Targeting burrows improves detection in giant pangolin *Smutsia gigantea* camera-trap surveys

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Abstract The Endangered giant pangolin *Smutsia gigantea* is rare and elusive across its Central African range. Because of its solitary and nocturnal nature, the species is difficult to study and so its ecology is little known. Pangolins are considered the most trafficked mammals in the world. Therefore, confirming presence accurately and monitoring trends in distribution and abundance are essential to inform and prioritize conservation efforts. Camera traps are popular tools for surveying rare and cryptic species. However, non-targeted camera-trap surveys yield low camera-trapping rates for pangolins. Here we use camera-trap data from surveys conducted within three protected areas in Uganda to test whether targeted placement of cameras improves giant pangolin detection probability in occupancy models. The results indicate that giant pangolin detection probability is highest when camera traps are targeted on burrows. The median number of days from camera deployment to first giant pangolin detection event was 12, with the majority of events captured within 32 days from deployment. The median interval between giant pangolin events at a camera-trap site was 33 days. We demonstrate that camera-trap surveys can be designed to improve the detection of giant pangolins and we outline a set of recommendations to maximize the effectiveness of efforts to survey and monitor the species.

Keywords Camera trap, detection probability, giant pangolin, occupancy modelling, *Smutsia gigantea*, survey design, targeted survey, Uganda

Introduction

Pangolins (Order: Pholidota) are considered the most trafficked mammals in the world (Heinrich et al., 2017). Because of growing international demand for their meat and scales, they are under increasing threat of extinction (Soewu & Adekanola, 2011; Boakye et al., 2015). The giant pangolin *Smutsia gigantea* is the largest of all eight extant pangolin species and is distributed widely throughout the forests and savannahs of equatorial Africa (Kingdon et al., 2013; Hoffmann et al., 2020). Despite its extensive range, the giant pangolin is categorized as Endangered on the IUCN Red List (Nixon et al., 2019). Their nocturnal, elusive and burrowing habits make them difficult to detect and challenging to study, with most of what is known about their ecology coming from a single study conducted in Gabon (Pagès, 1970). As such, detailed information on the status, ecology and life history of giant pangolins is needed to inform conservation actions and better understand the impacts of human exploitation and disturbance on the populations of this species (Kingdon et al., 2013; Challender et al., 2014; Morin et al., 2020).

To date there have been few efforts to develop effective and standardized survey and monitoring methods for pangolins (Ingram et al., 2019). As a result, the IUCN Pangolin Specialist Group identified the development of such methods as a priority in the global pangolin Action Plan (Challender et al., 2014). Reviews of methods used previously to survey both pangolins and other ecologically similar species suggest that passive monitoring approaches, including camera-trap surveys, offer great promise (Ingram et al., 2019; Willcox et al., 2019).

Camera-trap surveys should maximize effectiveness by balancing the available resources and required survey effort. Detection of species through camera-trap surveys is imperfect as it is dependent on the focal species moving through the detection zone of the camera (Randler & Kalb, 2018; McIntyre et al., 2020). Imperfect detection, where a species is not detected despite being present, must therefore be considered carefully during both the design and analysis of such studies (Rowcliffe & Carbone, 2008; Tobler et al., 2008; Guillera-Arroita & Lahoz-Monfort, 2017). Failure to detect a species is particularly common when populations are small, rare or cryptic, or when sampling effort is insufficient (Gu & Swihart, 2004). Survey designs that minimize the chance of detection error, and thus improve the effectiveness of camera trapping, are vital.

The encounter rate and detection of certain taxa can be improved using baits or lures (Bischof et al., 2014; Mills et al., 2019; Holinda et al., 2020) or by targeted deployment of cameras at habitat features frequented by the focal species (Kolowski & Forrester, 2017; Iannarilli et al., 2021).

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Placement of cameras on roads or large trails is now considered standard practice for surveys targeting large felids (Tobler et al., 2008; Tobler & Powell, 2013). A previous study found that the capture rate of carnivores was highest on roads, whereas tapirs *Tapirus terrestris* were recorded more frequently by cameras placed on animal trails (Trolle & Kery, 2005). Another study found that nine-banded armadillos *Dasypus novemcinctus* and pacas *Cuniculus paca* were captured more frequently in forest areas without trails and at sites furthest from human-made trails used regularly by jaguars *Panthera onca* (Weckel et al., 2006). However, targeted placement is not always successful in maximizing detection: previous research found that trail-focused camera placement did not have a significant effect on the capture rate of any species recorded during a survey of a tropical forest in Gabon (Fonteyn et al., 2020).

Using camera-trap data to perform occupancy modelling allows researchers to estimate the occurrence of rare and elusive species (Hamel et al., 2013) by considering the occupancy ψ (the probability that a site is occupied by the species) and detection probability p (the probability of detecting a species at an occupied site during the sampling period). Occupancy modelling improves the accuracy of estimates by using presence/absence data collected during repeated sampling occasions to account for imperfect detection (MacKenzie et al., 2002; Guillera-Arroita, 2017). This is particularly important for cryptic species such as pangolins, which often go undetected despite being present. A previous study presented an analysis of global data from non-pangolin-focused camera-trap surveys to determine the utility of camera-trap methods as a survey and monitoring tool (Khwaja et al., 2019). The study was able to model the occupancy of three species of pangolin, including giant pangolins, using contributed data. However, the occupancy and detection probability of all species were low, suggesting that targeted deployment of cameras could increase detection probability. Targeted placement of camera traps has been conducted at small scales for white-bellied pangolins *Phataginus tricuspis* (Simo et al., 2020) and giant pangolins (Bruce et al., 2018) but is yet to be trialled at a large scale for giant pangolins, and its effect on detection probability has not been quantified. Increasing detection probability through targeted deployment of cameras would improve the accuracy of occupancy modelling, better informing population estimates and assessments of the impacts of exploitation.

Here we use data from long-term camera-trap surveys conducted within three protected areas in Uganda to investigate whether targeted placement of cameras improves giant pangolin detection and to identify which target features were most effective. We hypothesize that targeting camera traps on features that giant pangolins frequently interact with, such as burrows, would generate a higher detection probability than other features. We use occupancy models (Royle & Nichols, 2003; MacKenzie, 2006) and focus on differences in detection probabilities. We also determine the optimum duration of camera-trap deployment and period to first detection. Finally, we make recommendations for future giant pangolin surveys to maximize the effectiveness of efforts to survey and monitor the species.

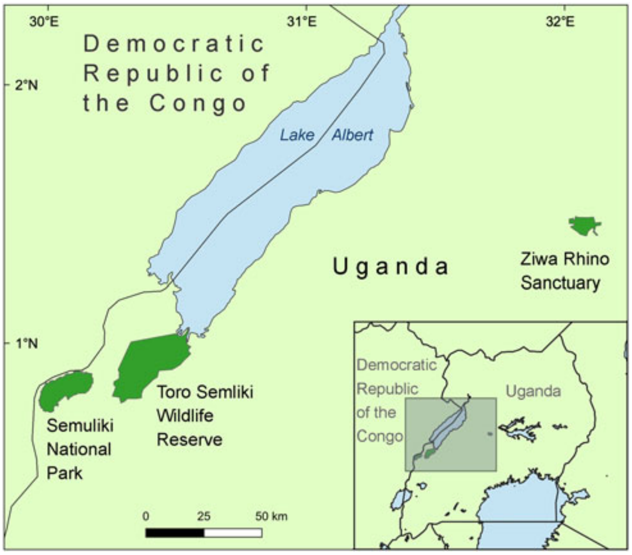

FIG. 1 Locations of protected areas in Uganda where we deployed camera traps to survey for the giant pangolin *Smutsia gigantea*.

Study area

We conducted camera-trap surveys within three protected areas in Uganda (Fig. 1). Ziwa Rhino Sanctuary (65 km^2) in central Uganda is a fenced sanctuary for introduced white rhinoceroses *Ceratotherium simum*. The sanctuary consists of a mosaic of woodland dominated by *Combretum* sp., dense bushland, open grasslands and swamp zones (Brett, 2002). Semuliki National Park (220 km^2) is a lowland rainforest dominated by *Cynometra alexandri* in south-western Uganda on the border with the Democratic Republic of the Congo. The Park is predominantly flat, with an elevation range of 670–760 m (Forbes, 2018). A 20-km^2 area in the east of the Park was selected as the study area because of its accessibility and there being recent records of giant pangolins (Nixon et al., 2018). Approximately 9 km to the east lies Toro Semliki Wildlife Reserve (540 km^2), with an elevation range of 900–1900 m (Patrick et al., 2012). It consists of savannah dominated by *Combretum ghasalense*, with gallery forest patches of *Celtis* sp. and *C. alexandri* (Patrick et al., 2012; Samson & Hunt, 2012). Here we selected a 30-km^2 area of gallery forest around the Mugiri and Wasa River systems as our study area for both logistical reasons and based on a recent record of a giant pangolin (R. Reyna, pers. comm., 2019).

TABLE 1 Summary of camera-trap data from three protected areas surveyed for giant pangolins *Smutsia gigantea* in Ziwa Rhino Sanctuary, Semuliki National Park and Toro Semliki Wildlife Reserve in Uganda.

	Ziwa Rhino Sanctuary	Semuliki National Park	Toro Semliki Wildlife Reserve
Survey period	Sep. 2018–Dec. 2019	Sep. 2019–Jan. 2020	Oct. 2019–Feb. 2020
Images/video	Both	Video	Images
Total trap-days (sampling occasions)	17,837	2,495	3,935
Camera traps per target feature			
Animal trail	69	14	58
Burrow	238	8	2
Other	37	21	9
Termite mound	10	6	10
Total camera traps	354	49	79
Giant pangolin events[1]	252	11	7
Giant pangolin locations[2]	39	5	5
Camera-trapping rate[3]	1.413	0.441	0.178
Naïve occupancy[4]	0.110	0.102	0.063

[1] Number of independent giant pangolin events. An independent event is defined as any giant pangolin activity recorded by a camera trap at least 60 minutes after a previous trigger.

[2] Number of camera-trap sites where giant pangolins were detected.

[3] Number of giant pangolin events per 100 trap-days.

[4] Proportion of sites at which giant pangolins were detected.

Methods

Camera-trap surveys

We conducted camera-trap surveys during September 2018–February 2020. We deployed camera traps in randomly selected 500 × 500 m grid cells. Beginning at the centre, we surveyed each selected cell on foot and deployed a camera trap at the first target feature encountered that we considered to be of potential importance to giant pangolins. Such target features were animal trails, burrows, termite mounds and others (Table 1). We grouped features on which camera traps were rarely targeted as 'other'. These included thickets (22), the centre point of a grid cell (13), streams (9), clearings (8), roads (7), swamps (5), animal wallows (2) and fallen trees (1). We secured the camera traps to a tree or stake 30–50 cm above the ground (Dillon & Kelly, 2007; Rovero & Zimmermann, 2016). We deployed 577 cameras throughout the three protected areas.

We used a combination of Reconyx Hyperfire HC550 and HP2W (Reconyx, Holmen, USA), Bushnell Aggressor Trophy HD11987 (Bushnell, Overland Park, USA) and Browning Recon Force Advantage (Browning Trail Cameras, Birmingham, USA) cameras throughout the study. We set the cameras to record a combination of images and video, dependent on the camera model, to optimize the performance of each camera. We deployed cameras for a median of 49 days (range 1–351 days). Cameras remained in place for longer-term monitoring at sites where giant pangolins were detected more frequently, resulting in a higher number of trap-days at some sites.

We excluded from the analysis cameras that malfunctioned or where the target field of view had changed or become obscured during the study (e.g. where cameras had been knocked out of position by animals). We included 482 cameras in the analysis. Upon retrieval we reviewed all camera-trap images and videos and recorded the dates and locations of any giant pangolin events. We discarded any photographs of people to protect their privacy.

Data analysis

We conducted all data analyses using *R 3.63* (R Core Team, 2020), through *RStudio IDE 1.2.5033* (R Studio Team, 2020).

We calculated the camera-trapping rate by dividing the number of independent giant pangolin events by the total number of camera-trap days (24-h periods during which cameras were active) and multiplying this by 100 for each protected area (Rovero & Marshall, 2009). We defined an independent event as any giant pangolin activity recorded by a camera trap at least 60 minutes after a previous trigger (Bowkett et al., 2008; Rovero & Zimmermann, 2016). We calculated naïve occupancy (the proportion of sites at which giant pangolins were detected) for each protected area (Rovero & Zimmermann, 2016).

We used occupancy models to investigate the effect of protected area, type of target feature and precipitation on detection probability (Royle & Nichols, 2003, MacKenzie, 2006). We constructed detection histories using daily data on giant pangolin presence and absence at each camera-trap site. Each camera-trap day was considered one sampling occasion as this is assumed to be long enough to consider captures as independent events, and short sampling occasions provide more information on detection probability, therefore optimizing the accuracy of estimates (Rovero & Zimmermann, 2016).

We included target feature, protected area and precipitation as covariates potentially affecting detection probability. Understanding the effect of a target feature was the main objective of our research. We included protected area to account for differences such as habitat type, and daily precipitation (mm/day) to account for seasonality. We sourced precipitation data from NASA's GMAO MERRA-2 (Bosilovich et al., 2017). As we were interested in the covariates that influenced detection most strongly, we did not investigate the covariates that influenced occupancy.

We ran single-season occupancy models using the *occu* function in the *unmarked* package in *R* (Fiske & Chandler, 2011). To account for the possibility of abundance-induced heterogeneity in detection probability (Royle & Nichols, 2003), we also ran all models as Royle–Nichols occupancy models using the function *occuRN* in the *unmarked* package. The detection probability (r) estimated by a Royle–Nichols occupancy model is the unconditional probability of a single individual being detected and therefore cannot be compared directly to the detection probability estimated by single-season occupancy models (i.e. p = the probability of detecting the species at a site if present). To obtain comparable measures of p from our Royle–Nichols occupancy models, we therefore transformed our estimates of r following the formulas provided in previous studies (Royle & Nichols, 2003; MacKenzie et al., 2017). We selected models based on the Akaike information criterion corrected for small sample size (AICc; Burnham & Anderson, 2002). Where the ΔAICc between the top-ranking model and subsequent models was < 4, we used the *model.avg* function in the *MuMIn* package in *R* to perform model averaging on the best-fitting models (Bartoń, 2020).

To determine the optimum duration for camera-trap deployment, we fitted a generalized linear model to the data from camera-trap sites where giant pangolins were detected. We used a negative binomial error structure to reduce the impact of over-dispersion (Zuur et al., 2007). We tested for the effect of protected area and target feature on the number of days from camera-trap deployment to first giant pangolin event, and we used the AICc to select the best-fitting model.

To investigate the effect of camera density on detection probability, we used a subset of data from Ziwa Rhino Sanctuary (March–September 2019) as this had the largest number of giant pangolin events (Table 1). We calculated camera-trap density using the number of camera traps deployed synchronously in 1-km^2 grid cells across the Sanctuary. We confirmed giant pangolin presence if we detected at least one giant pangolin during that period. We then fitted a generalized linear model with a binomial error structure using density to predict the presence or absence of giant pangolins.

Table 2 Model selection results for the fitted Royle–Nichols occupancy models. Covariates considered for detection probability (p): target feature (TF), protected area (PA) and precipitation (PP). Occupancy (ψ) was considered constant (.) for all models. Models selected for model averaging (ΔAICc < 4) are highlighted with asterisks (*).

Model	df	AICc[1]	ΔAICc[2]	Cumulative AICc weight
$\psi(.) \sim p$ (TF + PA)*	7	1987.368	0.000	0.570
$\psi(.) \sim p$ (TF + PA + PP)*	8	1989.353	1.985	0.211
$\psi(.) \sim p$ (TF)*	5	1989.922	2.554	0.159
$\psi(.) \sim p$ (TF + PP)	6	1991.877	4.510	0.060
$\psi(.) \sim p$ (PA)	4	2003.715	16.348	0.000
$\psi(.) \sim p$ (PA + PP)	5	2005.584	18.216	0.000
$\psi(.) \sim p$ (.)	2	2007.250	19.883	0.000
$\psi(.) \sim p$ (PP)	3	2009.076	21.709	0.000

[1] AICc, Akaike information criterion adjusted for small sample size.
[2] ΔAICc, difference in AICc values from the best-fitting model.

Results

We used data from 24,267 camera-trap days in the analysis. During this period, we recorded 270 independent giant pangolin events, resulting in an overall camera-trapping rate of 1.113 events per 100 camera-trap days.

We detected giant pangolins at 49 of the 482 camera-trap sites, resulting in a naïve occupancy of 0.102. The camera-trapping rate differed between protected areas and was highest at Ziwa Rhino Sanctuary. Naïve occupancy was similar at Ziwa Rhino Sanctuary and Semuliki National Park but lower at Toro Semliki Wildlife Reserve (Table 1).

We detected 270 independent events over 205 sampling occasions. All of the fitted Royle–Nichols occupancy models outperformed the single-season occupancy models (ΔAICc of the best-fitting single-season occupancy model from the worst Royle–Nichols occupancy model = 99.349), suggesting heterogeneity in abundance affected detection probability. We therefore report only the model selection results of the Royle–Nichols occupancy models in Table 2. The best-fitting model included target feature and protected area (Table 2). However, the three top-ranking models all had a ΔAICc < 4, so we model-averaged these models. Target feature was included in each of these three models, suggesting it has the largest influence on the detection probability of giant pangolins.

Detection probability was highest when camera traps were targeted on burrows, followed by animal trails and termite mounds (Table 3, Fig. 2). We recorded no giant pangolin events at any of the features grouped as 'other'. These results were consistent between protected areas.

Protected area also influenced detection probability, with Semuliki National Park having the highest detection probability, followed by Ziwa Rhino Sanctuary and Toro Semliki Wildlife Reserve (Fig. 2). There was no evidence of a

TABLE 3 Model-averaged estimates for detection probability (p) for all Royle–Nichols occupancy models with ΔAICc < 4. Estimates of detection probabilities (logit scale) for different target features and different protected areas are contrasts from the baseline intercept (Int; animal trail in Semuliki National Park).

Detection covariate	Estimate ± SE
p (Int)	-3.893 ± 0.576
p (termite mound)	-1.576 ± 1.120
p (burrow)	0.459 ± 0.276
p (other)	-8.779 ± 74.497
p (Toro Semliki Wildlife Reserve)	-1.603 ± 0.643
p (Ziwa Rhino Sanctuary)	-0.769 ± 0.444
p (precipitation)	0.004 ± 0.016

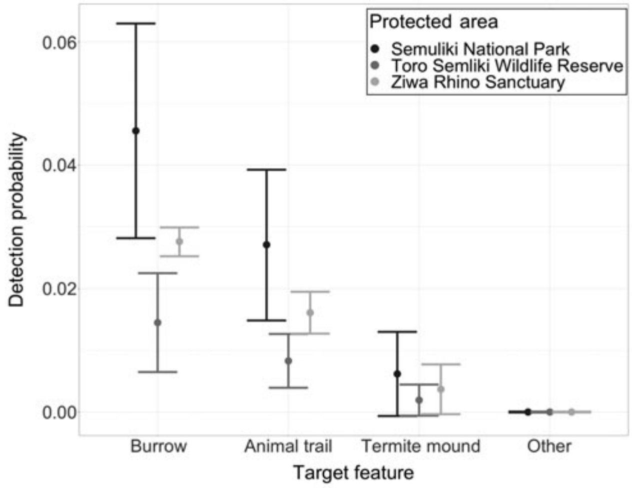

FIG. 2 Detection probability for target feature and protected area, with standard errors, using model-averaged estimates for the best-supported models (ΔAICc < 4) and mean daily precipitation (3.133 mm/day).

relationship between giant pangolin detection probability and precipitation.

The median number of days from camera-trap deployment to first giant pangolin event captured at sites where giant pangolins were confirmed was 12 days (interquartile range = 7–37 days).

The results of the negative binomial generalized linear model to determine the optimum camera-trap deployment duration showed that the best-fitting model did not include target feature or protected area as covariates (Table 4). The 95% confidence interval went from 18 to 32 days.

To determine the average interval between giant pangolin events at a camera-trap site, we calculated the median interval between events at each site and then used these results to calculate an overall median of 33 days (interquartile range = 17–55 days).

TABLE 4 Model selection results for the generalized linear model on the number of days from camera-trap deployment to first giant pangolin event (trap-days).

Model	df	AICc	ΔAICc
Trap-days ~ 1	2	415.066	0.000
Trap-days ~ target feature	4	418.323	3.257
Trap-days ~ protected area	4	418.839	3.773

When testing the effect of camera-trap density on detection probability, ΔAICc of the null model was < 4, indicating that there is no evidence that camera-trap density has a strong effect on the probability of capturing a giant pangolin event.

Discussion

As expected, deploying camera traps to target burrows increased the detection probability of giant pangolins compared to camera traps targeting animal trails, termite mounds and other habitat features. Where targeting of burrows is not possible, camera traps should be placed on animal trails as this yielded the second highest detection probability in our study.

Our results support previous findings demonstrating that targeting camera traps on burrows can increase the probability of locating giant pangolins (Bruce et al., 2018). To our knowledge, no other studies have used occupancy modelling to determine the effect of targeting camera traps on animal burrows on the detection probability of a species. Previous research has focused primarily on camera-trap placement on roads and animal trails (Trolle & Kéry, 2005; Weckel et al., 2006; Tobler & Powell, 2013). Our method could be applicable to other cryptic species that use burrows.

Although giant pangolins are known to use burrows as dens and feeding sites (Pagès, 1970; Bruce et al., 2018; Hoffmann et al., 2020), giant pangolins were observed entering or exiting burrows rarely in our study. Giant pangolins were recorded more regularly entering the field of view from elsewhere and investigating the burrow entrance before moving on. Little is known about how giant pangolins use burrows, and about the socio-ecological importance of this habitat feature to the species. The infrequency and long intervals between detections at burrows in this study suggest that burrow use is transient and irregular, and that individuals could use networks comprising multiple burrows simultaneously. In our study, the targeted burrows were used by multiple mammal species (N. Matthews, unpubl. data, 2022) and had no reliable diagnostic features that readily identified them as giant pangolin burrows. Giant pangolins only entered a small proportion of the burrows surveyed and it is not clear why they chose these burrows in particular. Further research utilizing data on the presence of other species, burrow morphometrics and habitat features at the burrow location is needed to ascertain giant pangolin preferences and behaviours associated with the use of burrows.

There were differences in the relative magnitudes of detection probability between protected areas. This could be the result of habitat differences reducing the field of view of the camera trap, or dense understory promoting the use of animal trails, for example. During this study, we found that visually locating burrows in the rainforest habitats of Semuliki National Park and Toro Semliki Wildlife Reserve was more challenging than in the relatively open grassland and woodland mosaic in Ziwa Rhino Sanctuary. Ground substrate type and the presence of other burrowing species (e.g. aardvarks *Orycteropus afer*) could also affect the quantity of burrows available in different research areas. However, detection probabilities of giant pangolins at burrows were consistently higher than at other target features in each protected area.

It has been suggested previously that using guides with local ecological knowledge could help to identify active giant pangolin burrows (Bruce et al., 2018). Similarly, it has been demonstrated previously that utilizing local ecological knowledge regarding pangolin-specific field signs, including feeding sites, burrows and tree cavities, resulted in effective targeting of camera traps for white-bellied pangolins (Simo et al., 2020). Using detection dogs has also been suggested to help identify potentially active pangolin burrows, which could then be verified using camera traps (Willcox et al., 2019). These alternative techniques to locate burrows could further increase the detection probability of giant pangolins. However, our results show that targeting burrows encountered randomly, without prior knowledge of their use by giant pangolins, also improves detection probability and is an effective stand-alone survey technique for the species, regardless of burrow abundance or habitat type. Furthermore, targeting camera traps at burrows encountered randomly does not introduce as much bias as deploying a camera outside a permanent dwelling of a species, where frequent detection would be probable. However, to account for bias as a result of targeted placement during camera-trap surveys, information on the target feature should always be recorded and incorporated into analyses (Kolowski & Forrester, 2017).

Increasing the number of detections of giant pangolins during a camera-trap survey will improve the estimation of detection probability and thus of occupancy. More accurate estimates of occupancy will enable better-informed decisions to be taken regarding the effective conservation of this species, both locally and across its range. Deploying camera traps to target burrows also increases the cost efficiency of surveys, providing more data with less effort and consequently requiring less funding, which is often a limiting factor when conducting wildlife surveys (Bischof et al., 2014).

Determining the optimum duration for a camera-trap survey is complicated and depends on the particular research questions to be answered (Kays et al., 2020). This is made especially difficult when there is little prior knowledge regarding the target species to inform design decisions. Our study revealed that the majority of first detections at occupied sites occurred within 32 days after cameras were deployed. It has been stated previously that camera trapping at a burrow can potentially detect a giant pangolin within 2 days of deployment (Bruce et al., 2018). Although our study confirms that detection can be this rapid, with our shortest period to first detection being within the first trap-day, our generalized linear model for estimating time to first detection had a 95% confidence interval of 18–32 days, with the longest period to first detection being 94 days.

To account for the time to first detection and the average interval between events, we therefore recommend leaving camera traps in place for 30–35 days when surveying for giant pangolins. This is considerably shorter than previous simulations that suggest a deployment period of 6.1–7.9 months for giant pangolins, depending on population status and number of camera-trap sites (Khwaja et al., 2019). These simulations suggest 75–130 camera-trap sites are required. Following our recommendations, a larger number of camera-trap sites could be achieved more quickly by moving cameras to a new location every 30–35 days. In a recent review of global camera-trap data, it was recommended that camera traps should be deployed for 3–5 weeks to obtain precise estimates of species richness, occupancy and detection rates (Kays et al., 2020). Similarly, it was found previously that accuracy and precision stabilized after 20–30 days for seven focal species in the arctic tundra (Hamel et al., 2013); this study advised that camera traps should be deployed for 30 days for rare species, supporting our findings.

Leaving camera traps in place for longer than 30–35 days would probably result in few additional data, whereas prioritizing additional camera-trap sites could increase the amount of data obtained within a study area and improve the accuracy of analyses. For example, of the 354 camera traps deployed at Ziwa Rhino Sanctuary, only 39 detected giant pangolins and the median period of deployment in this protected area was 48 days. Our results suggest that moving cameras earlier could have increased our ability to confirm giant pangolin presence and the accuracy of our estimates across a larger geographical area. Increasing the density of camera traps deployed simultaneously had no effect on detecting giant pangolins in this study.

Our study highlights the considerations needed when using camera traps to monitor rare and cryptic species. Because of the lack of existing information on giant pangolin ecology, developing an appropriate survey design had been challenging previously. Little is known about giant pangolin home ranges, and it is probable that we observed the same individuals at multiple sites as the home ranges of this species are probably larger than the minimum distance between cameras. Analyses could be improved if this information was made available by grouping detection data from multiple camera traps within a certain area (e.g. larger grid cells) or by substituting space for time (Srivathsa et al., 2018). Another consideration is that the detection probability of giant pangolins probably varies across their range, particularly where local population densities, and therefore camera trapping rates, are higher because of heterogeneity in the detection probability caused by variation in abundance (Royle & Nichols, 2003). We addressed this in our study using Royle–Nichols occupancy models (Royle & Nichols, 2003), and even within our study areas, which were limited to protected areas in Uganda, we found evidence of heterogeneity of abundance affecting detection probability. We therefore recommend considering heterogeneity in abundance in future studies to obtain more accurate estimates of detection probability and thus of occupancy.

The camera-trap model was not included as a covariate in the models because of an unbalanced survey design between study areas. However, it could be valuable to consider the impact of this factor as studies have shown that trigger sensitivity and detection distance vary between camera-trap models (Apps & McNutt, 2018; Heiniger & Gillespie, 2018) and therefore could affect detection probability (Urlus et al., 2014).

Several studies have examined whether camera-trap survey design could be modified to increase detection probability, but few focused on rare species (Hamel et al., 2013; Tourani et al., 2020). This study highlights the difficulties in surveying and monitoring rare species with low detection probabilities, such as giant pangolins. The results illustrate that time to first detection and intervals between events are long. The effort to survey the species is high, requiring a large number of camera-trap sites and cameras to be deployed for 30–35 days. Our study shows how an optimized survey design can be used to improve detection probability and therefore gather more information on the target species. Specifically, targeting burrows can significantly improve the estimation of detection probability of giant pangolins. Our study therefore provides much-needed insight into developing suitable monitoring and surveying methods for giant pangolins, which is a priority for this species (Challender et al., 2014) as it could help us to assess its status and inform conservation management decisions.

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Author contributions Study design: NM, SN; fieldwork: NM, SI; data analysis: NM, AvH, MG; writing: NM, SN, AvH, MG.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards and was approved by the University of Chester's Faculty of Medicine, Dentistry and Life Sciences Research Ethics Committee (reference: 1606/19/NM/BS).

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