

Original Research Article

Pangolins in global camera trap data: Implications for ecological monitoring



Hannah Khwaja ^{a, b, *}, Claire Buchan ^{a, c, **}, Oliver R. Wearn ^d, Laila Bahaa-eldin ^e, Drew Bantlin ^f, Henry Bernard ^g, Robert Bitariho ^h, Torsten Bohm ^{i, j}, Jimmy Borah ^{k, l}, Jedediah Brodie ^m, Wanlop Chutipong ⁿ, Byron du Preez ^o, Alex Ebang-Mbele ^p, Sarah Edwards ^{i, q}, Emilie Fairet ^r, Jackson L. Frechette ^s, Adrian Garside ^t, Luke Gibson ^u, Anthony Giordano ^v, Govindan Veeraswami Gopi ^w, Alys Granados ^x, Sanjay Gubbi ^y, Franziska Harich ^z, Barbara Haurez ^{aa}, Rasmus W. Havmøller ^{ab, ac}, Olga Helmy ^m, Lynne A. Isbell ^{ac}, Kate Jenks ^{ad}, Riddhika Kalle ^{ae}, Anucha Kamjing ⁿ, Daphawan Khamcha ⁿ, Cisquet Kiebou-Opepa ^{r, af}, Margaret Kinnaird ^{ag}, Caroline Kruger ^{ah}, Anne Laudisoit ^{ai}, Antony Lynam ^{aj}, Suzanne E. Macdonald ^{ak}, John Mathai ^{i, al}, Julia Metsio Sienne ^{am, an}, Amelia Meier ^{ao}, David Mills ^{e, l}, Jayasilan Mohd-Azlan ^{al}, Yoshihiro Nakashima ^{ap}, Helen C. Nash ^{a, aq}, Dusit Ngoprasert ⁿ, An Nguyen ^{i, ar}, Tim O'Brien ^{aj}, David Olson ^d, Christopher Orbell ^{i, as}, John Poulsen ^{ao}, Tharmalingam Ramesh ^{ae}, DeeAnn Reeder ^t, Rafael Reyna ^{at}, Lindsey N. Rich ^{au}, Johanna Rode-Margono ^b, Francesco Rovero ^{av, aw}, Douglas Sheil ^{ax}, Matthew H. Shirley ^{ay}, Ken Stratford ^{az}, Niti Sukumal ⁿ, Saranphat Suwanrat ^{ba}, Naruemon Tantipisanuh ⁿ, Andrew Tilker ^{i, ar}, Tim Van Berkel ^{bb}, Leanne K. Van der Weyde ^{bc}, Matthew Varney ^{bd}, Florian Weise ^{be}, Ingrid Wiesel ^{bf}, Andreas Wilting ⁱ, Seth T. Wong ⁱ, Carly Waterman ^{a, bg}, Daniel W.S. Challender ^{a, bh}

^a IUCN SSC Pangolin Specialist Group, % Zoological Society of London, Regents Park, London, NW1 4RY, UK

^b The North of England Zoological Society / Chester Zoo, Cedar House, Caughall Road, Chester, CH2 1LH, UK

^c School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

^d Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK

^e School of Life Sciences, University of KwaZulu-Natal, Durban, 4000, South Africa

^f Carnivore Coexistence Lab, Nelson Institute for Environmental Studies, University of Wisconsin-Madison, 122 Science Hall, 550 North Park Street, Madison, WI, 53706, USA

^g Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400, Kota Kinabalu, Sabah, Malaysia

^h Institute of Tropical Forest Conservation, Kabale, Uganda

ⁱ Leibniz Institute for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Straße 17, 10315, Berlin, Germany

^j African Parks, POB: 62, Brazzaville, Republic of the Congo

^k WWF-India, 172 B, Lodhi Estate, New Delhi, 110003, India

^l Panthera, 8 West 40th Street, 18th Floor, NY, 10018, USA

^m Division of Biological Sciences, Wildlife Biology Program, University of Montana, 32 Campus Drive, Missoula, MT, 59812, USA

ⁿ Conservation Ecology Program, King Mongkut's University of Technology Thonburi, 49 Thakham, Bangkhuntien, Bangkok, 10150, Thailand

* Corresponding author. IUCN SSC Pangolin Specialist Group, % Zoological Society of London, Regents Park, London, NW1 4RY, UK.

** Corresponding author. IUCN SSC Pangolin Specialist Group, % Zoological Society of London, Regents Park, London, NW1 4RY, UK.

E-mail addresses: h.khwaja@chesterzoo.org (H. Khwaja), c.buchan@uea.ac.uk (C. Buchan).

^o PO Box CH254, Chisipite, Harare, Zimbabwe

^p Agence Nationale des Parcs Nationaux (ANPN) Kalikak, BP20379, Libreville, Gabon

^q The Society for Environmental Exploration / Frontier, 50-52, Rivington Street, London, EC2A 3QP, UK

^r Wildlife Conservation Society Congo, 151 Avenue du General de Gaulle, BP, 14537, Brazzaville, Republic of the Congo

^s Conservation International, 3rd Floor, Building F, Room, 371, Phnom Penh Center, Phnom Penh, Cambodia

^t Department of Biology, Bucknell University, Lewisburg, PA, 17837, USA

^u School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen, China

^v The Society for the Preservation of Endangered Carnivores & their International Ecological Study, P.O. Box 7403, Ventura, CA, 93006, USA

^w Wildlife Institute of India, PO Box 18, Chandrabani, Dehra Dun, 248 001, Uttarakhand, India

^x Biodiversity Research Centre, University of British Columbia, 2212 Main Mall, Vancouver, British Columbia, V6T 1Z4, Canada

^y Nature Conservation Foundation, 1311 Amritha, 12th Main, Vijayanagar 1st Stage, Mysore, 570 017, India

^z University of Hohenheim, Department of Agroecology in the Tropics and Subtropics (490f), Garbenstr. 13, 70599, Stuttgart, Germany

^{aa} Forest Is Life, Gembloux Agro-Bio Tech, University of Liège, Passage des Déportés 2, 5030, Gembloux, Belgium

^{ab} Center for Macroecology, Evolution & Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100, OE, Copenhagen, Denmark

^{ac} Department of Anthropology, University of California-Davis, One Shields Ave, Davis, CA, 95616, USA

^{ad} Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA

^{ae} Sâlim Ali Centre for Ornithology and Natural History, Anaikatty, Coimbatore, Tamil Nadu, 641108, India

^{af} Tropical Ecology Assessment and Monitoring (TEAM) Network, USA

^{ag} World Wide Fund for Nature, The Mvuli House, Mvuli Road, Westlands, Nairobi, Kenya

^{ah} Mogalakwena Research Centre, Limpopo Province, South Africa

^{ai} EcoHealth Alliance, 460 West 34th Street - Ste. 1701, New York, NY, 10001-2320, USA

^{aj} Wildlife Conservation Society – Center for Global Conservation, 2300 Southern Boulevard, Bronx, NY, 10460, USA

^{ak} Department of Psychology, York University, Toronto, Ontario, Canada

^{al} Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, 94300, Kota Samarahan, Sarawak, Malaysia

^{am} Vegetation Science and Nature Conservation Group, Carl von Ossietzky University, 26111, Oldenburg, Germany

^{an} Gessner Landschaftsökologie, Im Ermesgraben 3, 54338, Schweich, Germany

^{ao} Nicholas School of the Environment, Duke University, Durham, NC, 27708, USA

^{ap} College of Bioresource Science, Nihon University, Fujisawa, Kanagawa, Japan

^{aq} National University of Singapore, 14 Science Drive 4, 117543, Singapore

^{ar} Global Wildlife Conservation, Global Wildlife Conservation, 500 N Capital of Texas, Austin, TX, USA

^{as} School of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, Scotland, United Kingdom

^{at} El Colegio de la Frontera Sur (ECOSUR), Av. Rancho Polígono 2-A, Ciudad Industrial, 24500, Lerma Campeche, Camp, Mexico

^{au} Department of Fish and Wildlife Conservation, 318 Cheatham Hall, Virginia Tech, Blacksburg, VA, 24061-0321, USA

^{av} MUSE - Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38122, Trento, Italy

^{aw} Department of Biology, University of Florence, Via Madonna del Piano 6, 50019, Sesto Fiorentino, Italy

^{ax} Faculty of Environmental Sciences and Natural Resource Management (MINA), Norwegian University of Life Sciences (NMBU), Box 5003, 1432, Ås, Norway

^{ay} Tropical Conservation Institute, Florida International University, 11200 SW 8th Street, ECS 314, Miami, FL, 33199, USA

^{az} Ongava Research Centre, 102A Nelson Mandela Avenue, Klein Windhoek, Windhoek, Namibia

^{ba} Department of Biology, Faculty of Science, Silpakorn University, Sanam Chandra Palace Campus, 6 Rajamankha Nai Road, Amphoe Muang, Nakhon Pathom Province, 73000, Thailand

^{bb} Heart of Borneo Project, 16 Whinney Knowe, North Queensferry, Inverkeithing, KY11, 1JL, UK

^{bc} Cheetah Conservation Botswana, B5-Kgale Siding Office Park, Gaborone, Botswana

^{bd} Fauna & Flora International, David Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, UK

^{be} N/a'an ku sê Research Programme, P.O. Box 99292, Windhoek, Namibia

^{bf} Brown Hyena Research Project, P.O. Box 739, Lüderitz, 9000, Namibia

^{bg} Conservation Programmes, Zoological Society of London, Regents Park, London NW1 4RY, UK

^{bh} Department of Zoology and Oxford Martin School, University of Oxford, Zoology Research and Administration Building, 11a Mansfield Road, Oxford, OX1 3SZ, UK

ARTICLE INFO

Article history:

Received 11 June 2019

Received in revised form 30 August 2019

Accepted 31 August 2019

Keywords:

Camera trap

Detection

Occupancy modelling

Pangolin

Macroecology

Monitoring

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.

© 2019 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Pangolins are considered to be the world's most trafficked wild mammals (Challender and 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 and 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 few exceptions (e.g. *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 and Glover-Kapfer, 2017). They thereby create large volumes of potentially informative data on a wide range of species (Wearn and 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 with 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 and 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 and 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 and Anderson, 2002) using the Akaike Information Criterion corrected for small sample size (AICc). We carried only those parameters contained in models with $\Delta\text{AICc} \leq 6$ 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 $\Delta\text{AICc} \leq 6$ compared with the top-ranking model using the R package *AICcmovg* (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 (Fig. 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 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 (Fig. 2).

Probability of occupancy for both *S. gigantea* and *P. tricuspis* declined with increasing elevation across a range from 0 to 2395 m asl (Fig. 3A and B). *S. gigantea* occupancy also declined with increasing distance from the nearest river, while that of *M. javanica* increased (Fig. 3C and D). 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 (Fig. 4), although only 12% of camera trap locations 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

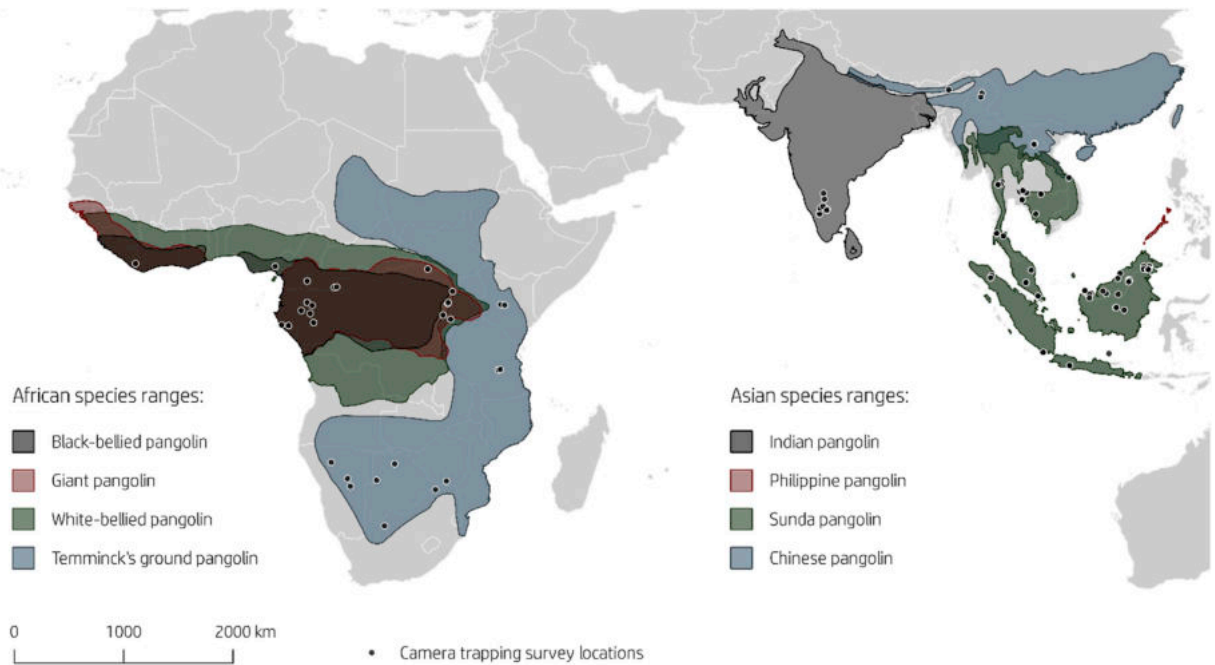


Fig. 1. Map of camera trap survey locations across the range of African and Asian pangolin species. Points represent the mean camera trap location for each survey.

of 26 (Fig. 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 (Figs. 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*.

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 the 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

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

Species	Represented range countries	Studies (n)	Camera traps (n)	Five-day trap occasions (n)	Trap occasions with detections (n)	Naive occupancy ^a	Naive detection probability ^b
Indian pangolin <i>Manis crassicaudata</i>	India	8	361	9405	29	0.07	<0.01
Philippine pangolin <i>Manis culionensis</i>	No data obtained	N/A	N/A	N/A	N/A	N/A	N/A
Sunda pangolin <i>Manis javanica</i>	Cambodia Indonesia Laos Malaysia Singapore Thailand Vietnam	43	2944	33,857	162	0.04	<0.01
Chinese pangolin <i>Manis pentadactyla</i>	India Laos Vietnam	5	737	9547	3	<0.01	<0.01
Black-bellied pangolin <i>Phataginus tetradactyla</i>	Cameroon Gabon Liberia Republic of the Congo	12	834	8186	0	N/A	N/A
White-bellied pangolin <i>Phataginus tricuspis</i>	Cameroon DRC Gabon Liberia Republic of the Congo Rwanda South Sudan Uganda	18	2287	29,083	275	0.10	<0.01
Giant pangolin <i>Smutsia gigantea</i>	Cameroon DRC Gabon Liberia Republic of the Congo Rwanda South Sudan Uganda	17	1993	27,249	414	0.13	0.02
Temminck's ground pangolin <i>Smutsia temminckii</i>	Botswana Kenya Namibia South Africa Tanzania Zimbabwe	13	708	12,654	5	<0.01	<0.01

^a Proportion of surveyed camera trap locations with pangolin detections.

^b Proportion of sampling occasions with pangolin detections.

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

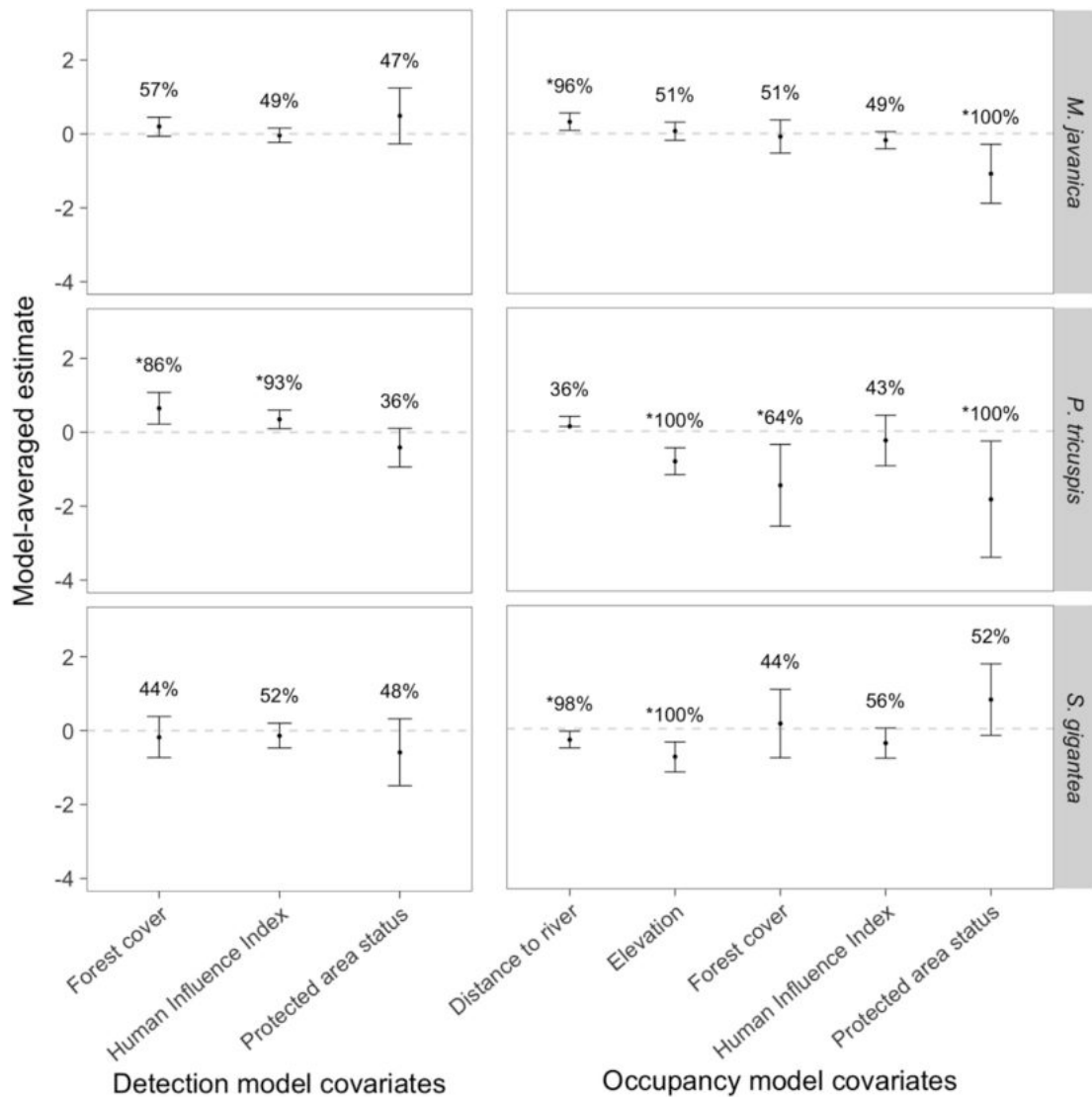


Fig. 2. Model-averaged covariate estimates for detection and occupancy, averaged across the best-supported models ($\Delta AICc \leq 6$). Error bars represent 95% confidence intervals. Values above error bars indicate the percentage of candidate models in which each covariate was present. Significant covariates are denoted by an asterisk.

sufficiently large scale, but could aid broad understanding of how pangolins respond to this threat, including potentially useful information on 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 and 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 and 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

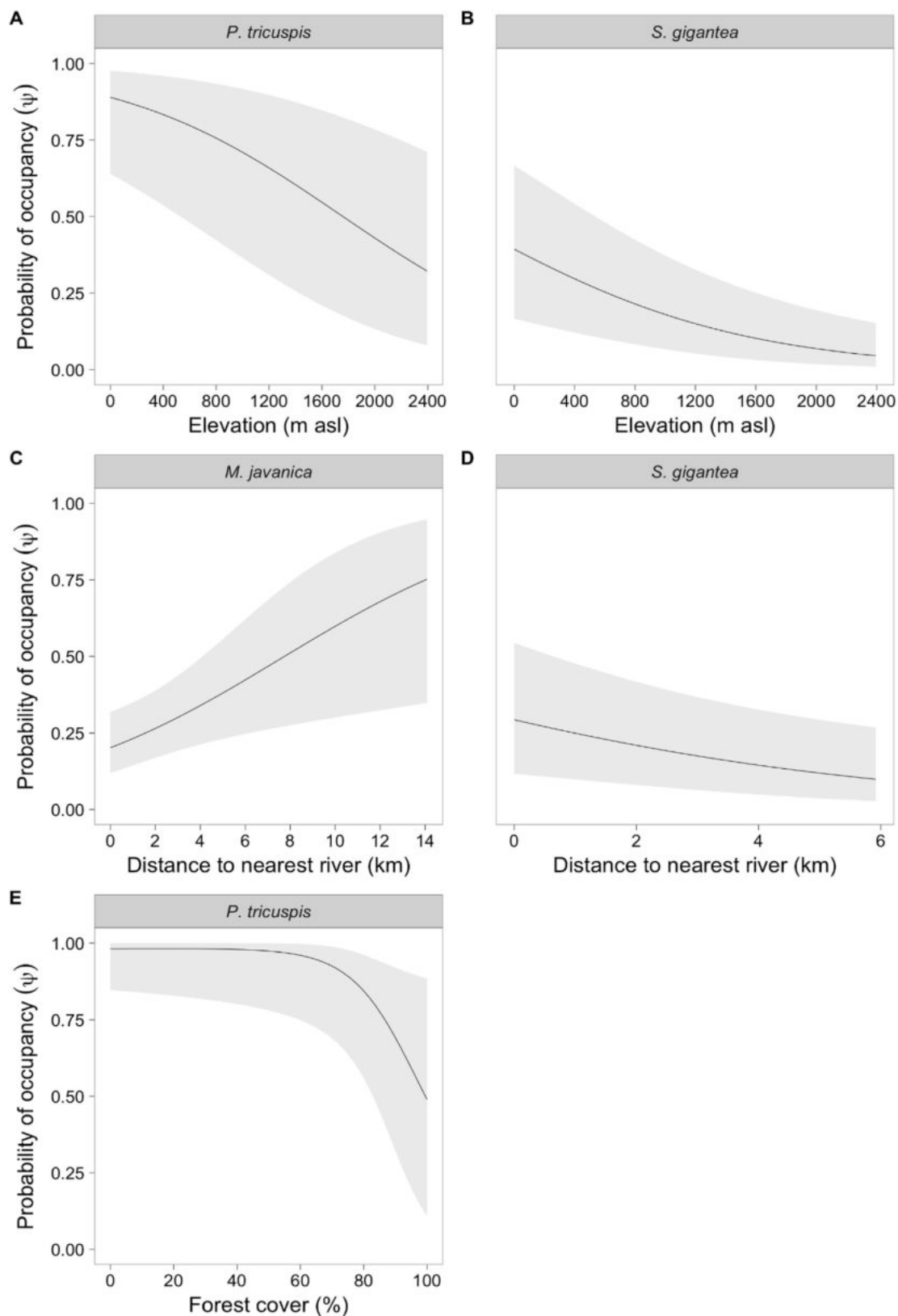


Fig. 3. Probability of occupancy of (A) white-bellied pangolin *Phataginus tricuspis* and (B) giant pangolin *Smutsia gigantea* based on elevation; (C) Sunda pangolin *Manis javanica* and (D) giant pangolin based on distance to the nearest river; and (E) white-bellied pangolin based on forest cover.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

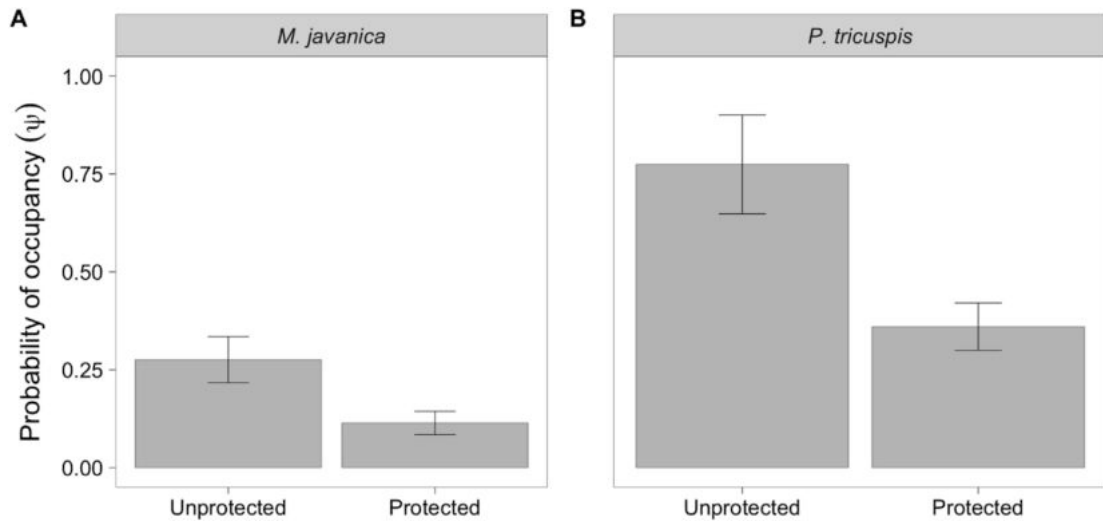


Fig. 4. Probability of occupancy of (A) Sunda pangolin *Manis javanica* and (B) white-bellied pangolin *Phataginus tricuspis* based on protected area status. Error bars represent 95% confidence intervals.

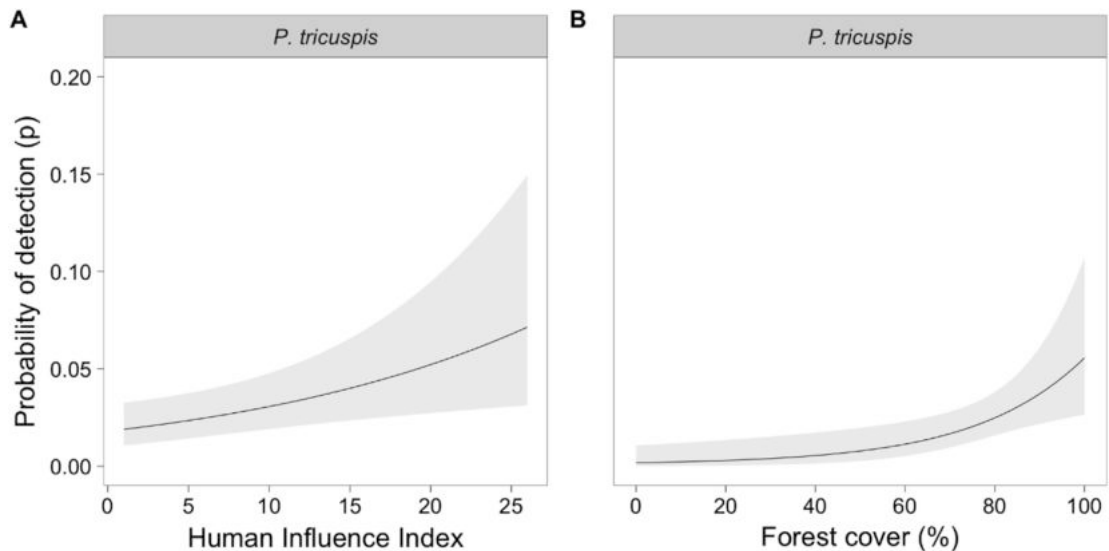


Fig. 5. Probability of detection of white-bellied pangolin *Phataginus tricuspis* based on (A) the Human Influence Index (WCS and CIESIN, 2005) and (B) percentage forest cover. Shaded areas represent 95% confidence intervals.

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 professional 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

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 <i>P. tricuspis</i> , <i>S. gigantea</i> and <i>M. javanica</i> 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 <i>P. tetradactyla</i> , 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 <i>P. tricuspis</i> , <i>S. gigantea</i> and <i>M. javanica</i> , 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 N pangolins recorded alongside a suite of other species		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, <i>S. gigantea</i> , 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 Y? targeted camera placement for pangolins		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. Limited, 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).

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 and 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 the 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 and 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.

Declarations of interest

None.

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/SO/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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00769>.

References

- Akpona, H.A., Djagoun, C.A.M.S., Sinsin, B., 2008. Ecology and ethnozoology of the three-cusped pangolin *Manis tricuspis* (Mammalia, Pholidota) in the Lama forest reserve, Benin. *Mammalia* 72, 198–202.
- Anon, 2015. First Pangolin Range State Meeting Report. June 24–26, 2015. Da Nang, Vietnam. Pp.1–68.
- Apps, P.J., McNutt, J.W., 2018. Are camera traps fit for the purpose? A rigorous, reproducible and realistic test of camera trap performance. *Afr. J. Ecol.* 56, 710–720.
- Baillie, J., Challender, D., Kaspal, P., Khatiwada, A., Mohapatra, R., Nash, H., 2014. *Manis crassicaudata*. The IUCN Red List of Threatened Species 2014: e.T12761A45221874. Available at: www.iucnredlist.org/species/12761/45221874.
- Bruce, T., Kamta, R., Mbobda, R.B.T., Kanto, S.T., Djibrilla, D., Moses, I., Deblauwe, V., Njabo, K., LeBreton, M., Ndjassi, C., Barichiev, C., Olson, D., 2018. Locating giant ground pangolins (*Smutsia gigantea*) using camera traps on burrows in the Dja Biosphere Reserve, Cameroon. *Tropical Conservation Science* 11, 1–5.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*, second ed. Springer-Verlag, New York, USA.
- Challender, D. W. S., Alvarado, D., Archer, L., Brittain, S., Chong, J. L., Copesey, J., Davies, A., Fletcher, L., Gudehus, M., Hartmann, J., Hoffmann, R., Ichu, I.G., Ingram, D., Johnston, A., Khwaja, H., Kim, H.J., Klailova, M., Lees, C., Mahmood, T., Nash, H. C., Nixon, S., O'Neill, H., Panaino, W., Panjang, E., Parker, K., Pollini, B., Shirley, M.H., Sun, N. C. M., Suwal, T. L., Tayleur, C., Wang, Y., Waterman, C., Wearn, O.R., Whytock, R., Wu, S. B. and Morin, D. (in prep.) Developing Ecological Monitoring Methods for Pangolins (Pholidota: Manidae). *Global Ecology And Conservation*.
- Challender, D., Baillie, J., Ades, G., Kaspal, P., Chan, B., Khatiwada, A., Xu, L., Chin, S., KC, R., Nash, H., Hsieh, H., 2014a. *Manis pentadactyla*. The IUCN Red List of Threatened Species 2014: e.T12764A45222544. Available at: www.iucnredlist.org/species/12764/45222544.
- Challender, D., Nguyen Van, T., Shepherd, C., Krishnasamy, K., Wang, A., Lee, B., Panjang, E., Fletcher, L., Heng, S., Seah Han Ming, J., Olsson, A., Nguyen The Truong, A., Nguyen Van, Q., Chung, Y., 2014b. *Manis javanica*. The IUCN Red List of Threatened Species 2014: e.T12763A45222303. Available at: www.iucnredlist.org/species/12763/45222303.
- Challender, D., Waterman, C., 2017. Implementation of CITES Decision 2 17.239 B) and 17.240 on pangolins (*Manis* spp.). CITES SC69 Doc. 57 Annex. Available at: www.cites.org/sites/default/files/eng/com/sc/69/E-SC69-57-A.pdf.
- Challender, D.W.S., Waterman, C., Baillie, J.E.M., 2014c. Scaling up Pangolin Conservation: IUCN SSC Pangolin Specialist Group Conservation Action Plan. Zoological Society of London, London, UK.
- Convention on the International Trade in Endangered Species (CITES), 2017. Convention on the International Trade in Endangered Species (CITES), 2017. Resolution Conf. 17.10: Conservation of and Trade in Pangolins. Available at: www.cites.org/sites/default/files/document/E-Res-17-10.pdf.
- de Ferranti, J., 2012. Digital elevation data. Available at: www.viewfinderpanoramas.org/dem3.html.
- Dorazio, R.M., Gotelli, N.J., Ellison, A.M., 2011. Modern methods of estimating biodiversity from presence-absence surveys. In: Grillo, O., Venora, G. (Eds.), *Biodiversity Loss in a Changing Planet* (IntechOpen).
- Fischer, J.H., Jones, S.E.L., Brodie, J.F., Marshall, A.J., Setiawan, E., Wain, A., van Berkel, T.B.T., Wearn, O.R., van der Kaaden, A., Granados, A., Mathai, J., Cheyne, S.M., Denny, M.J.H., 2017. The potential value of camera-trap studies for identifying, ageing, sexing and studying the phenology of Bornean *Lophura* pheasants. *Forktail* 33, 92–102.
- Fiske, I., Chandler, R., 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* 43, 1–23.
- Glover-Kapfer, P., Soto-Navarro, C.A., Wearn, O.R., 2019. Camera-trapping version 3.0: current constraints and future priorities for development. *Remote Sens. Ecol. Conserv.* <https://doi.org/10.1002/rse2.106>. Online before Print.
- Guillera-Arroita, G., Ridout, M.S., Morgan, B.J.T., 2010. Design of occupancy studies with imperfect detection. *Meth. Ecol. Evol.* 1, 131–139.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853. Available at: earthenginepartners.appspot.com/science-2013-global-forest.
- Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6, e4794.
- Heinrich, S., Wittman, T.A., Ross, J.V., Shepherd, C.R., Challender, D.W.S., Cassey, P., 2017. The global trafficking of pangolins: a comprehensive summary of seizures and trafficking routes from 2010–2015. Petaling Jaya, Malaysia: Traffic. Available at: www.traffic.org/publications/the-global-trafficking-of-pangolins.html.
- Hofmeester, T.R., Cromsigt, J.P.G.M., Odden, J., Andrén, H., Kindberg, J., Linnell, J.D.C., 2019. Framing pictures: a conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution* 9, 2320–2336.
- Hossain, A.N.M., Barlow, A., Greenwood Barlow, C., Lynam, A.J., Chakma, S., Savini, T., 2016. Assessing the efficacy of camera trapping as a tool for increasing detection rates of wildlife crime in tropical protected areas. *Biol. Conserv.* 201, 314–319.
- Howe, E.J., Buckland, S.T., Després-Einspinner, M., Kühl, H.S., 2017. Distance sampling with camera traps. *Methods in Ecology and Evolution* 8, 1558–1565.
- Ingram, D.J., Coad, L., Abernethy, K.A., Maisels, F., Stokes, E.J., Bobo, K.S., Breuer, T., Gandiwa, E., Ghiurghi, A., Greengrass, E., Holmern, T., Kamgaing, T.O.W., Obiang, A.M.N., Poulsen, J.R., Schleicher, J., Nielsen, M.R., Solly, H., Vath, C.L., Walther, M., Whitham, C.E.L., Wilkie, D.S., Scharlemann, J.P.W., 2017. Assessing Africa-wide pangolin exploitation by scaling local data. *Conservation Letters* 11, e12389.
- IUCN, 2018. The IUCN red list of threatened species, version 2018-2. Available at: www.iucnredlist.org.
- Jansen, P.A., Ahumada, J., Fegraus, E., O'Brien, T.G., 2014. TEAM: a standardised camera trap survey to monitor terrestrial vertebrate communities in tropical forests. In: Meek, P.D., Fleming, P.J.S., Ballard, G., Banks, P., Claridge, A., Sanderson, J., Swann, D. (Eds.), *Camera Trapping: Wildlife Management and Research*. CSIRO Publishing, Melbourne, Australia, pp. 263–270.
- Karawita, H., Perera, P., Gunawardana, P., Dayawansa, N., 2018. Habitat preference and den characterisation of Indian pangolin (*Manis crassicaudata*) in a tropical lowland forested landscape of southwest Sri Lanka. *PLoS One* 13, e0206082.
- Kays, R., Tilak, S., Kranstauber, B., Jansen, P.A., Carbone, C., Rowcliffe, M., Fountain, T., Eggert, J., He, Z., 2009. Camera traps as sensor networks for monitoring animal communities. *International Journal of Research and Reviews in Wireless Sensor Networks* 1, 19–29.
- Kingdon, J.S., Hoffman, M., 2013. *Mammals of Africa Volume V: Carnivores, Pangolins, Equids and Rhinoceroses*. Bloomsbury Publishing PLC, London, UK.
- Lagrada, L., Schoppe, S., Challender, D., 2014. *Manis culionensis*. The IUCN Red List of Threatened Species 2014: e.T136497A45223365. Available at: www.iucnredlist.org/species/136497/45223365.
- Latif, Q.S., Ellis, M.M., Amundson, C.L., 2016. A broader definition of occupancy: comment on Hayes and Monfils. *J. Wildl. Manag.* 80, 192–194.
- Lehner, B., Verdin, K., Jarvis, A., 2008. New global hydrography derived from spaceborne elevation data. *Eos* 89, 93–94.
- Lin, J.S., 2011. Home Range and Burrow Utilisation in Taiwanese Pangolins (*Manis Pentadactyla Pentadactyla*) at Luanshan, Taitung (MSc Thesis). National Pingtung University of Science and Technology. Available at: <http://aa.npust.edu.tw/html/832-932-grade/991%E6%91%98%E8%A6%81/M9617012.doc>.
- Linkie, M., Guillera-Arroita, G., Smith, J., Ario, A., Bertagnolio, G., Cheong, F., Clements, G.R., Dinata, Y., Duangchantrasiri, S., Frederiksson, G., Gumal, M.T., Horng, L.S., Kawaniishi, K., Khakim, F.R., Kinnaird, M.F., Kiswayadi, D., Lubis, A.H., Lynam, A.J., Maryati, Maung, M., Ngoprasert, D., Novarino, W., O'Brien, T. G., Parakkasi, K., Peters, H., Priatna, D., Rayan, D.M., Seuaturien, N., Shwe, N.M., Steinmetz, R., Sugesti, A.M., Sunarto, Sunquist, M.E., Umponjan, M., Wibisono, H.T., Wong, C.C.T., Zulhami, 2013. Cryptic mammals caught on camera: assessing the utility of range wide camera trap data for conserving the endangered Asian tapir. *Biol. Conserv.* 162, 107–115.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- MacKenzie, D.I., Royle, J.A., 2005. Designing efficient occupancy studies: general advice and tips on allocation of survey effort. *J. Appl. Ecol.* 42, 1105–1114.

- Mazerolle, M.J., 2017. AICcmmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-1. Available at: cran.r-project.org/web/packages/AICcmmodavg/index.html.
- Moeller, A.K., Lukacs, P.M., Horne, J.S., 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. *Ecosphere* 9, e02331.
- Mugume, S., Isabirye-Basuta, G., Otali, E., Reyna-Hurtado, R., Chapman, C.A., 2015. How do human activities influence the status and distribution of terrestrial mammals in forest reserves? *J. Mammal.* 96, 998–1004.
- Nijman, V., 2015. Pangolin seizures data reported in the Indonesian media. *Traffic Bull.* 27, 44–46.
- Pei, K.J.C., Lai, Y.C., Corlett, R.T., Suen, K.Y., 2010. The larger mammal fauna of Hong Kong: species survival in a highly degraded landscape. *Zool. Stud.* 49, 253–264.
- Pietersen, D., Jansen, R., Swart, J., Kotze, A., 2016. A conservation assessment of *Smutsia temminckii*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T. (Eds.), *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South Africa: South African National Biodiversity Institute and Endangered Wildlife Trust.
- Pietersen, D., Waterman, C., Hywood, L., Rankin, P., Soewu, D., 2014. *Smutsia temminckii*. The IUCN Red List of Threatened Species 2014: e.T12765A45222717. Available at: www.iucnredlist.org/species/12765/45222717.
- Plummer, M., 2012. JAGS: Just another Gibbs sampler. Astrophysics source code library. Available at: ascl.net/1209.002.
- QGIS Development Team, 2017. QGIS geographic information system. Open source geospatial foundation project. Available at: qgis.org.
- Rich, L.N., Davis, C.L., Farris, Z.J., Miller, D.A.W., Tucker, J.M., Hamel, S., Farhadinia, M.S., Steenweg, R., Di Bitetti, M.S., Thapa, K., Kane, M.D., Sunarto, S., Robinson, N.P., Paviolo, A., Cruz, P., Martins, Q., Gholikhan, N., Taktehrani, A., Whittington, J., Widodo, F.A., Yoccoz, N.G., Wulfsch, C., Harmsen, B.J., Kelly, M.J., 2017. Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. *Glob. Ecol. Biogeogr.* 26, 918–929.
- Rowcliffe, J.M., Field, J., Turvey, S.T., Carbone, C., 2008. Estimating animal density using camera traps without the need for individual recognition. *J. Appl. Ecol.* 45, 1228–1236.
- Royle, J.A., Dorazio, R.M., 2008. *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Academic Press, Amsterdam.
- Schank, C.J., Cove, M.V., Kelly, M.J., Mendoza, E., O'Farrill, G., Reyna-Hurtado, R., Meyer, N., Jordan, C.A., González-Maya, J.F., Lizcano, D.J., Moreno, R., Dobbins, M.T., Montalvo, V., Sáenz-Bolaños, C., Carillo Jimenez, E., Estrada, N., Díaz, J.C.C., Saenz, J., Spinola, M., Carver, A., Fort, J., Nielsen, C.K., Botello, F., Montuy, G.P., Rivero, M., de la Torre, J.A., Brenes-Mora, E., Godínez-Gómez, O., Wood, M.A., Gilbert, J., Miller, J.A., 2017. Using a novel model approach to assess the distribution and conservation status of the endangered Baird's tapir. *Divers. Distrib.* 23, 1459–1471.
- Scotson, L., Fredriksson, G., Ngoprasert, D., Wong, W.M., Fieberg, J., 2017a. Projecting range-wide sun bear population trends using tree cover and camera-trap bycatch data. *PLoS One* 12, e0185336.
- Scotson, L., Johnston, L.R., Iannarilli, F., Wearn, O.R., Mohd-Azlan, J., Wong, W.M., Gray, T.N., Dinata, Y., Suzuki, A., Willard, C.E., Frechette, J., 2017b. Best practices and software for the management and sharing of camera trap data for small and large scale studies. *Remote Sensing in Ecology and Conservation* 3, 158–172.
- Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J.T., Burton, C., Townsend, S.E., Carbone, C., Rowcliffe, J.M., Whittington, J., Brodie, J., Royle, J.A., Switalski, A., Clevenger, A.P., Heim, N., Rich, L.N., 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology & Evolution* 15, 26–34.
- Stuart, C.T., 1980. The distribution and status of *Manis temminckii* Pholidota Manidae. *Säugetierkundliche Mitteilungen* 28, 123–129.
- Trageser, S.J., Ghose, A., Faisal, M., Mro, P., Mro, P., Rahman, S.C., 2017. Pangolin distribution and conservation in Bangladesh. *PLoS One* 12, e0175450.
- UNEP-WCMC, IUCN, 2015. *Protected planet: the world database on protected areas (WDPA)*. Cambridge, UK: UNEP-WCMC and IUCN. Available at: www.protectedplanet.net.
- Waterman, C., Pietersen, D., Hywood, L., Rankin, P., Soewu, D., 2014a. *Smutsia gigantea*. The IUCN Red List of Threatened Species 2014: e.T12762A45222061. Available at: www.iucnredlist.org/species/12762/45222061.
- Waterman, C., Pietersen, D., Soewu, D., Hywood, L., Rankin, P., 2014b. *Phataginus tetradactyla*. The IUCN Red List of Threatened Species 2014: e.T12766A45222929. Available at: www.iucnredlist.org/species/12766/45222929.
- Waterman, C., Pietersen, D., Soewu, D., Hywood, L., Rankin, P., 2014c. *Phataginus tricuspis*. The IUCN Red List of Threatened Species 2014: e.T12767A45223135. Available at: www.iucnredlist.org/species/12767/45223135.
- Wearn, O.R., Glover-Kapfer, P., 2017. *Camera-trapping for Conservation: A Guide to Best-Practices*. WWF-UK, Woking, UK.
- Wearn, O.R., Glover-Kapfer, P., 2019. Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *R. Soc. Open Sci.* 6, 181748.
- Wearn, O.R., Rowcliffe, M.J., Carbone, C., Pfeifer, M., Bernard, H., Ewers, R.M., 2017. Mammalian species abundance across a gradient of tropical land use intensity: a hierarchical multi-species modelling approach. *Biol. Conserv.* 212, 162–171.
- Welsh, A.H., Lindenmayer, D.B., Donnelly, C.F., 2013. Fitting and interpreting occupancy models. *PLoS One* 8, e52015.
- Wildlife Conservation Society (WCS) and Center for International Earth Science Information Network (CIESIN), 2005. Last of the wild project, version 2 (LWP-2): global human influence index (HII) dataset (geographic). Palisades, NY: NASA socioeconomic data and applications center (SEDAC). <https://doi.org/10.7927/H4BP00QC>. Available at:
- Willcox, D., Bull, R., Nguyen, V.N., Tran, Q.P., Nguyen, V.T., 2017. Small carnivore records from the U Minh wetlands, Vietnam. *Small Carniv. Conserv.* 55, 4–25.
- Willcox, D., Nash, H.C., Trageser, S., Kim, H.J., Hywood, L., Connelly, E., Ichu Ichu, G., Kambale Nyumu, J., Mousset Momboulou, C.L., Ingram, D.J., Challender, D.W.S., 2019. Evaluating methods for detecting and monitoring pangolin populations (Pholidota: Manidae). *Global Ecology and Conservation*, e00539.
- Willi, M., Pitman, R.T., Cardoso, A.W., Locke, C., Swanson, A., Boyer, A., Veldhuis, M., Fortson, L., 2018. Identifying animal species in camera trap images using deep learning and citizen science. *Methods in Ecology and Evolution* Online before print. <https://doi.org/10.1111/2041-210X.13099>. Available at:
- Wu, S., Ma, G., Chen, H., Xu, Z., Li, Y., Liu, N., 2004. A preliminary study on burrow ecology of *Manis pentadactyla*. *Chin. J. Appl. Ecol.* 15, 401–407.
- Zoological Society of London (ZSL), 2016. *Asia conservation programme: new hope for Thailand's Sunda pangolins*. Available at: www.zsl.org/blogs/asia-conservation-program/new-hope-for-thailand%E2%80%99s-sunda-pangolins.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Meth. Ecol. Evol.* 1, 3–14.