Journal Pre-proof

Pangolins in global camera trap data: Implications for ecological monitoring

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PII: S2351-9894(19)30310-5

DOI: https://doi.org/10.1016/j.gecco.2019.e00769

Reference: GECCO 769

To appear in: *Global Ecology and Conservation*

Received Date: 11 June 2019

Revised Date: 30 August 2019

Accepted Date: 31 August 2019

Please cite this article as: Khwaja, H., Buchan, C., Wearn, O.R., Bahaa-EL-Din, L., Bantlin, D., Bernard, H., Bitariho, R., Bohm, T., Borah, J., Brodie, J., Chutipong, W., Preez, B.D., Ebang-Mbele, A., Edwards, S., Fairet, E., Frechette, J.L., Garside, A., Gibson, L., Giordano, A., Veeraswami GOPI, G., Granados, A., Gubbi, S., Harich, F., Haurez, B., Havmøller, R.W., Helmy, O., Isbell, L.A., Jenks, K., Kalle, R., Kamjing, A., Khamcha, D., Kiebou-Opepa, C., Kinnaird, M., Kruger, C., Laudisoit, A., Lynam, A., Macdonald, S.E., Mathai, J., Sienne, J.M., Meier, A., David, M.I.L.L.S., Mohd-Azlan, J., Nakashima, Y., Nash, H.C., Ngoprasert, D., Nguyen, A., O'Brien, T., Olson, D., Orbell, C., Poulsen, J., Ramesh, T., Reeder, D., Reyna, R., Rich, L.N., Rode-Margono, J., Rovero, F., Sheil, D., Shirley, M.H., Stratford, K., Sukumal, N., Suwanrat, S., Tantipisanuh, N., Tilker, A., Berkel, T.V., Weyde, L.V., Varney, M., Weise, F., Wiesel, I., Wilting, A., Wong, S.T., Waterman, C., Challender, D.S., Pangolins in global camera trap data: Implications for ecological monitoring, *Global Ecology and Conservation* (2019), doi: https://doi.org/10.1016/j.gecco.2019.e00769.

Pangolins in global camera trap data: implications for ecological monitoring

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Declarations of interest: none.

Abstract

Despite being heavily exploited, pangolins (Pholidota: Manidae) have been subject to limited research, resulting in a lack of reliable population estimates and standardised survey methods for the eight extant species. Camera trapping represents a unique opportunity for broad-scale collaborative species monitoring due to its largely non-discriminatory nature, which creates considerable volumes of data on a relatively wide range of species. This has the potential to shed light on the ecology of rare, cryptic and understudied taxa, with implications for conservation decision-making. We undertook a global analysis of available pangolin data from camera trapping studies across their range in Africa and Asia. Our aims were (1) to assess the utility of existing camera trapping efforts as a method for monitoring pangolin populations, and (2) to gain insights into the distribution and ecology of pangolins. We analysed data collated from 103 camera trap surveys undertaken across 22 countries that fell within the range of seven of the eight pangolin species, which yielded more than half a million trap nights and 888 pangolin encounters. We ran occupancy analyses on three species (Sunda pangolin *Manis javanica,* white-bellied pangolin *Phataginus tricuspis* and giant pangolin *Smutsia gigantea*). Detection probabilities varied with forest cover and levels of human influence for *P. tricuspis*, but were low (< 0.05) for all species. Occupancy was associated with distance from rivers for *M. javanica* and *S. gigantea*, elevation for *P. tricuspis* and *S. gigantea*, forest cover for *P. tricuspis* and protected area status for *M. javanica* and *P. tricuspis*. We conclude that camera traps are suitable for the detection of pangolins and large-scale assessment of their distributions. However, the trapping effort required to monitor populations at any given study site using existing methods appears prohibitively high. This may change in the future should anticipated technological and methodological advances in camera trapping facilitate greater sampling efforts and/or higher probabilities of detection. In particular, targeted camera placement for pangolins is likely to make pangolin monitoring more feasible with moderate sampling efforts.

Keywords: camera trap, detection, occupancy modelling, pangolin, macroecology, monitoring

1. Introduction

Pangolins are considered to be the world's most trafficked wild mammals (Challender & Waterman, 2017; Heinrich et al., 2017). With contemporary illegal trade largely involving whole pangolins and their scales (Nijman, 2015), pangolins are threatened by overexploitation for both international and local use. Pangolin products are trafficked within Asia and, increasingly, from West and Central Africa to East and Southeast Asia, mainly China and Vietnam (Heinrich et al., 2017). All eight species are listed as threatened on The IUCN Red List of Threatened Species™ (hereafter 'Red List'; IUCN, 2018) and in 2016 were included in CITES Appendix I, establishing an international ban on commercial trade in wild-caught pangolins and their derivatives. Nonetheless, pangolin poaching and trafficking continues seemingly unabated (Heinrich et al., 2017).

Despite high levels of exploitation, pangolins have received little research attention and, until the last decade, scant conservation investment. Consequently, their biology and ecology remain poorly understood, with even basic ecological knowledge lacking for multiple species (Willcox et al., 2019). Of the eight recognised pangolin species, the black-bellied pangolin *Phataginus tetradactyla*, white-bellied pangolin *Phataginus tricuspis*, giant pangolin *Smutsia gigantea*, and Temminck's ground pangolin *Smutsia temminckii* are distributed across sub-Saharan Africa. The Indian pangolin *Manis crassicaudata*, Philippine pangolin *Manis culionensis*, Sunda pangolin *Manis javanica*, and Chinese pangolin *Manis pentadactyla* are found across large parts of South, East and Southeast Asia. Pangolins are solitary, predominantly nocturnal (with the exception of *P. tetradactyla*) and myrmecophagous (Kingdon & Hoffman, 2013). They are known from a variety of habitats including primary and secondary tropical forests, moist and dry lowland and montane forests, shrublands, grasslands, and swamplands, ranging up to a maximum elevation of around 3000 m asl (Baillie et al., 2014; Challender et al., 2014a, 2014b; Lagrada et al., 2014; Pietersen et al., 2014; Waterman et al., 2014a,b,c). While the Chinese, Indian, giant and Temminck's pangolins are ground-dwelling, the Philippine, Sunda and white-bellied pangolins are semi-arboreal, and the black-bellied pangolin almost exclusively arboreal. The ground-dwelling species use different types of burrows for feeding and resting, to which they show low fidelity (e.g. Karawita et al., 2018; Lin, 2011). Indian, Chinese and giant pangolins are thought to remain in close proximity to water sources (e.g. Karawita et al., 2018; Wu et al., 2004), while Temminck's ground pangolins are considered to be largely water-independent (Stuart, 1980). Beyond this, little is understood about the natural history of pangolins, including home range size, habitat use, activity patterns and reproductive behaviours.

Population estimates for any pangolin species at the national or international level are almost non-existent, with the exception of *S. temminckii* in South Africa (Pietersen et al., 2016). Monitoring of pangolin populations is constrained by the absence of standardised survey methods (Challender et al., in prep). A range of approaches have been applied with mixed success, including burrow counts, camera trapping, detection dog teams, social research, and telemetry (see Willcox et al., 2019). Camera trapping is one of the few methods that has been attempted for most pangolin species, although its use has varied widely in terms of sampling strategy and intensity. Willcox et al. (2019) report that large-scale survey efforts using camera traps as part of general biodiversity monitoring activities, in which cameras are frequently located along trails, typically result in very low detection rates for pangolins. In many places in Southeast Asia, this is thought to be because populations have declined severely and occur at very low densities, but camera placement strategies may also be suboptimal for pangolins (Willcox et al., 2019). Cameras targeted at potential pangolin field signs, such as ant nests or burrows, have had more success in confirming presence (e.g. Bruce et al., 2018; ZSL, 2016), as have cameras placed in strictly random locations (Wearn et al., 2017). However, camera placement strategies may be less critical where populations of ground-dwelling pangolins are still relatively abundant because, hypothetically, detection rates should be higher (Challender et al., in prep; Willcox et al., 2019).

Collaborative biodiversity monitoring across multiple studies and locations offers the potential for broad-scale ecological assessments with extensive geographic coverage (Rich et al., 2017; Steenweg et al., 2017). Remote camera trapping methods offer an ideal opportunity for collaborative research, as they are effective at sampling a wide variety of terrestrial mammals and birds (> 100 g body size) and are non-exclusive to any particular species of interest (Wearn & Glover-Kapfer, 2017). They thereby create large volumes of potentially informative data on a wide range of species (Wearn & Glover-Kapfer, 2019; Steenweg et al., 2017). These data are increasingly being used to assess understudied species of conservation concern (e.g. Fischer et al., 2017; Linkie et al., 2013; Schank et al., 2017; Scotson et al., 2017a). Although lack of standardisation across studies can preclude the incorporation of fine-scale covariates (e.g. site-specific vegetation or climatic variables), cross-site analysis of camera trap data using global covariate datasets (such as those based on remote sensing) can assist with answering basic questions regarding the distribution and ecology of threatened species. Pangolins are potentially well suited to camera trap monitoring, because they are relatively large (> 1 kg), endothermic (and therefore suitable for the passive infrared sensors most commonly used on camera traps), and most species are at least partially terrestrial. A collaborative range-wide assessment that brings together small numbers of records from a multitude of studies has the potential to contribute significantly to our understanding of pangolin populations and monitoring methods. This knowledge is urgently needed in order to inform targeted conservation interventions, including identifying potential strongholds, influencing national and international policy, and evaluating the impact of both exploitation and conservation interventions (Challender et al., 2014c; CITES, 2017). These needs have been recognised as priorities by the IUCN SSC Pangolin Specialist Group (Challender et al., 2014c), pangolin range states (Anon, 2015) and the Parties to CITES (CITES, 2017).

In this study, we combined camera trap efforts on an unprecedented scale, aiming to (1) assess the utility of existing camera trapping efforts as a method for monitoring pangolin populations, and (2) improve understanding of pangolin distribution and ecology. This is the first attempt at modelling the probability of occurrence (hereafter, occupancy; MacKenzie et al., 2002) of pangolins throughout their known range, enabling us to offer insights into the broad factors determining pangolin distribution patterns and the challenges of monitoring pangolins using camera trap methods.

2. Materials and methods

2.1 Data collection and preparation

We performed extensive literature reviews of camera trap research conducted in regions within the predicted range of all pangolin species published between 2010 and 2016 using ISI Web of Science in December 2015 (Asia) and September 2016 (Africa). We included all articles regardless of target species using the generic search terms (“camera trap*” AND “Asia”) and (“camera trap*” AND “Africa”). We used these data to create a database of correspondence authors from whom we requested data. In addition, we reviewed the activities of major regional and international NGOs and obtained data from publicly advertised camera trapping projects within relevant regions, as well as using freely available camera trap data provided by the Tropical Ecology Assessment and Monitoring (TEAM) Network. We obtained further datasets where correspondence authors and NGO representatives connected us with colleagues working on relevant projects. The data we requested comprised latitudes and longitudes of camera trap stations, capture histories for cameras that recorded pangolins, and summary data for all other cameras. We accepted reported pangolin species identifications without further verification.

We overlaid individual camera trap locations with each species distribution (as defined by the Red List) and created detection histories for each species using all cameras located within their respective ranges (Baillie et al., 2014; Challender et al., 2014a, 2014b; Lagrada et al., 2014; Pietersen et al., 2014; Waterman et al., 2014a, 2014b, 2014c). In the detection matrix, a value of 1 indicated that the species was detected on a given day at a given camera trap station, while 0 represented the absence of detection. In the absence of empirical data, we defined the maximum length of a sampling session (in which we assume that camera trap locations were closed to changes in occupancy) as six months based on recommendations in Wearn & Glover-Kapfer (2017) for medium to large mammals. Where sampling in a given study took place over more than 6 months, we split sampling into multiple sessions. We then stacked data from different studies and sessions to create a single detection history matrix (in which each row is therefore a given camera trap station in a given session). We note that, because sampling in different studies was not concurrent, our occupancy estimates do not apply to a specific time period, but to the occupancy state as it existed across the different study areas when they were sampled. In addition, by stacking data from different sessions within a study, we have introduced some dependence across rows of the detection matrix where camera trap stations were repeat-surveyed. However, we felt the benefits of providing models with more data were larger than the cost of potentially under-estimating sampling variances. Due to a low number of records, we collapsed five-day sampling periods into single trap occasions in order to increase per-occasion detection probability. We used ArcGIS Desktop Version 10.0 (ESRI, Redlands, CA) and QGIS Version 2.18 (QGIS Development Team, 2017) to ensure independence of camera trap samples by establishing a minimum distance of 25 m between cameras (Kays et al., 2009), using random selection to eliminate stations where necessary. Given that the spacing between some of our camera trap stations was likely less than the home-range diameter of pangolins, we interpret occupancy estimates as the probability of a location being used over the period of sampling, rather than the probability it was occupied (Latif et al., 2016).

Due to lack of standardisation across studies included in our dataset, we extracted station-level covariates for each camera trap using GIS software and freely available global datasets. These consisted of distance to the nearest river (based on HydroSHEDS; Lehner et al., 2008); a binary indicator of protection status, where protected areas were defined as land falling under any of the IUCN protected area categories (World Database on Protected Areas; UNEP-WCMC & IUCN, 2015); elevation (Viewfinder Panoramas; de Ferranti, 2012); percentage forest cover for 2015, which was the year most represented in our dataset (extracted from Hansen et al., 2013); and an index of human influence inferred from datasets on human population density, land use and infrastructure (built-up areas, night-time lights and land cover), and potential for human access (coastlines, roads, railroads and navigable rivers) (Global Human Influence Index v2; WCS and CIESIN, 2005). We expected that these global datasets would capture aspects of pangolin ecology based on current knowledge, as well as the threats they face from hunting and human-induced habitat changes. All continuous covariates were scaled using the mean and standard deviation in R. All variance inflation factors were < 3 (Zuur et al., 2010).

2.2 Occupancy models

For species with sufficient captures, we analysed the detection data with single-season occupancy models (MacKenzie et al., 2002) using the R package *unmarked* (Fiske & Chandler, 2011). We used occupancy models to analyse two key parameters: occupancy (ψ) and detectability (*p*), initially creating a null model that assumed both parameters were constant across all camera trap stations. Given the low number of pangolin records obtained, we were unable to fit a maximal model containing all detection and occupancy covariates simultaneously. We therefore built a set of candidate models for each species in a two-staged process that first identified significant detection covariates, and then carried these forward to assess the influence of occupancy covariates. We considered a subset of covariates to have a potential influence on detection probability, namely protected area status, human influence and forest cover. We hypothesised that protected area status and human influence might be a determinant of hunting pressure, which in turn may affect the movement patterns of pangolins and therefore detectability. We hypothesised that forest cover might be associated with variation in understorey vegetation density, which in turn may affect the size of the detection zone of camera traps. We incorporated all previously described station-level covariates as potential influencers of occupancy.

In the first stage of modelling, we followed an information theoretic approach to determine the importance of detection covariates (Burnham & Anderson, 2002) using the Akaike Information Criterion corrected for small sample size (AICc). We carried only those parameters contained in models with ΔAICc ≤ 6 forward into the second stage (Harrison et al., 2018). Our model selection process therefore consisted of: (1) detection models, in which occupancy was held constant and detection probability was assumed to be either constant or a function of the covariates protected area status, human influence and/or forest cover; and (2) variable detection and occupancy models, in which both occupancy and detection probability were assumed to be either constant or a function of study covariates. We compared models containing all possible covariate combinations and conducted model averaging across all models with ΔAICc ≤ 6 compared with the top-ranking model using the R package *AICcmodavg* (Mazerolle, 2017). We inferred the relative importance of variables based on their standardised effect sizes and considered effects to be significant when their model-averaged confidence intervals did not cross zero.

Given the paucity of pangolin detections, we also attempted to fit similar occupancy models in a Bayesian framework, using Just Another Gibbs Sampler (v4.3.0; Plummer, 2012). We provide details of this modelling (including prior specification) in Appendix S3. We hypothesised that a Bayesian approach might perform better with the small sample sizes, and be robust to boundary effects caused by low detection probabilities (Welsh et al., 2013). The results we obtained were qualitatively similar to those from *unmarked*, and we were still only able to fit occupancy models with covariates for the Sunda pangolin, white-bellied pangolin and giant pangolin. We therefore present these results in the Supplementary Material (Appendix S3).

3. Results

3.1 Data overview

We obtained camera trap data from 103 studies distributed across fourteen African countries and eight Asian countries (Figure 1), totalling 508,312 trap nights. This effort yielded 888 pangolin detections (Table 1). Studies were primarily targeting specific medium to large terrestrial mammals (e.g. sun bear *Helarctos malayanus*, leopard cat *Prionailurus bengalensis*) or taxonomic groups (e.g. felids, carnivores), or otherwise were assessing the whole community of terrestrial mammals and birds. Camera traps were sited on a mixture of wildlife trails, man-made trails, active roads, abandoned roads and random off-trail locations.

3.2 Occupancy models

Detections of *M. crassicaudata*, *M. culionensis*, *M. pentadactyla*, *P. tetradactyla* and *S. temminckii* were too few to implement occupancy models. The models suffered from boundary estimates or otherwise failed to produce sensible estimates (e.g. very large standard errors for one or more parameters). We obtained very low detection estimates from null models for the remaining species (*M. javanica*: 0.025 ± 0.004 SE; *P. tricuspis*: 0.026 ± 0.003; *S. gigantea*: 0.039 ± 0.003). Through our

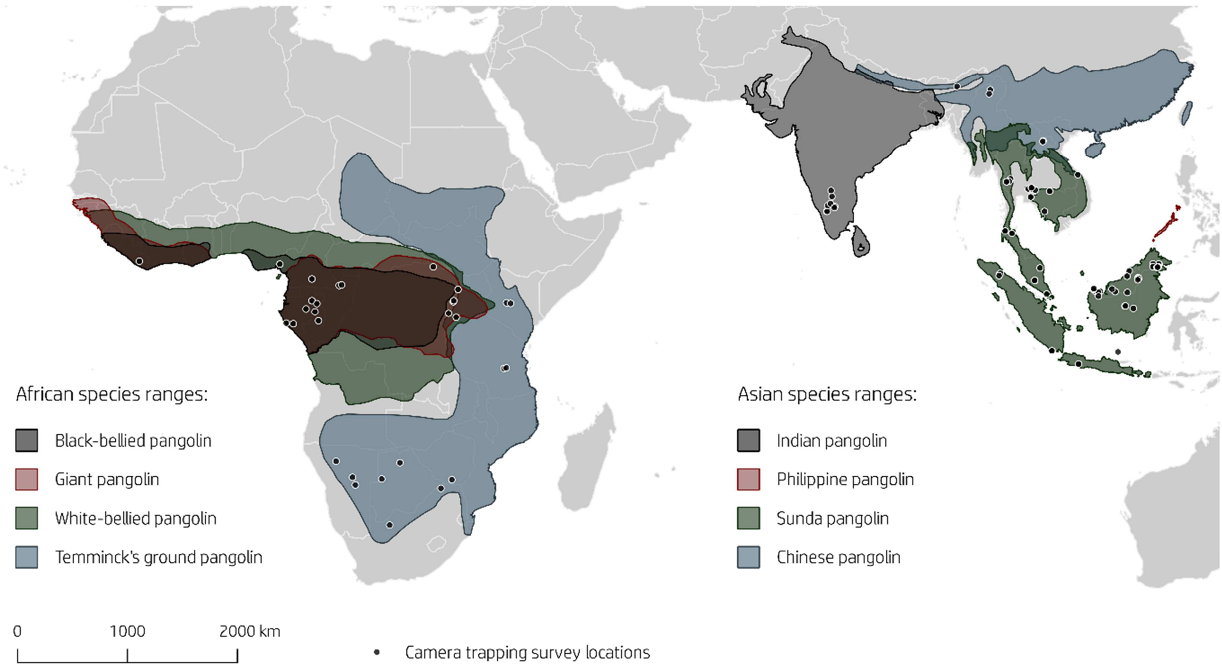

Figure 1. Map of camera trap survey locations across the range of African and Asian pangolin species. Points represent the mean camera trap location for each survey.

Table 1. Summary of camera trap data obtained for analysing occupancy of pangolins across their range.

two-staged model selection process, we obtained 51 candidate models for *M. javanica*, 14 for *P. tricuspis* and 52 for *S. gigantea*. Following model averaging, our results indicated significant influences of forest cover and human influence on detection probability, and of elevation, distance from rivers, protected area status and human influence on occupancy (Figure 2).

Species	Represented range countries	Studies (*n*)	Camera traps (*n*)	Five-day trap occasions (*n*)	Trap occasions with detections (*n*)	Naive occupancy[1]	Naive detection probability[2]
Indian pangolin *Manis crassicaudata*	India	8	361	9,405	29	0.07	<0.01
Philippine pangolin *Manis culionensis*	*No data obtained*	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
Sunda pangolin *Manis javanica*	Cambodia Indonesia Laos Malaysia Singapore Thailand Vietnam	43	2,944	33,857	162	0.04	<0.01
Chinese pangolin *Manis pentadactyla*	India Laos Vietnam	5	737	9,547	3	<0.01	<0.01
Black-bellied pangolin *Phataginus tetradactyla*	Cameroon Gabon Liberia Republic of the Congo	12	834	8,186	0	*N/A*	*N/A*
White-bellied pangolin *Phataginus tricuspis*	Cameroon DRC Gabon Liberia Republic of the Congo Rwanda South Sudan Uganda	18	2,287	29,083	275	0.10	<0.01
Giant pangolin *Smutsia gigantea*	Cameroon DRC Gabon Liberia Republic of the Congo Rwanda South Sudan Uganda	17	1,993	27,249	414	0.13	0.02
Temminck's ground pangolin *Smutsia temminckii*	Botswana Kenya Namibia South Africa Tanzania Zimbabwe	13	708	12,654	5	<0.01	<0.01

[1]Proportion of surveyed camera trap locations with pangolin detections.
[2]Proportion of sampling occasions with pangolin detections.

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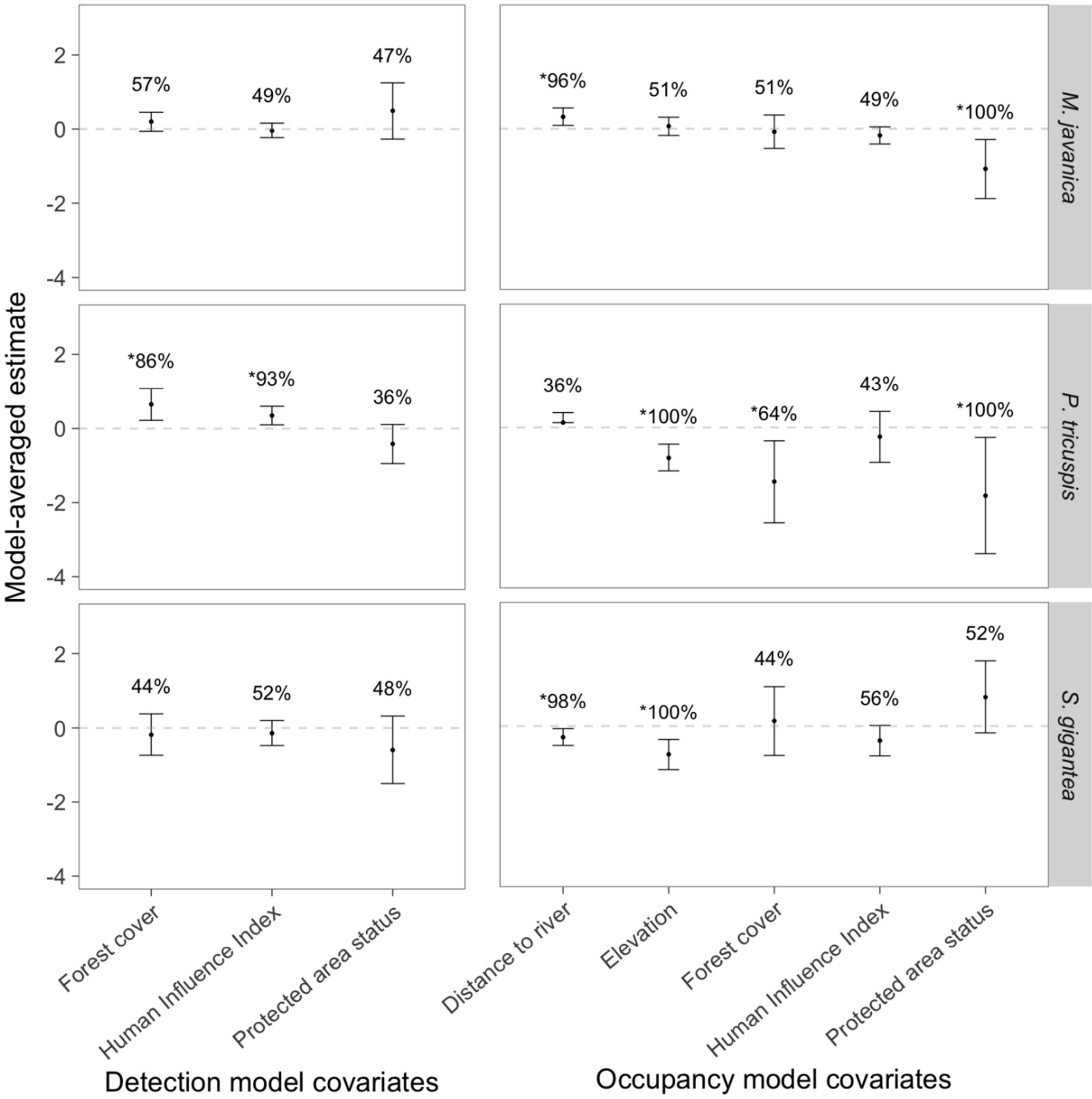

Figure 2. Model-averaged detection and occupancy estimates for Sunda pangolin *Manis javanica*, white-bellied pangolin *Phataginus tricuspis* and giant pangolin *Smutsia gigantea* based on environmental covariates presented in candidate models (ΔAICc ≤ 6). Error bars represent 95% confidence intervals. Values above error bars indicate the percentage of candidate models in which each covariate was present. Significant covariates are denoted by an asterisk.

Probability of occupancy for both *S. gigantea* and *P. tricuspis* declined with increasing elevation across a range from 0 – 2395 m asl (Figures 3A and 3B). *S. gigantea* occupancy also declined with increasing distance from the nearest river, while that of *M. javanica* increased (Figures 3C and 3D). The maximum distance from rivers varied for camera traps within each species range, with no cameras beyond 6 km for *S. gigantea* (mean 1.9 km), compared with a maximum of 14 km for *M. javanica* (mean 2.3 km). Both *P. tricuspis* and *M. javanica* were more likely to use locations outside of protected areas than within them (Figure 4), although only 12% of camera trap locations

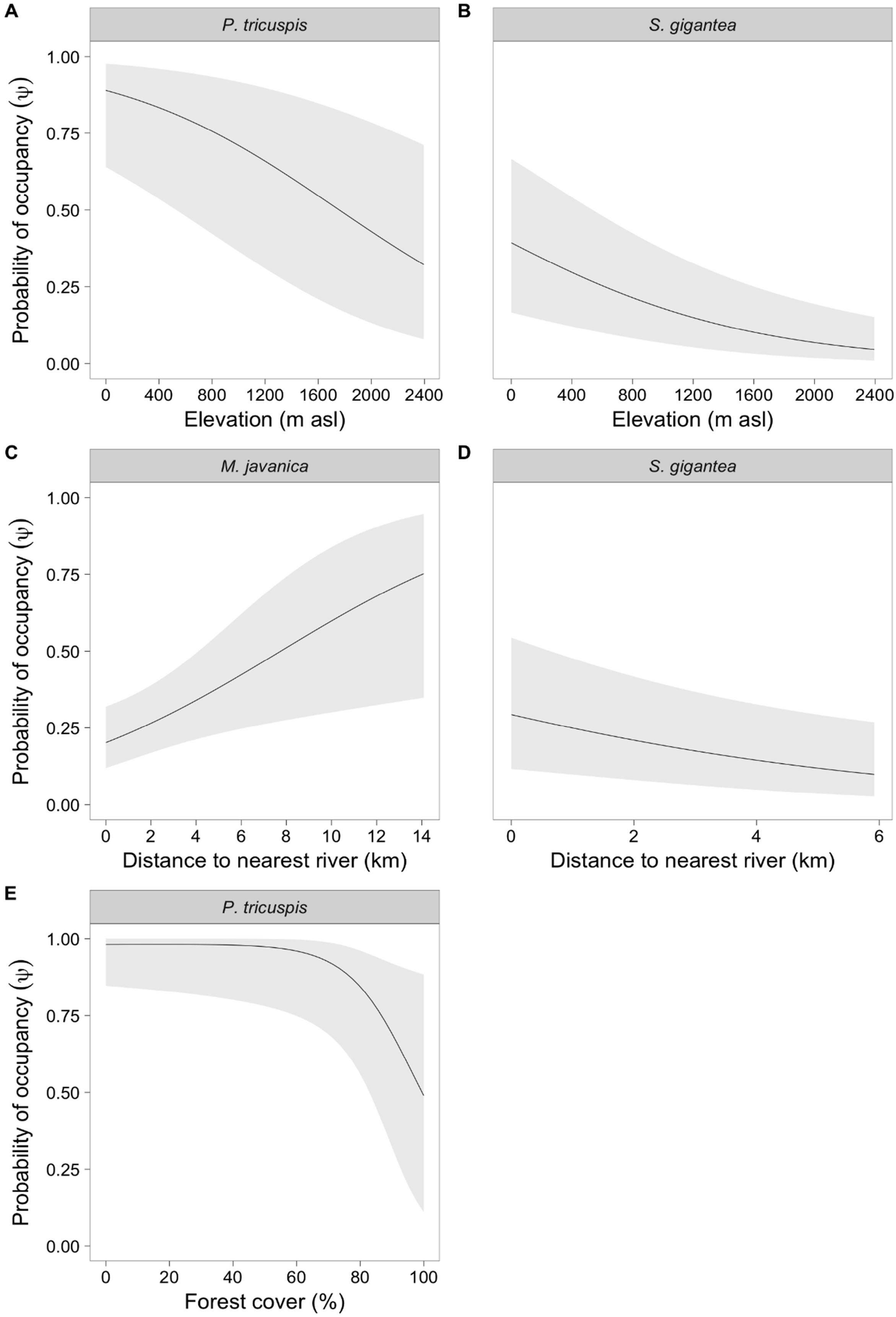

Figure 3. Probability of occupancy of (**A**) white-bellied pangolin *Phataginus tricuspis* and (**B**) giant pangolin *Smutsia gigantea* based on elevation; (**C**) Sunda pangolin *Manis javanica* and (**D**) giant pangolin based on distance to the nearest river; and (**E**) white-bellied pangolin based on forest cover. All other covariates were set to their mean value. Shaded areas represent 95% confidence intervals.

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for *P. tricuspis* were located outside of protected areas, compared with an even distribution for *M. javanica*. Detectability of *P. tricuspis* was positively associated with levels of human influence up to a score of 26 (Figure 5A), where the maximum possible index of human influence is 64 (WCS and CIESIN, 2005). In addition, both detection and occupancy of *P. tricuspis* were significantly influenced by forest cover, but in opposing directions (Figures 3E and 5B). This result should, however, be treated cautiously, as there were very few records of *P. tricuspis* in areas of low forest cover (only 3% of camera traps were situated in locations with < 50% forest cover). None of the tested detection covariates were found to be significant for *M. javanica* and *S. gigantea*.

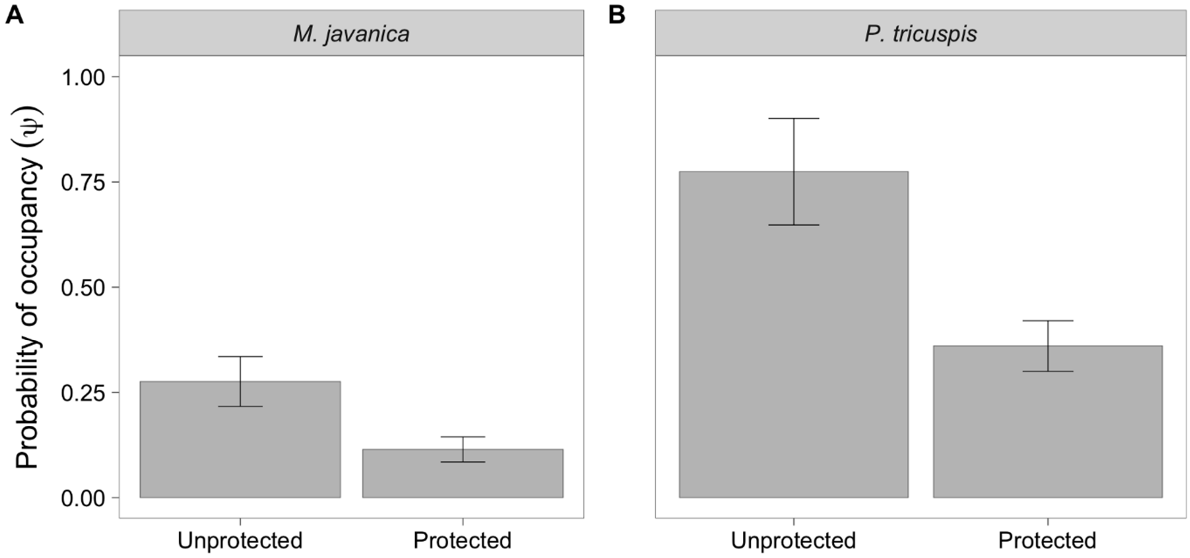

Figure 4. Probability of occupancy of (**A**) Sunda pangolin *Manis javanica* and (**B**) white-bellied pangolin *Phataginus tricuspis* based on protected area status. Error bars represent 95% confidence intervals.

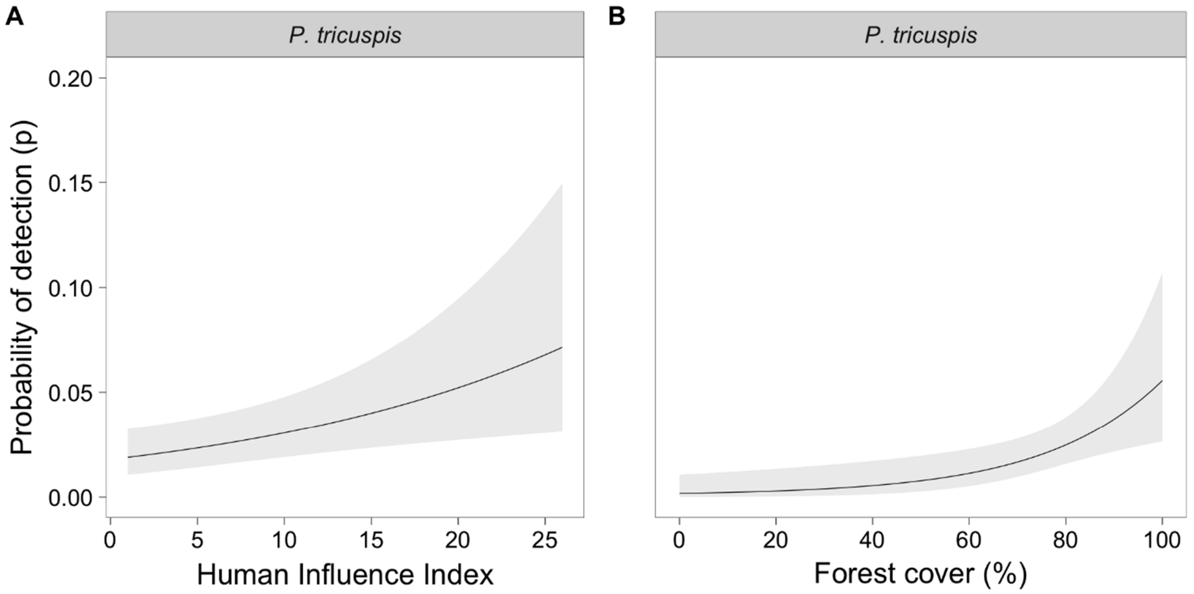

Figure 5. Probability of detection of white-bellied pangolin *Phataginus tricuspis* based on (**A**) the Human Influence Index (WCS and CIESIN, 2005) and (**B**) percentage forest cover. Shaded areas represent 95% confidence intervals.

4. Discussion

As solitary, predominantly nocturnal species, pangolins have historically proven difficult to detect. Despite a global approach and unprecedented number of trap nights collated in our study, we recorded a very low number of detections for all species. Nevertheless, we obtained meaningful results regarding distribution and ecology of the Asian species *M. javanica* and African species *P. tricuspis* and *S. gigantea*, but gained limited insights into the threats that pangolins face, likely due to the coarse nature of the data supporting our tested variables. Our findings help inform future camera trapping efforts for detecting and monitoring pangolins in a given study area, and have broader implications regarding the feasibility of using camera traps for robust monitoring of pangolins across their ranges (Table 2).

4.1 Coarse-scale drivers of pangolin occupancy

Our model results align with current understanding of *S. gigantea* ecology, indicating decreasing occupancy with increasing elevation and distance from rivers, as this species is believed to occur primarily in lowland tropical moist and swamp forest (Waterman et al., 2014a). The contrasting finding that *M. javanica* occupancy increases with distance from rivers may reflect the fact that this more arboreal species uses a much wider range of habitat types, and is thought to have been pushed out of lowland areas by human disturbance and hunting pressure across much of its range (see Challender et al., 2014b). Combined with low reported abundances of *M. javanica* in peat-swamp forests in east and central Kalimantan, Indonesia and Sarawak, Malaysia (Challender et al., 2014b), our results suggest that this species may be less suited to riverine and swamp forest habitats compared with *S. gigantea*. It may also be that rivers serve as transport routes for hunters, particularly in very dense forests without roads, which could lead to increased hunting pressure in proximal areas and therefore decreased population density and/or detectability. However, *M. javanica* has been recorded in wetland habitat in Vietnam in an area of considerable hunting pressure (Willcox et al., 2017). Further research is required to determine optimal habitat requirements for this species.

Across our sample of studies, we found evidence for a higher probability of occupancy outside protected areas for both *M. javanica* and *P. tricuspis*, which contradicted our initial expectations. Our measure of protection was necessarily coarse (a binary variable of protected status), meaning that actual levels of protection on the ground may have been poorly captured. Even so, our findings are supported by previous studies that have demonstrated the ability of multiple pangolin species to inhabit degraded habitats (*M. crassicaudata:* Karawita et al., 2018; *M. javanica:* Wearn et al., 2017; *M. pentadactyla:* Pei et al., 2010; Trageser et al., 2017; *P. tricuspis*: Akpona et al., 2008; *S. gigantea:*

Mugume et al., 2015). In Benin, for example, Akpona et al. (2008) detected no significant difference in the number of *P. tricuspis* recorded in natural forest and old teak plantations. Similarly, in Borneo, *M. javanica* was found at higher local abundances in intensively logged sites compared to old-growth forest, under very low levels of hunting pressure (Wearn et al., 2017). This could be related to prey availability in disturbed sites, and/or reduced natural predation pressure outside of protected areas. The fact that some pangolin species appear able to cope with some level of disturbance and habitat degradation gives hope for their future persistence in increasingly human-dominated environments. However, we stress that our results do not mean that protection measures are not needed; nor do they indicate that pangolins prefer degraded habitat over intact habitat. In order to test these hypotheses, a sampling design with matched treatment replicates, or better fine-scale covariates, would be needed, and is highly recommended for future studies.

Despite the well-documented impacts that hunting has on local pangolin populations (see Challender et al., 2014b), none of the modelled species showed an association between occupancy and the human influence index. However, it should be noted that there were no camera traps located in highly disturbed habitats within the range of the African species, with maximum indices reaching 26 out of a potential 64. More direct measures of hunting pressure are not currently available at sufficiently large scale, but could aid broad understanding of how pangolins respond to this threat, including potentially informing us about the levels of offtake that pangolin populations might be able to withstand. This would require a concerted and coordinated effort across studies in order to measure hunting pressure in a comparable way. Alternatively, at more local scales or at site level, hunting data could be used to inform modelling (Ingram et al., 2017).

4.2 Influencing factors for pangolin detectability

The low detectability of all pangolin species in our dataset is likely to be due to a combination of factors, including low population densities (especially in the case of exploited populations; Willcox et al., 2019); sub-optimal placement, operation and suitability of camera traps for detecting pangolins (Apps & McNutt, 2018); the arboreal and/or burrowing behaviours of pangolins (which reduces their availability for detection by ground-based cameras) (Challender et al., in prep; Kingdon & Hoffman, 2013); and perhaps relatively slow movement rates (meaning that cameras are encountered infrequently) (Hofmeester et al., 2019). Human influence and forest cover were found to affect detectability only for *P. tricuspis*. Probability of detection was higher for this species in locations affected by greater human influence, perhaps because pangolins move further, spend more time on the ground, and/or occur at higher density in disturbed areas, thereby triggering cameras more frequently. Detectability was also higher in locations with more forest cover, possibly due to reduced understorey vegetation density (and therefore larger camera detection zones) in such habitats. Detectability was not found to vary according to the protection status of a location.

Although the data presented here are extensive, they are restricted by the limits of the contact network of the authors, and by the response rate to our data requests. They therefore do not provide full coverage of the possible range of the eight pangolin species, nor constitute a complete representation of camera trap surveys that took place within known pangolin distributions between 2010 and 2016. Due to the scarcity of pangolin records in our final dataset, we were only able to fit relatively simple occupancy models with few variables, limiting our ability to fully account for heterogeneity in detection (likely causing a negative bias in our occupancy estimates) and allowing us to test only a narrow range of hypotheses about the potential drivers of pangolin occurrence. In addition, we were constrained to use coarse-scale global variables due to the lack of standardised and ecologically-relevant variables collected across our contributed data, and not all variables were found in all combinations. These are common problems when using data from many disparate studies, each using different methods (e.g. Scotson et al., 2017a). Heterogeneity could be reduced and better accounted for with greater consistency across camera trap studies in data collection and recording protocols (Scotson et al., 2017b), which would also facilitate much greater ease of data sharing for large-scale analyses. It might be possible to increase model precision by 'borrowing' information about detectability from other species recorded in the same studies, using a Bayesian hierarchical modelling approach (Royle & Dorazio, 2008). However, this multi-species approach may involve trading off accuracy in order to gain increased precision if species do not form a coherent ecological group that can be modelled together (Dorazio et al., 2011).

4.3 Implications for pangolin detection and monitoring using camera traps

Camera traps might conceivably be used to a) detect pangolins, i.e. confirm their presence in a study area, and b) monitor pangolins over space or time, i.e. by modelling their occupancy or density. Studies in our dataset successfully detected pangolins, demonstrating that camera traps can be useful, even when the focus of surveys might be on other species. However, our results suggest that moderately large sampling efforts are required to detect pangolins. Modelled detection probabilities for the three species suggest that minimum sampling efforts required to ensure a 90-95% chance (using a simple binomial model) of detecting *P. tricuspis, S. gigantea* and *M. javanica* if present are 446-580, 288-375, and 457-594 camera trap nights, respectively. As an example, this could be achieved using 20 camera traps, each deployed for 30 nights.

Our results suggest that monitoring pangolins over space or time remains very challenging with camera traps. At coarse scales, we have shown that it is possible to monitor pangolin occupancy across space. With better, fine-scale variables that capture the likely drivers of pangolin occurrence (in particular hunting and habitat variables), as well as methodological standardisation across studies (for example, as implemented by TEAM Network; Jansen et al., 2014), this approach has the potential to further inform our knowledge of pangolin ecology and their conservation. However, within a single study area, it seems that monitoring pangolins over space or time is unlikely to succeed in most cases, at least using commonly-applied methods and current camera trap technology. Following the occupancy survey design recommendations in Mackenzie & Royle (2005) and Guillera-Arroita et al. (2010), we deduced that a minimum of 130 locations would need to be camera-trapped for six months for *S. gigantea*, or 10 months for *P. tricuspis* and *M. javanica* in order to obtain a reasonably precise occupancy estimate (with a standard error < 0.075) for a 'depleted' pangolin population (occupancy = 0.1) (Supplementary Material, Appendix S2). For an 'unexploited' pangolin population (occupancy = 0.5), the same approach yields a recommendation with fewer required locations (100), monitored for the same time period (Appendix S2). Sampling for such extended periods risks violating the closure assumption of occupancy modelling, and is likely to be prohibitively costly or logistically difficult (although it is being done in some sites, for example to monitor large felids). In addition, if the modelling of occupancy as a function of covariates is desired, an even larger sample of locations will likely be required.

Although Bayesian approaches to leveraging information on detectability from other detected species can help with the low number of detections (e.g. Wearn et al., 2017), model estimates will likely remain imprecise. In addition, occupancy does not provide information on abundance, and other statistical methods would be needed to infer this. To date, no camera trap studies have estimated pangolin density, although methods do in principle exist for species such as pangolins that are not individually recognisable (Moeller et al., 2018; Howe et al., 2017; Rowcliffe et al., 2008). In practice, pangolin density might be more efficiently obtained using other methods (e.g. non-invasive genetic methods; Challender et al., in prep.).

Developments in camera trap methods and technology have the potential to improve the feasibility of monitoring pangolins at the site level. The sampling effort recommendations provided above are based on studies in which pangolins were not generally the focus, meaning that the detection probabilities could potentially be improved by targeting pangolin tracks, feeding signs, or burrows. For example, in a recent study of *S. gigantea* at a site in Uganda, naïve detection probabilities were increased tenfold by transitioning from systematic grid-based surveys to targeted camera trapping focusing on burrows, tracks and feeding signs located using reconnaissance surveys (N. Matthews, S. Isoke & S. Nixon, unpubl. data). The increased volume of records is in turn helping to facilitate improved understanding of *S. gigantea* ecology to further refine targeted camera trapping methods in future. A deeper understanding of the ecology of all pangolin species, including home range size, habitat use, speed of movement, proportion of time spent on the ground (for semi-arboreal species), and microhabitat preferences could contribute significantly towards optimisation of camera trap placement strategies (Hofmeester et al., 2019). In addition, camera trap technology is constantly improving in terms of battery life, memory capacity and cost (Glover-Kapfer et al., 2019), which increases the feasibility of achieving the very high sampling efforts required for monitoring pangolins. The labour costs of processing large amounts of camera trap data are also decreasing with the advent of new citizen-science and machine learning approaches (e.g. Willi et al., 2018). We present a summary of recommendations for the use of camera trapping in pangolin detection and monitoring in Table 2. Finally, camera trap images have other benefits beyond monitoring, including their value as tools for outreach, engagement and law enforcement (Steenweg et al., 2017; Hossain et al., 2016).

5. Conclusions

Our results suggest that standard camera trapping protocols for generic biodiversity surveys and/or targeting other medium to large mammals are insufficient to reliably estimate pangolin occupancy for a single study area. Pangolins were nevertheless detected in multiple studies in our dataset, and we were able to uncover relationships between pangolin occurrence and landscape variables on a broad scale. Should a coordinated approach to future camera trapping surveys bring about standardised methods and recording of covariate data, future large-scale, cross-study analyses such as this could deliver greater insights into pangolin ecology. On an individual survey scale, refined methods could improve the utility of camera trapping for monitoring pangolin occupancy, but abundance estimation remains to be tested, and might be better achieved with alternative methods. Future technological and methodological advances may facilitate the large sampling efforts required to obtain meaningful pangolin population estimates from camera trapping surveys in a cost-effective manner.

Table 2. Recommended current and potential uses of camera traps in pangolin detection and spatial or temporal monitoring.

Study aim	Are camera traps suitable?		Justification
	Currently	Potentially in future	
Detection	Y	Y	Detection of *P. tricuspis, S. gigantea* and *M. javanica* has been achieved across multiple sites. It is feasible to ensure 90-95% confidence of detecting these species with moderate sampling effort, and may be feasible for other pangolin species with moderate or high sampling efforts. For *P. tetradactyla*, this would likely involve at least some arboreal camera trapping.
Large-scale modelling of pangolin distribution	Y	Y	Large-scale modelling of pangolin occupancy has been possible for *P. tricuspis, S. gigantea* and *M. javanica*, although better standardisation of methods and covariates would improve the inferences that can be made. This could also be possible for other pangolin species through more widespread collaborative sharing of datasets.
Monitoring pangolin occupancy in a study area with pangolins recorded alongside a suite of other species	N	Y	Prohibitively high sampling efforts are required for robust monitoring of pangolin occupancy at the study area scale using prevailing methods. This is likely the case even for the most detectable species, *S. gigantea*, and even in the case of a population with relatively high abundance. However, it may be possible in future as camera traps become more efficient per unit of labour (thereby increasing detection probabilities) and surveys become more ambitious in scale (i.e. involving many more stations within a study area).
Monitoring pangolin occupancy in a study area with targeted camera placement for pangolins	Y?	Y?	Higher detectability of pangolins may be achieved using methods specifically targeted at pangolins, with location and duration of camera trapping informed by overall understanding of the ecology of each species and identification of potential sites of activity using reconnaissance surveys. This might make pangolin monitoring more feasible with moderate sampling efforts. We acknowledge that current understanding of pangolin ecology, and specifically microhabitat use, is a key knowledge gap preventing immediate application.
Monitoring density of pangolins in a study area	Y?	Y?	It might be possible to estimate pangolin density with camera traps in future, assuming that developments in camera trap technology lead to 1) higher detectability and 2) greater sampling intensities per study (i.e. more stations, sampled for longer periods).

Acknowledgments

Thank you to the many individuals and institutions who generously made their data available for this study, and to the Zoological Society of London and donors to the IUCN SSC Pangolin Specialist Group for supporting the time of HK and CB during their research internships. The authors are grateful to Fondation Segré for supporting this research. AL would like to thank the Biodiversity Monitoring Centre (Centre de Surveillance de la Biodiversité) at the Faculty of Sciences of the University of

Kisangani and the Centre for International Forestry Research (CIFOR) for financial, academic and logistical support. AM would like to thank Agence Nationale des Parcs Nationaux and Centre National de la Recherche Scientifique et Technologique for kindly granting permission to conduct research in Gabon. CKO and TB would like to thank the Nouabalé-Ndoki Foundation and Ministry of Forest Economy, Republic of Congo for kindly providing research permissions. GVG would like to gratefully thank the Department of Science and Technology, Government of India for their funding (DST. No. SR/S0/AS-100/2007), Mr. K. M. Selvan and Mr. S. Lyngdoh for their support in field data collection, and the Department of Environment & Forest, Government of Arunachal Pradesh for permissions. JAM was supported by Ministry of Education Malaysia (NRGS 2013/1088/02). LAI acknowledges support from the U.S. National Science Foundation (BCS 1266389). ORW was supported by an AXA Research Fellowship. SE would like to thank R. Mueller and R. Roder for their input into data processing. Some data in this publication was provided by the Tropical Ecology Assessment and Monitoring (TEAM) Network, a collaboration between Conservation International, the Smithsonian Institution, and the Wildlife Conservation Society, and partially funded by these institutions, the Gordon and Betty Moore Foundation, and other donors.

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