measures.

slightly, but the ranking between methods still holds regardless of the chosen model.

Method comparison – primate species by field method

For the six diurnal primate species, naïve occupancy ranged from only 0.0556 for the *Cercopithecus mona* up to 0.9444 for *C. mitis* and *C. lhoesti*. Occupancy probability could not be estimated for two of the species, *C. mona* and *Lophocebus albigena*, because they were only detected one or two times, respectively, and only by line transect surveys. For the other four species, estimated occupancy probability was 0.947 (SE 0.054) for *C. lhoesti*, 0.963 (SE 0.056) for *C. mitis*, 0.688 (SE 0.567) for *Colobus angolensis*, and 0.694 (SE 0.314) for *Pan troglodytes*. The estimated theta value was 0.741 (SE 0.604) for *P. troglodytes* and 1 for the other three species. In terms of estimated probability of detection by field method, line transect surveys had the highest estimated detection for *C. angolensis* [$P = 0.162$ (SE 0.150)], ground cameras had the highest estimated detection for *C. lhoesti* [$P = 0.822$ (SE 0.066)] and *P. troglodytes* [$P = 0.486$ (SE 0.354)], and arboreal cameras had the highest detection for *C. mitis* [$P = 0.693$ (SE 0.082); Fig. 4].

Arboreal camera traps – effect of camera height in tree

Using the null model [i.e., $\psi()p()$], we added height as a covariate on both the probability of occupancy and detection [i.e., ψ(height)p(height)]. Height was not a significant predictor of the probability of occupancy ($\beta = -0.090 \pm 0.095$) or the probability of detection ($\beta = -0.130 \pm 0.164$) as the 95% confidence interval on the beta coefficient for height on both parameters crossed zero.

Discussion

We compared species richness and detection probability estimates between species occurrence data collected simultaneously using three field methodologies (1) line transect surveys,

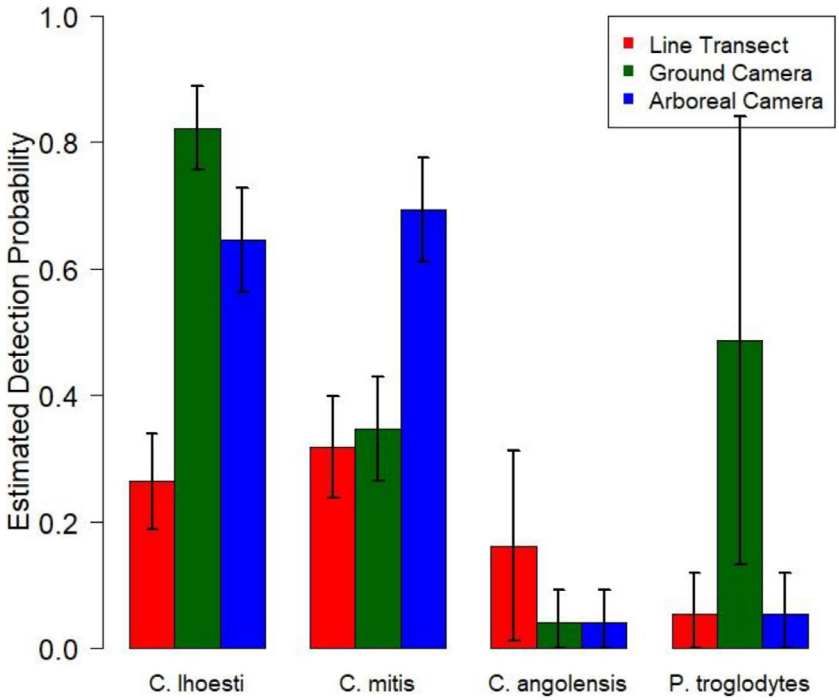

Figure 4 Estimated probability of detection (±SE) by field method for each of the four primate species that were detected during the study.

(2) ground camera traps, and (3) arboreal camera traps. Combining all three field methods was the most effective for detection of tropical forest mammals as measured by the number of species detected but using ground cameras alone was the most precise estimate of occupancy probability. Ground and arboreal cameras combined had the highest estimated detection probability, while using all three methods or ground and arboreal cameras combined had the highest precision for detection probability. For each primate species, a different method had the highest estimated detection probability, suggesting that all three methods were important for detecting the full primate community. Overall, our results suggest that the combination of all methods is most effective; however, if only two methods can be employed, the combination of ground and arboreal cameras is recommended, and ground cameras are likely the best single field method. Previous studies have concluded that ground cameras are a more effective methodology for detecting species than line transects (Silveira, Jácomo & Diniz-Filho, 2003; Srbek-Araujo & Chiarello, 2005); however, few studies have evaluated the effectiveness of arboreal cameras in combination with other methods (but see Whitworth *et al.*, 2016). We are unaware of any studies that have compared these particular methods while also accounting for imperfect detection.

Comparison of field data collection methods

Using all available data, we found only a small difference between the top 10 models, suggesting that there is no clear best covariate predictor for the probability of occupancy. Detection probability was affected by the average adult body mass of each species as well as whether or not the species lives in groups. Contrary with findings from other studies (Tobler *et al.*, 2008) which found a higher detection for larger species, we found that detection probability was higher for smaller species. In NNP, a majority of the large-bodied species are rare, while the small-bodied species such as squirrels are common (Plumptre, 2012; Wildlife Conservation Society, unpublished data). This variation in abundance affects detection probability with more abundant species having a higher detection (Tanadini & Schmidt, 2011; McCarthy *et al.*, 2013). However, it is important to note that some of our ground cameras were placed higher or lower than the average height due to the slope of the terrain surrounding the camera site, which could have also affected the detection probability of some species. As for group-living versus solitary species, we found a higher detection probability for group-living species. Group-living species were found to have higher detection probability in a study in Uganda too (Treves *et al.*, 2010), which they attributed to gregarious species revisiting cameras sites more often.

As expected, the highest estimated occupancy probability and thus species richness was based on data collected using all three field methods; however, the highest estimated detection probability was using both ground and arboreal camera traps together. Therefore, if resources were only available to deploy two of the three methods with an objective to estimate species richness, we would suggest that line transect surveys not be conducted. That being said, it does depend whether the interest is a particular species or the highest detected species richness. Additionally, if other metrics, such

as density, are desired line transect surveys may still be necessarily coupled with distance sampling analyses (Thomas *et al.*, 2011); however, recent studies have shown that camera traps could also be adapted for using with distance sampling for estimating density (Rowcliffe *et al.*, 2008). Our analyses show that for diurnal primate species, which are a tourism and management focus for NNP, two of the six species were only detected using line transect surveys and one additional species had the higher estimated detection probability using line transect surveys. Yet, one of these two species have been detected in a previous survey using arboreal camera traps (*Lophocebus albigena*). Additionally, the nocturnal species of primates were only detected on arboreal cameras (galagos and pottos). Therefore, it seems that cameras traps could be a recommended field method for detecting primate species; however, further research needs to be conducted to determine why particular species are less likely to be detected than others (e.g. *Cercopithecus mona*). This could have to do with camera placement and orientation or tree species in which the camera is deployed.

The height at which the arboreal cameras were deployed was not a significant predictor of detection probability, but the coefficient was negative implying a higher detection probability at lower heights. This is contrary with the positive trend found in a previous study (Bowler *et al.*, 2017). However, in Bowler *et al.* (2017), cameras were placed higher (16.6–29.9 m) than in our study (4–17 m).

NNP mammal community

During our study, the three field methods combined, detected 35 mammal species within NNP (Table 1). One species, the Central African oyan *Poiana richardonsii*, was added to the species list for this park as a result of arboreal camera deployment (Moore & Niyigaba, 2018). Five additional mammal species that were not observed in this study are known to occur in the park: the owl-faced guenon *Cercopithecus hamlyni*, which resides in bamboo forest – a habitat type that was not surveyed, the red-tailed guenon *Cercopithecus ascanius*, the African wildcat *Felis silvestris* and two species of mongoose, the marsh mongoose *Atilax paludinosus* and the slender mongoose *Galerella sanguinea*. These five species may not have been observed because of low abundances or patchy distributions. Historical records suggest that additional felids, such as the leopard *Panthera pardus* and African golden cat *Caracal aurata* could also occur in the park as well as the giant forest hog *Hylochoerus meinertzhageni*; however, none have been detected in the past 20 years (Wildlife Conservation Society, unpublished data), and thus it is possible that they have been extirpated likely due to poaching activity.

Arboreal cameras may provide a useful tool for studying small mammals and birds when identification at the species level is possible. Because some mice and rat species in NNP have not been described taxonomically, we were unable to identify them. However, some notable birds detected during the study were the great blue turaco *Corythaeola cristata*, Ruwenzori turaco *Ruwenzorornis johnstoni*, black-billed turaco *Tauraco schuetti*, African wood owl *Strix woodfordii*, Cassin's hawk-eagle *Aquila africana*, and the African harrier hawk *Polyboroides typus*.

Conclusion

We found that the three field methods, line transects, ground camera traps, and arboreal camera traps each have advantages and disadvantages and the choice of field methods to use depends on the specific questions being addressed (Supporting Information, Appendix S3). Ground camera traps are now a common method for assessing wildlife populations and are frequently incorporated into species monitoring programs (Ahumada *et al.*, 2011; Tobler *et al.*, 2015). Because arboreal species are missed using ground cameras alone, some monitoring programs combine line transect surveys in conjunction with ground cameras to survey the arboreal community. Line transects are also particularly common for surveying primate populations (Voss & Emmons, 1996; Peres, 1999). Based on our results, we recommend using ground cameras in conjunction with arboreal cameras. This setup provided the second highest species richness estimate (14 species vs. 15 species), but with a higher precision, measured as the standard error of the estimates (0.096 vs. 0.101). In addition, these methods combined provided the highest estimated detection probability (0.706) with close to the highest precision (0.239 vs. 0.237). Additionally, ground and arboreal cameras together detected 24 species which were not detected by line transect surveys. Line transect surveys only detected three species that were not detected by other methods, two primate species and one squirrel species. One of these species has previously been detected on an arboreal camera during a different survey; thus, longer sampling periods could lead to these three species being detected with camera traps. Also, because arboreal cameras are still a new technology, future research on the effects of camera orientation, deployment, and other features on the detection of different species groups could improve this field method, as we would expect arboreal cameras to detect primate and squirrel species. The use of ground cameras and arboreal cameras together have the potential to detect all species, regardless of substrate use and activity period. We recommend that future studies interested in all species within an area should use a combination of arboreal and camera traps for species monitoring programs. These cameras could prove particularly important in areas like tropical forest, where species detection rates are often low due to poor visibility (Plumptre, 2000). Using a combination of ground and arboreal camera traps will improve system-specific knowledge and will better inform species monitoring plans and concomitant management actions within protected areas.

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Authors' contributions

JFM, FM, MM, and PN conceived the ideas and designed the field methodology; PN, GG collected the data; JFM and WEP analyzed the data; JFM, WEP, and LB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data will be archived in a public repository in GitHub prior to publication.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Mammal species list for Nyungwe National Park, Rwanda including all species (excluding small mice and rats) that were detected at least once during the study period.

Appendix S2. Full Model selection table for single-season occupancy models with multi-species data using data from all three field methods combined.

Appendix S3. Methodological advantages and disadvantages.