Distribution, range connectivity, and trends of bear populations in Southeast Asia

A Dissertation
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Francesca J Cuthbert

June 2017

Acknowledgements

Thank you to all in the Government of Laos who facilitated my work in Lao PDR. This includes the Ministry of Natural Resources and Environment, Vientiane and Provincial Offices of Natural Resources and Environment of Bokeo, Luang Namtha, Huaphanh, Bolikhamxai, Khammouan, Savannahket, Sekong, Saravane and Champasack Provinces.

Thank you to the talented and courageous Lao BSc and MSc students who helped me in the field, including Oudone Phakphotong, Kongseng Vannachomchan, Phianxay Xiongyiadong, Ommany Leudedmounsone and Sonenaline Inthavong. Thank you also to the Wildlife Conservation Society and to the faculty at the National University of Laos, particularly Ajan Bounthop and Ajan Kamla, for assistance with field permits and for facilitating Lao student projects.

Thank you to the bear experts Gabriella Fredriksson, Dave Garshelis, Rob Steinmetz and Siew Te Wong, for their valuable input into my project design and field training, and for providing essential guidance and inspiration throughout my field research in Lao PDR.

Thank you to all the faculty at the University of Minnesota for all I've learned during my time at the University. I am especially grateful to my PhD Advisor, Professor Francie Cuthbert, for her advice and guidance in the completion of my thesis. I am indebted to Sue Galatowitsch, Karen Oberhauser, and Andrew Simons, for their unwavering support, advice and guidance throughout my final year.

I thank my PhD Committee, Todd Arnold, John Fieberg and Michael Proctor, for their input and collaboration. I have gained so much from working with you. Thank you also to Robert Steinmetz and James Forester, for your input as committee members in my earlier years.

Thank you also to all of those who collaborated on my thesis chapters, Chapter 1: Steve Ross and Todd Arnold, Chapter 2: Michael Proctor, Gabriella Fredriksson, Robert Steinmetz, Dusit Ngoprasert, Wai Ming Wong and John Fieberg; Chapter 3: Michael Proctor, Chapter 4: Lisa Johnston, Fabiola Iannarilli, Oliver Wearn, Jayasilan Mohd-Azlan, Wai Ming Wong, Thomas Gray, Yoan Dinata, Ai Suzuki, Claire Willard, Jackson Frechette, Brent Loken, Robert Steinmetz, Alexander Moßbrucker and John Fieberg.

Thank you to my peers at the University of Minnesota, for the solidarity and friendships I found during my time here, including Mark Ditmer, Roshan Guharajan, Fabiola Iannarilli, Pornkamol (Joob) Jornburom, Worata (Pai) Klinsawat, Lindsey Novak, Jeta Rudi, Kelsey Vitense and all the Fieberg and B52 Lab. I hope that we stay in touch.

Thank you to Free the Bears, and to my generous funders, for financial support and also friendship, for giving me confidence in the usefulness of my research, and for providing platforms to publicize my findings. Funders include Free the Bears, Perth Zoo, Karine and Anna Hauser from the Hauser Bear Foundation, The International Bear Association's Research and Conservation Grant and Experience and Exchange Grant, Alertis Fund for Bear and Nature Conservation, the Margaret Dawbarn Foundation and Estate Robin Vincent Udney Rothwell Account Wildlife Preservation Trust (Perpertual Philanthropic), Cholchester Zoo's Action for the Wild Fund and Kölner Zoo. I am also very grateful for funding received from the University of Minnesota's Doctor Dissertation Fellowship program and the Conservation Biology summer grant and travel fund.

Thank you to all those who helped me during my field research in Lao PDR. Thank you especially to Shi Ji Seingtaow, for being the best field assistant anyone could ask for, and for always making me feel safe in the forest. A special thank you to Mike Brocklehurst, who always answered the phone when I found signal at the tops of mountains and who drove things around the country for me without question or complaint. Thank you also to Phouyavong Khathalangsy, Ben Swanepoel, Mai Heim, Ai Senjilo, Ai Wongphet, Sinthone Phoukhanouane, Bounthavy Phommachanh and all others I had the pleasure of meeting and working with during my work in Lao PDR.

Thank you to Vicki Hartman, and her menagerie at Carisbrooke farm, for making my final year's writing so colorful, and for giving me a warm winter office in the horse barn, in between the furnace and Stella the potbellied pig.

Thank you Mum and Dad, for keeping me going through the hard times, and for giving me an office in the Scottish countryside. Thank you to Robert and Keith Redford, my new Canadian family, for accepting and supporting me, and for giving me so much to look forward to.

Finally, thank you to Matt Hunt, for your support and encouragement. Thank you for sending me on that first adventure into the Cambodian jungle, and for getting me hooked on searching for bears in the amazing forests of southeast Asia.

My first bear sign, 13th January, 2007,Cardamon Mountains, Cambodia

Dedication

This thesis is dedicated to my Mum and Dad

- Nancy and Angus Scotson -

who taught me to search for adventures in foreign lands

Abstract

Sun bears and Asiatic black bears co-occur in Southeast Asia with wide areas of overlapping range. Both species are in decline, and are vulnerable to extinction due mainly to habitat loss and illegal hunting. Efforts to conserve bears in Southeast Asia are hampered by a lack of basic knowledge of distribution, population trends and habitat configuration. To advance the scientific understanding of sun bears and Asiatic back bears in this region I investigated fine and broad scale patterns of distribution. In Lao PDR, I gathered data on bear occurrence using bear sign transects walked in multiple forest blocks throughout the country. To model the country-wide relative abundance of bears and habitat quality, I related bear sign to environmental factors associated with bear occurrence. Within global sun bear range, I gathered camera trap records of sun bear detections from seven sun bear range countries. To generate quantitative measures of sun bear population trends, I related sun bear detection rates to tree cover and estimated related changes in country and global-level sun bear populations based on tree cover loss. To evaluate the global extent of sun bear range connectivity, I used the modelled relationship between sun bears and tree cover to create a habitat suitability index, and I identified areas of fractured range that have created unnatural subpopulations that are at risk from isolation. In Lao PDR, bears selected for areas of high elevation, rugged terrain, and areas of high tree density far from roads. My model-based estimates of sun bear global population trends predicted that over a 30-year period, sun bear populations in mainland southeast Asia have potentially declined by close to 20%, and insular sun bear populations have declined by ~50%. I identified seven potential sun bear subpopulations; two that are fully isolated with no potential for inter-subpopulation movement, and in the other five, inter and intra-subpopulation habitat fragmentation occurs in a continuum of severity. My findings advance the understanding of patterns in bear distribution and trends in southeast Asia, identify research priorities, and lay a framework for future monitoring efforts at country and region-level scales. I conclude with recommendations on how to better manage camera trap data for secondary research and sharing.

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Introduction

One thousand years ago, scientists thought the world was flat, and cartographers wrote the words "*Here be dragons*" on maps to signify dangerous and uncharted territories (Best 1988). Now, in the apparent luxuries of the 3rd millennium, we can use Google Earth to zoom into a spherical earth for a bird's eye view of any region of the world. Despite all this progress, large portions of the geographic range of many of the world's most charismatic wildlife species remain in a state of uncertainty. Asia's bear species are a prime example, as species for which we are still uncovering the most basic information on their habitat and inhabitable ranges. For Asia's bears, we are now in a period of exponential knowledge growth; for every new piece of information obtained, a new portion of the map is illuminated.

Of the eight extant species of bears in the world, brown bears (in Europe and North America) and American black bears are faring well in most areas, and are afforded the highest levels of scientific understanding, so enabled by adequate funding, technological capacity, and long-term data sets (Garshelis et al. 2016, McLellan et al. 2016). By contrast, in developing countries, most notably in Southeast Asia, we have very low levels of understanding of bears and populations are thought to be eroding, potentially disappearing virtually unnoticed. My research focuses on both bear species that inhabit this region: Sun bears *Helarctos malayanus* and Asiatic black bears *Ursus thibetanus*. Both species are listed as 'Vulnerable' by the International Union for Conservation of Nature (IUCN; Garshelis and Steinmetz 2016, Scotson et al. 2017). Sun bears and Asiatic black bears occupy the same habitats (not just on a broad scale, but in the same small forest patches) across much of mainland Southeast Asia. A narrow isthmus on the Thai-Malay Peninsula marks the southern geographical range limit for Asiatic black bears; southward, sun bears occur alone and at higher densities (Steinmetz 2011). Between 2010 - 2013 I conducted field work in the forest of Lao People's Democratic Republic (hereafter Lao PDR), where no other scientific work on bears had been done prior to my study. Lao PDR's extent of natural forest cover is among the highest in the region (over 40%) and it is generally believed to be a stronghold for bears in Southeast Asia. As such, Lao PDR represents not only an ideal country for studying the ecologies of these two species in varying habitats, but also a country where it is possible to implement thoughtful, proactive strategies to preserve ecosystems with both species of bears as fundamental functioning components, rather than remnant, isolated, sparse populations. Southeast Asia is experiencing the highest rate of deforestation in the world, resulting in dramatic shrinkage of bear habitat (Miettinen et al. 2011). Moreover, bears are illegally hunted for their parts, in particular, bile from the gall bladder, which is a highly efficacious in treating degenerative and inflammatory ailments and is much sought after Traditional Chinese Medicine (Feng et al. 2009).

My dissertation is built across several scales. Chapter one centers on mapping the country-wide distribution of sun bears and black bears in Lao PDR. I detected the presence of bears by the sign they left in the forest — mainly claw marks on trees they climbed for foraging (Steinmetz and Garshelis 2008). I examined every tree in narrow strip transects within eight forest blocks throughout Lao PDR. I captured the full range of eco-geographic variation across the country, while also ensuring adequate, pseudo-random and independent sampling within each forest block so that I could make valid inferences from the data. In addition to bear presence, I collected data on ecological and anthropogenic variables thought to influence bear abundance. These data allowed me to create a data driven species distribution map that reveals fine scale patterns of bear distribution in Lao PDR, and a tool that can be repeatedly applied through time as human factors continue to influence patterns of bear distribution change.

Chapters two and three focus solely on sun bears, and broaden out to examine the entire sun bear range across mainland and insular Southeast Asia. Southeast Asia has experienced a higher rate of forest loss than any other region of the world, due largely to conversion to oil palm and other crops. As such, the range of the forest dependent sun bear is shrinking and becoming increasingly fragmented. In chapter two, I undertake the first quantitative assessment of the decline of bears over a broad region, based on the extent of habitat loss and fragmentation. Prior estimates of sun bear population decline are based on expert opinion, inferred from perceived levels of hunting and published estimates of forest loss within sun bear range (Scotson et al. 2017). I obtained detection data from 2845 camera traps, collected from other studies throughout the region. I have combined these data with recently-available high-resolution satellite imagery depicting tree cover across all Southeast Asia to relate bear presence to tree cover density (Hansen et al. 2013). Using the relationship between tree cover and sun bear detections, I estimated related changes in country and global-level sun bear populations based on tree cover loss between 2000 and 2014, and have projected declines over a 30-year period.

In Chapter 3, I examine the present-day range connectivity of sun bears and identify subpopulations and isolated populations at risk from the nefarious effects of habitat fragmentation. In the Pleistocene, sun bear range occurred on one continuous continent, stretching northwards from Sundaland, an ancient continent formed collectively by the Indo-Malay islands of Borneo, Sumatra and Java, when areas in-between were dry land, and limited naturally by the Red River, in north-eastern Vietnam, and unfavorable climate and elevations, and competitive exclusion by the Indian Sloth Bear, in Southern China and northeast India (Wallace 1869, Erdbrink 1953, Steinmetz 2006). In present day, sun bear range is unnaturally broken up into many subpopulations, created by habitat loss and disturbance due to human activities. Characterizing sun bears as modern day subpopulations allows us to consider their ability to persist as unnatural metapopulations, and steers research by prioritizing investigation into areas where bears may be most at risk from local extirpation.

Finally, in Chapter 4, I take the experiences gained from my previous chapters, and provide a range of data management best practices and software to improve the management and sharing of camera trap data. To build on scientific knowledge of Asian bears, and other threatened tropical species, scientists must harness the power of data collected and shared from multiple sources. My thesis research is a small step in a long journey to research and conserve bears in Southeast Asia. Rigorous population monitoring is essential for adaptive conservation, because it highlights what is working and what is not. Here I make a start, by shedding some light on the distribution, trends and range connectivity of bear populations in Southeast Asia. I provide a framework for future population monitoring, that is reproducible and can be improved upon, as more data become available and the techniques I propose here are developed further.

Chapter 1

Monitoring sun bears and Asiatic black bears in Lao PDR with remotely sensed predictors of distribution and relative abundance

Scotson L., Ross S., Arnold, T.

Synopsis

Asiatic black bears *Ursus thibetanus* and sun bears *Helarctos malayanus* co-occur throughout Lao PDR, and populations are thought to be faring better than those in neighboring countries. However, bears are in decline throughout Southeast Asia, due to habitat loss and human disturbance and knowledge of the distribution and status of populations is limited, and based largely on anecdotal information. Range maps are coarse, compiled by expert opinion, and basic information on the presence or absence of bears is unknown in large portions of Lao PDR. Here we identify biological and anthropogenic factors related to bear relative abundance and habitat selection. We use these factors to explore patterns of bear distribution by generating species distribution maps that reflect the country-wide relative abundance of bears and relative habitat suitability. We sampled bear populations within eight study sites in the north, east and south of Lao PDR between 2010 – 2013. To create a proximate measure of relative bear abundance, and an indicator of habitat suitability, we collected bear sign along forest transects and modeled bear sign as a log-linear function of environmental predictors associated with habitat assemblages and levels of human disturbance. We found that bears tended to favor higher elevation, rugged terrain in areas less accessible by humans. Bears were most abundant, and habitat most suitable, in the north and along the eastern border with Vietnam. The southern lowland plains are largely devoid of suitable habitat and abundance was relatively low. By using low tech bear sign transects, we created a replicable GIS-based monitoring and assessment tool for bears in Lao PDR that can be used to identify conservation opportunities and monitor changes in bear distribution through time. Bear populations in Lao PDR are threatened by habitat loss and human disturbance. Declines will likely continue in the

absence of proactive conservation measures that effectively reduce deforestation within bear habitat, and combat illegal hunting and trade.

Introduction

Asiatic black bears *Ursus thibetanus* and sun bears *Helartos malayanus* are sympatric in Lao PDR, and previously occurred throughout all provinces (Erdbrink 1953, Lekagul and McNeely 1977). Both species are classed as ‘Vulnerable’ on the IUCN Red-list of Threatened species, and populations are projected to decline globally by more than 30% in the next 30+ years, due to habitat loss and hunting (Garshelis and Steinmetz 2016, Scotson et al. 2017). The IUCN range map, which is identical for sun bears and Asiatic black bears in Lao PDR, suggests that currently, bears occur within all national protected areas (NPAs) and some provincial protected areas (PPAs; Garshelis and Steinmetz 2016, Fig 1), highlighting Lao PDR as a core area for bear conservation, However, the fine scale distribution of bears within PAs and their status within forested areas outside PAs is uncertain. In order to sufficiently assess and protect bears there is a need for baseline survey data that can quantify bear distribution, habitat suitability and status within Lao PDR.

Sun bears and Asiatic black bears are currently protected under Lao national legislation, the Wildlife and Aquatic Law, 2007, as a Category 1 species, and globally, under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; Fredriksson et al. 2008, Garshelis and Steinmetz 2016). Despite the high levels of conservation concern for bears, they are heavily exploited in Lao PDR for commercial trade in their parts and as cubs (Servheen et al. 1991, Duckworth et al. 1999, Foley et al. 2011). Bear trade occurs both locally and internationally, with China, Thailand and Vietnam (Servheen et al. 1991, Nooren and Claridge 2001). Bear poaching appears to be on the rise, and is thought to be the main factor limiting population size and growth (Hunt and Scotson 2011). Bears are also killed when they depredate crops, with the value of a poached bear often exceeding the annual value of a crop yield (Scotson et al. 2014). The high value of bear products is one reason that pressure from poaching is very high, at the same time law enforcement is inadequate and is failing to protect bears in Lao PDR.

Sun bear and Asiatic black bears are dependent on tropical forest to survive. Although they are known to exploit plantations and agricultural fields, there is no evidence that bears can survive without access to natural forest. Southeast Asia has experienced the highest rates of forest loss in the world in the past two decades (Miettinen et al. 2011) and the deforestation rate per annum between 2000-2005 was around 1.5% (Sodhi et al. 2010). The Food and Agricultural Organization (FAO 2015) reported forest cover in Lao PDR to be 81.3% in 2015, but this figure includes unquantified areas of non-native vegetation and the extent of natural forest is presumably much lower. Agricultural land expanded exponentially between 2000 – 2014, and now covers more than 10% of total land area (World Bank, 2017). Lao PDR has a well-developed protected area network, with 23 NPAs, and various provincial and district-level PAs (MacKinnon 1997, Berkmuller 2000). The success of PA's, however, is hindered by the rural population's reliance on natural resources, and the lack of internal funding for forest protection and enforcement of wildlife laws (MacKinnon 1997, Berkmuller 2000). Protected area management relies heavily on external funding, but currently, only a few sites have long term external funding (Wildlife Conservation Society; World Wildlife Fund); in one case, a NPA is managed with revenue from a hydropower dam (Molle et al. 2009). Despite deficiencies in protection from habitat loss and illegal hunting in Lao PDR, bear populations may be faring better than in neighboring Thailand, Vietnam and Cambodia, due to a comparatively low human population size and large areas of intact habitat. Lao PDR represents an increasingly rare opportunity for proactive conservation, where it is possible to implement strategies to preserve ecosystems with bears as fundamental functioning components, rather than remnant, isolated, sparse populations. Efforts to conserve highly threatened species such as tigers *Panthera tigris,* Asian elephants *Elephas maximus,* and Sumatran and Javan rhinos; *Dicerorhinus sumatrensis* and *rhinoceros sondaicus,* have been reactive, representing a struggle, or in some cases a failure, to pull species back from the brink of extinction (Berkmüller et al. 1995, Johnson et al. 2016). Proactive conservation of bears in Lao PDR may still be possible, but is hampered by lack of the most basic information on bear distribution and status. Limited applied research has been conducted on bears, and most information in Lao PDR is either anecdotal or a by-product of other studies. In support of the conservation management of bears, the development of a Species Distribution Model for bears in Lao PDR is needed to improve understanding of the consequences of environmental change to bear populations, and inform proactive conservation and monitoring plans through time (McShea 2014).

Aims and Objectives

Using bear occurrence data collected on transects in Lao PDR, we explored bear distribution in Lao PDR, by 1) identifying biological and anthropogenic predictors that are related to bear habitat use, 2) generating species distribution maps that reflect bear habitat suitability, and the relative abundance of bears, throughout Lao PDR and 3) creating a replicable GIS-based monitoring and assessment tool for bears in Lao PDR that can be used to identify conservation opportunities and monitor changes in bear distribution through time.

Methods

Study Area

Lao People's Democratic Republic (Lao PDR) in Southeast Asia is landlocked between Vietnam, Cambodia, Thailand, Myanmar and China and has a land mass of 236,800 km^2. Human population density is the lowest in southeast Asia, at 29 people/km^2, estimated at 6.8 million people in 2015, with an annual growth rate of 1.7% (World Bank, 2017). Around 80% of the population lives rurally and depends on agriculture (i.e. rice cultivation, sweetcorn) for income, and on wild meat and other forest products for subsistence (Berkmuller et al. 1995, Johnson et al. 2016). Lao PDR is one of the poorest countries in the region, with a Gross National Income of $5,049, ranking 138 out of 187 countries and territories on the 2015 Human Development Index (UNDP 2016). Foreign investment, particularly in natural resources (land, mining, hydropower) is the main driver of economic growth (UNDP 2016).

Study sites

We sampled within the three biological subunits of Lao PDR; the central Indochina tropical lowland plains, the northern Indochina hilly sub-tropical sector, and the Annam Trung Son mountain chain (Fig 2). Study sites had a range of elevations and varied in the number of villages located with and around sites (Table 1). In the northwest, the Nam Kan National Protected Area (NPA) is dominated by semi-evergreen forest, with a steep mountainous terrain. The NPA spans two provinces and four districts, Muang (district) Houayxai, Muang Mung, and Pha-oudom in Bokeo Province and Viangphongkha in Luang Namtha. The adjacent and smaller forest blocks of Gnot Namthi Provincial PA and Sam Meuang Product Forest have similar terrain and vegetation as the Nam Kan NPA. In the northeast, Nam Et Phou Louey (NEPL) NPA has a steep mountainous terrain, with mixed evergreen and deciduous forest, interspersed by dry evergreen and upper montane forest. Secondary forest, agricultural lands and anthropogenic grasslands are distributed patchily throughout. In the east, Nakai Nam Theun NPA, Laving Lavern NPA and Xe Sap NPA, all share similar eco-geographical characteristics with steep and mountainous topography. The most ecologically distinct feature of these sites is their shared location along the Annamite Mountain spine that forms much of the eastern border between Lao PDR and Vietnam. The southern-most site, Xe Pian NPA, straddles Chamapsack and Attapeu Provinces, and is the largest NPA in southern Lao PDR (Berkmuller et al. 1995). Xe Pian is a mosaic of semi-evergreen, mixed deciduous and dry dipterocarp forests, and wetland habitat. Xe Pian is in the lowland plains; elevation is primarily < 200-m, but reaches 844m within the mountainous region of the northern section.

Data collection

Between 2010-2013 we sampled study sites by searching for bear sign while walking 500m long line transects, of between 6 - 10-m width, at distances of 2 – 20-km from villages. The number of transects ranged from 10 – 36 per site. Transect start points were chosen randomly with a random point generator in ArcGIS Geospatial Modelling Environment. To reduce time constraints, as some random locations could take up to 5-days to reach, we stratified our sampling by generating a pool of random points within park boundaries, and chose a number to visit depending on the time available at a given site. We chose points to be spread evenly throughout sites and had no prior knowledge of the habitat conditions at each chosen point. We entered the forest from villages closest to the random points, walked directly towards each point and completed 500-m transects within different distance gradients from villages (0 - 5 km, 5 - 10 km, 10 - 15 km, 15 – 20 km). In Xe Pian NPA, where habitat is very open, we walked long continuous transects. Following data entry, to maintain independence between the Xe Pian transects, we created gaps of 1500-m between 500-m segments by systematically withdrawing data. To maintain independence, we grouped data from Gnot Namthi Provincial PA and Sam Muang Product Forest, which were contiguous and had similar habitat conditions. Transects within all study sites were a minimum of 700-m apart (usually more than 1km).

Each line transect was surveyed by a team of four to five people. One person walked the midline, measuring the length of the transect with a 10-m rope, monitoring the rest of the team and recording all data. One to two people zigzagged within 5-m strips on either side of the mid-line, searching for bear sign. For continuity within field sites, team members held the same role for all transects, and those searching for sign alternated on each side of the midline. Team members changed between field sites, and all teams were trained and led by the same principal investigator (L.S.). Most transects were conducted in primary tropical forest (semi-evergreen and mixed deciduous), at elevations between 500 – 1700-m, and 25% fell within lowland dry dipterocarp forest. We recorded all bear sign within transects. These were mainly claw marks on trees (~80%), but also bear nests (in tree and on the ground), ground digging, broken rotten wood and broken open bee nests. We recorded human disturbance (any evidence of human activity), bear food availability (ripe fruit, acorns), forest composition and sign of ungulates. We recorded data only within transect boundaries. We included sign on trees that were partially within the transect boundaries. Claw marks, bear's nests, broken bee nests, digging sites, scat, tracks and trails were each recorded as one sign. If claw marks of different age categories were observed on one tree, we recorded only the most recent sign. We assumed all sign were detected within transects, or that sign were missed at a constant rate. Claw marks on trees are visible for more than two years. Sign were aged and identified to bear species (where possible) using protocol from Steinmetz & Garshelis (2008, 2010). Sign were left by sun bears and Asiatic black bears, and could rarely be identified to species, therefore both species were considered together. We grouped bear sign into two age categories: sign < 1 year old (recent sign), and sign of all ages (all sign). We assumed that the amount of recent bear sign is directly proportional to the number of bears using the site and therefore a measure of relative abundance. Older claw marks can remain visible for more than 2 years, and accumulates at variable rates compared with recent claw marks (Steinmetz & Garsheslis 2010). Therefore, we assumed that all sign is reflective of general habitat use and suitability.

Data analysis

To optimize the power to make predictions outside our sample sites, we used a generalized linear mixed modelling approach to model expected count of bear sign as a log-linear function of ecological and anthropogenic predictors. Mixed models are appropriate for modelling data that are collected within discrete study sites, because inclusion of study sites as a random effect assumes that data collected within the same site are more correlated than data collected from different sites (Fieberg et al. 2009). We calculated the number of predictors that can be modelled against our response variable based on their associated degrees of freedom and our limiting sample size (i.e. number of transects). We created an *a priori* model, prior to exploring univariate relationships between bear sign and predictor variables. This approach reduces the risk of model overfitting, and maximizes model strength in making predictions outside the area sampled (Babyak 2004, Giudice et al. 2012, Harrell 2015). We assumed our data followed a negative binomial distribution; counts are rarely Poisson distributed and are typically over dispersed (Gardner et al. 1995). The negative binomial distribution is usually suitable for count data with high frequencies of zeros that can be explained by model covariates (Warton 2005).

We considered environmental and anthropogenic variables thought to be associated with bear presence, collected locally, and extracted from a Geographic Information System (GIS). We screened predictors for variation between transects, correlation with other variables, data completeness, potentially influential observations and measurement errors. We grouped and reduced number of categories in categorical variables where possible. Degrees of freedom were calculated as the number of model generated non-intercept coefficients, if modelled as a linear predictor without interactions. The maximum allowance of model parameters (p) associated with predictors is calculated as p = m/15 where m is our limiting sample size (i.e. number of transects; Harrell 2015). In our sample, $m = 99$, therefore $p = 99/15 = 6.6$ model parameters allowed (rounded up to 7). Transects covered a very small area (0.3 – 0.5 hectares), and may not represent what bears are selecting at larger scales. Therefore, we measured predictors within a 350-m buffer from the center of transects (0.35 hectares), to explore how bears respond to their immediate surroundings. The buffer radius was also small enough to avoid overlaps in covariate extraction among adjacent transects.

Variable screening

We considered forest type, % tree cover, human influence (Sanderson et al. 2002), road density, distance to nearest wildlife trading hub, distance to road, latitude, distance to river, distance to village, human density, elevation, surface ruggedness, temperature and precipitation (Table 2). We selected variables for inclusion in the *a priori* model based on the following criteria:

i) biological importance to bears
ii) data availability outside our study sites
iii) probability that future updates will become available (for predictors that change through time)
iv) independence from other predictors ($r < 0.7$)
v) sample variation within study sites (because for variables that showed little variation within study sites, the effective sample size was closer to 7 than 99)

Considering these criteria, we selected the variables % tree cover, elevation, surface roughness, distance to village and distance to road for inclusion in our *a priori* model. We explored the effects of locally collected predictors, that could not be used for landscape level predictions (human disturbance, food abundance, and ungulate sign), separately. We chose % tree cover over forest type because of uncertainty in the accuracy of the forest type layer, and whether future releases will be available in the same format. We derived a 2012 tree cover layer by combining an existing 2000 tree cover layer with tree loss data between 2000 – 2012 (Hansen et al. 2013). Tree cover is also a good indicator of differences in forest type, as there is little overlap in % tree cover within semi-evergreen and mix-deciduous forest (combined, $\bar{x} = 83.9$, SD = 12.7), secondary forest ($\bar{x} = 62.6$, SD = 34.9), and dry dipterocarp forest ($\bar{x} = 39$, SD = 15). Elevation is linked to climate and patterns in habitat assemblage (Culmsee and Leuschner 2013), and may be related to food availability. We hypothesized that elevation is also linked to habitat security, with steeper elevation areas tending to be less accessible to humans, and further from human settlements and agriculture, creating natural sanctuaries for wildlife. Surface roughness, derived from a digital elevation model (DEM), is a measure of fine scale terrain ruggedness (i.e. steepness and undulations of terrain). We tested the prediction that bears use rugged terrain to avoid humans, due to the difficulty for humans to move through rugged habitat. Distance to road and distance to village are both related to accessibility by humans, measured from the center of each transect.

We modelled the relationship between the expected count of bear sign as a log-linear function of our chosen predictors:

$$\log(E[Y\mathrm{i}]/\text{transect area}) = \beta_0 + \beta_1 \text{ \% Tree Cover } + \beta_2 \text{ Elevation } + \beta_3 \text{ Slope roughness} + \beta_4 \text{ Distance to road } + \beta_5 \text{ Distance to village}$$

Predictors were centered using z-scores (x-mean/sd), and the transect area was scaled by dividing by 100. We ran two identical models with recent sign and all sign as the res**p**onse. We included log(transect area) as an offset in models to account for differences in transect area. We evaluated models with diagnostic plots (Pearson residual, residuals versus fitted values, scale-location and QQ), Intraclass Correlation Coefficients (ICCs) and Negative Binomial Dispersion Parameters (NBDPs). ICC is the ratio of the between-cluster variance to the total variation, and is the proportion of total variation in the response that is accounted for by clustering of observations. ICC can also be interpreted as the level of correlation among observations within the same cluster, and is an indicator of whether inclusion of a random effect is necessary (McCullough and Nelder 1989). NBDP is the dispersion parameter (theta that describes the relationship between the variance and the mean in the negative binomial model. Very large NBDP's would suggest that a Poisson distribution is more appropriate, whereas very small values are evidence of overdispersion and lend support for the negative binomial distribution.

We created a predictive distribution map by converting all GIS variables into rasters, and calculating predicted values for each pixel using our model coefficients in a predictive equation:

$$E[Yi|X] = \exp(\beta_0 + (\sigma^2 \div 2) + \beta_1 \text{ \% Tree Cover } + \beta_2 \text{ Elevation } + \beta_3 \text{ Slope roughness} + \beta_4 \text{ Distance to road } + \beta_5 \text{ Distance to village } + \log(\text{mean}(\text{transect area}))$$

where σ = the variance of the random effect ($\sigma^2 \div 2$ was included to generate population-level predictions by averaging over the site-level random effects (Young et al. 2007, Fieberg et al. 2009). We grouped predicted values into 4 categories: 0.0 – 0.5, 0.5 – 1.0, 1.0 – 3.0, >3.0, and calculated the proportion of transects where bears were detected within each predictive value category to generate a habitat suitability index. We interpreted the map generated from the recent sign model as reflective of relative bear abundance (Steinmetz and Garshelis 2010, Fredriksson 2012), and the map generated from the all sign model as reflective of general habitat suitability.

We validated models using Spearman's rank correlation between real and predicted values, and an ROC on binary observations (i.e. presence or absence of bear sign on transects) by plotting the true positives versus the false positives. We used 'leave-one-out' cross validation, alternately removing each transect from our data set, re-running the model and using the coefficients to predict the expected number of sign within each transect as if it were a new observation to generate more honest measures of predictive performance (Abdi and Williams 2010). We repeated the cross-validation process with individual study sites as the sample unit, to test how well our models perform at predicting counts at new sites.

Data were analyzed in R version 3.3.1, with R package "glmmADMB", and GIS covariates and predictive maps were generated in ArcGIS Version 10.3.

Results

Data overview

We walked 99 transects, surveying an area of 322.7 ha. We observed 165 recent signs (found within 43% of transects), and 455 total signs (found within 78% of transects). We identified bear species for 34 recent claw marks: 16 sun bear and 17 Asiatic black bear, with no apparent latitudinal trend in ratio of species from north to south. The average density of bear sign on transects was highest in northern Sam Meuang Product Forest and Gnot Namthi Provincial Protected Area (2 sites combined), and lowest in the southern Xe Pian National Protected Area. Proportions of recent sign and old sign (> 1 year) varied between sites, and the lowest incidence of recent sign occurred within southern sites (Fig 3).

A priori models of recent bear sign (< 1 year old), and bear sign of all ages

Our models included 5 fixed-effect covariates, 1 random effect, and 1 dispersion parameter (negative binomial distribution), for a total of 7 degrees of freedom (Table 2). Testing the appropriateness of a negative binomial distribution, we found that the negative binomial recent sign model had an NBDP of 1.89 (SE = 0.46). The negative binomial all sign model had an NBDP of 0.85 (SE = 0.30). We concluded that the very low NBDP values are evidence that the negative binomial distribution was appropriate for our models. When testing the significance of study site as a random effect, we found that the recent sign model had an ICC of 0.18, meaning 18% of stochastic variation recent sign, given the predictors, was explained by study site. The all sign model had an ICC of 0.017, meaning that only 1.7% of the variation in all sign, given the predictors, was explained by study site. We interpreted parameters from the recent sign model with a random effect and parameters from the all sign model without a random effect.

Bears were more often detected at higher elevations ($P < 0.01$), and further from roads ($P < 0.05$). All sign were detected more in areas of high tree cover ($P < 0.05$) and in rugged habitats ($P = 0.08$). The significance of parameter estimates varied between the recent sign model and the all sign model, and the 95% confidence intervals (profile confidence intervals generated by R function "confint") for all predictors are narrower in the all sign model (Table 3). The direction of effects was the same in both models, except for distance to village, where the effect changes from neutral, in the recent sign model, to positive in the all sign model, however confidence intervals for this variable suggested it may not be important (at least inside protected areas), or the effect could be a consequence of sampling bias (Fig 4). Elevation and distance to roads were the most important predictors in both models, and effect sizes were lower in the all sign model. Tree cover was statistically significant ($P < 0.05$) in the model with all bear sign (Table 3, Fig 4). The recent sign model predicted relative bear abundance to be highest in the mountainous areas of Lao PDR, particularly along the border areas. The all sign model predicted a wider area of suitable bear habitat than the recent sign model (Fig 5).

Models with local covariates

In the recent model that included only locally collected predictors the ICC was < 1. In the all sign model the ICC was 0.27. We interpreted parameters from the recent sign local model without a random effect and parameters from the all sign local model with a random effect. The negative binomial recent sign model had an NBDP of 1.2 (SE = 0.3) and the Poisson model failed to estimate standard errors. The negative binomial all sign model had an NBDP of 2.5 (SE = 0.82). We concluded that the negative binomial distribution was appropriate for our models. In both models, bear occurrence was negatively associated with human disturbance ($P < 0.001$), and had a positive but non-significant relationship with ungulate sign and food abundance (Table 4).

Model validation

A Spearman's rank correlation between observed versus predicted values was significant for both models, at 0.337 ($P = 0.0007$) for recent sign, and 0.535 ($P < 0.001$) for all sign. An ROC curve derived from the ‘leave-one-out’ cross validation that removed one transect at a time had a moderate AUC value for the fresh sign model (0.63, 95% CI = 0.46 – 0.77), and a good AUC value for the model with all bear sign (0.73, 95% CI = 0.53 – 0.89). There was very little difference in ROC curves generated from the ‘leave-one-out’ cross validation that removed one study site at a time, which had a moderate AUC value for the fresh sign model (0.67, 95% CI = 0.51 – 0.8), and a good AUC value for the model with all bear sign (0.73, 95% CI = 0.54 – 0.89).

Discussion

Our models of bear relative abundance and habitat suitability performed well with a small set of remotely sensed predictors. Remotely sensed predictors were best at explaining variation among transects of density of sign of all ages, for which study site explained 18% of variation. Conversely, locally collected predictors were best at explaining variation among transects of density of recent sign, for which study site explained 27% of variation. In our study, bears selected for areas of high elevation, high tree density and for sites at greater distance from roads. Contrary to expectations, proximity to villages had little association with bear occurrence, with either neutral or non-significant positive effects. Similarly, terrain ruggedness had neutral or weakly positive effects associated with bear sign intensity. Country-wide variation in eco-geographic conditions and levels of human disturbance had a pronounced effect on bear habitat suitability throughout Lao PDR. Most suitable bear habitat was concentrated in the northern Indochina hilly sub-tropical sector, and the eastern Annam Trung Son mountain chain. Data and predictions indicated bear abundance to be very low in the southern tropical lowland plains, where there are only small patches of suitable habitat. We also found no bear activity within dry dipterocarp forest (Fig 5). Our predictions have some notable differences from the IUCN range map, which has the bulk of definite range concentrated within the south of Lao PDR and relatively fewer patches of definite range in the north, where there are large areas of unknown range (Fig 1).

One of the most important predictors of the relative abundance of bears was elevation, with suitable habitat most concentrated in mountainous areas in the north and in the border regions of Lao PDR. We assume that the cooler, wetter conditions and the vegetation assemblages associated with higher elevations (Culmsee and Leuschner 2013) are preferred habitat of bears. Our results appear to contradict findings from a similar study in Kao Yai National Park, Thailand, where models of fresh Asiatic black bear sign, using sign < 3 months old, revealed no effect of elevation, and found that bear habitat selection was largely driven by food availability (Ngoprasert et al. 2011). We detected no significant relationship between bear occurrence and fruit abundance. The differences between the studies are most likely attributed to differences in sampling, in particular the time-scales captured by the age of signs included during surveys. By using a wider age category of bear sign, we captured a broad temporal range of habitat and elevation use by bears, spanning a wide seasonal variation in food availability, whereas using only fresh sign is more suitable to understanding short-term foraging sites of bears such as fruit trees and other pulsed food resources.

Bear occurrence in Lao PDR was negatively associated with closer distances to roads and human disturbance, and we expect that both of these predictors were closely associated with levels of hunting (Brodie et al. 2015). In Thailand, Ngoprasert et al (2011) detected no influence of human disturbance on bear habitat use; Thailand is the only country in Southeast Asia where bear populations are not in decline (Garshelis and Steinmetz 2016), and there is government investment in protected area management (Jenks et al. 2011). When hunting levels are low, as is the case in Thailand, bears may not be displaced by human activities. This is in contrast to Lao PDR, where evidence of hunting and illegal trade in bears was ubiquitous throughout all of our study sites. The strong effects of human influence on bears in Lao PDR suggests that protected areas are not providing sufficient protection to bears. However, observed levels of protection varied among sites, and this level of protection may have been reflected by study site, as a random effect, explaining 18% of variation in density of recent bear sign as a function of remotely sensed predictors. Conversely, the models of locally collected covariates, of which only local levels of human disturbance had a significant effect on bear sign, are opposite to what we found with the remotely sensed covariates. In models with local covariates, study site explained very little variation in density of recent sign, but explained 27% of variation in all sign. This result suggests that local levels of human disturbance may better explain among-transect variability in density of recent sign within study sites, and that the strength of this relationship is diluted over time, with local levels of human disturbance less able to explain differences in density of all sign, which accumulate over a long period (> 2 years).

In principle, forest protection in Lao PDR is the responsibility of Provincial and District offices of Natural Resource and Environment. In practice, however, the level of enforcement of wildlife protection laws varied widely among sites, and was dependent on external funding. For example, in the northern-most study site, Nam Kan NPA, forest patrols and vehicle inspections were commonplace during our surveys, and were a consequence of the protected area hosting a popular ecotourism project ‘The Gibbon Experience’. Similarly, NEPL NPA had long term financial backing from WCS (Johnson et al. 2016) and Nakai Nam Theun NPA has long term support from the Nam Theu 2 Power Company (Molle et al. 2009), and active forest patrols were observed in both protected areas during our surveys. This was also the case in Xe Sap NPA and Xe Pian NPA which are managed by WWF. In contrast, in Gnot Namthi Provincial PA and Sam Meuang Product Forest and Laving Lavern NPA, no active management was observed. With high financial incentives to poach bears, park funding and patrols are an essential part of protected area management. Without these measures, the relatively low risk of poachers being caught or penalized leave protected areas open to illegal exploitation. We believe our failure to detect bears in lowland dry dipterocarp forest was due to insufficient protection and high levels of human disturbance within this forest type. This included widespread domestic livestock grazing within Xe Pian NPA. Bears are known to use dry dipterocarp forest in Huai Kha Khaeng Wildlife Sanctuary (HKKWS), Thailand, where they feed on fruit and termites (Chongsomchai 2013). However, HKKWS is well protected, patrolled and free from livestock, whereas Xe Pian NPA was not. Therefore, bears presumably avoid (or do not survive in) dry dipterocarp forest in Lao PDR due to the high levels of human disturbance, and would otherwise utilize this habitat type if these pressures were absent.

Surprisingly, distance to village had either a neutral or non-significant positive effect on bear occurrence, despite villages being associated with human disturbance and hunter accessibility (Brodie et al. 2015). The lack of relationship may be an artifact of errors in village GIS location data, or possibly due to people from villages within protected areas being less likely to hunt. Alternatively, other predictors in our models may be explaining similar information as distance to village (i.e. distance to road, tree cover, elevation) and the correlation between distance to village with these predictors may be masking its true effect. The neutral effect of distance to village could also be attributed to bear’s propensity to forage in human crop fields (Fredriksson 2005, Ngoprasert et al. 2011, Guharajan 2016). In Lao PDR bears raid sweet corn crops during July – September. The corn ripening season coincides with a period of low fruit productivity in seasonal tropical forests, drawing bears into plantations (Ngoprasert et al. 2011). Similarly, in Japan, Asiatic black bears selected for agricultural areas in proximity to forest edges (Takahata et al. 2014). Feeding from crop fields puts bears at risk of mortality from farmers, seeking both to defend their crops, and to profit from the high trading values of bears and cubs (Scotson et al. 2014). Corn fields, may therefore bolster productivity in times of low food availability, but could also act as ecological traps for bears foraging for food during the lean season.

Our results suggest that the density of Asiatic black bears and sun bears in Lao PDR is approximately equal. Ngoprasert et al (2013) found that abundance of bear sign identified to species reflects real differences in population densities. However, only a small proportion of sign in our study was identifiable to species. We found sign from both species in all study sites, with a roughly equal ratio of sign of Asiatic black bears and Sun bears (52% Asiatic black bear, 48% Sun bear). We found no north to south trend in species ratio. Asiatic black bears are known to dominate in areas of high fruit availability, and sun bears incorporate a higher proportion of insects into their diet (Steinmetz et al. 2013). At fine scales, these dietary differences coincide with divergent elevational preferences; sun bears occur more in lower elevation forests where insect availability is high, and Asiatic black bears favor higher elevations, where fruit availability is high (Steinmetz et al 2011; Wong and Linkie 2013, Nazeri et al. 2014). At broad scales, there is a latitudinal gradient of abundance within overlapping range, with sun bears more abundant in the south and Asiatic black bears more abundant in the north (Steinmetz 2006). Therefore, in Lao PDR, Asiatic black bears probably occur at higher densities in the northern mountainous regions, and sun bears at higher densities in the southern lowlands.

Conservation outcomes

Contraction of bear range, from what was once continuous throughout Lao PDR (Erdbrink 1953, Lekagul and McNeely 1977), is a result of rapid habitat clearance, human development and exploitation of bears in the past 3 decades (Sodhi et al. 2010, Scotson and Brocklehurst 2013, UNDP 2016). Ongoing habitat loss and human development will continue to put pressure on bears in Lao PDR. Likewise, the high value and international demand for bear cubs, gallbladder and paws undermines the efforts of legislation and law enforcement. Despite these challenges, our study highlighted opportunities for bear conservation in the region. Our relative abundance maps indicated the large availability of suitable habitat for bears in Lao PDR, and highlighted several areas in the northern half of the country as highly suitable, in areas previously described as status unknown. However, the map also predicted relatively low bear abundance in several southern areas marked as definite bear habitat by the red list assessment (Scotson et al. 2017). Further work is needed to verify and track bear status in Lao PDR. Sign transects proved a viable alternative to other available methods, and were efficient, non-invasive, low tech and easily standardized, and could potentially be implemented as a ranger monitoring system. Our map and modeling system also has potential in predicting and monitoring the response of bear populations to future human developments, by updating future model with variables that are likely to change through time (e.g. distance to villages and roads, tree density). Future studies may also consider incorporating a measure of financial support on protected area management, to represent active protection status.

Our study collected data on bear presence at two time scales, sign < 1 year (recent) and sign of all ages (which can be > 2 years old). There was a large difference in the predicted bear relative abundance using the recent and all sign models, with high values of bear relative abundance over a much larger area using the all sign model. This can be interpreted in several ways: (1) all sign covered areas of between year movement of bears and picked up habitat and aerial use that may not be regularly used or typical; (2) the large decrease in aerial coverage from all sign to new sign maps can be attributed in part to a decrease in area of occupancy over time caused by a decrease in population size; and (3) the new sign map is a representation of bear distribution and relative abundance now, whereas the all sign map represents general bear habitat suitability, in other words, where bears should occupy if threats were reduced. Although all three interpretations are likely to be true, it is impossible to quantify the contribution of each to current bear distribution and abundance indicated by our map. Nevertheless, the data indicate a decline in bear populations, highlighting a need for action, and provide a habitat suitability map that can guide where conservation actions may have most impact. One of the biggest concerns highlighted by this and other studies is the need to deter poaching, through improved protected area management and enforcement, and restricting, and reducing the incentives driving trade in bears and bear parts in the region. Fundamental to resolving these issues is improved law enforcement. This requires funding for facilities and rangers within protected areas but also requires training of rangers to more effectively reduce the threat of poaching. Of particular concern is the widespread use of wire snares, which is decimating wildlife populations throughout much of Southeast Asia (Gray et al. 2017). Snares led to the extirpation of tigers from NEPL NPA in recent years, and considering this protected area is one of the most intensively managed in Lao PDR (Johnson et al. 2016), the need for new, improved strategies to combat poaching is evident. Without measures to reduce poaching, bear populations in Lao PDR will almost certainly continue to decline (Scotson and Brocklehurst 2013).

Table 1. Characteristics of study sites surveyed for bear sign in Lao PDR between 2010 - 2013.

Site Name	Area (km^2)	Elevation Range (m)	Villages[1]
Nam Kan National Protected Area	1,230 km^2	500 - 1500	60
Gnot Namthi Provincial Protected Area	161 km^2	600 - 800	12
Sam Meuang Production Forest	787 km^2	600 - 900	45
Nam Et Phou Louey National Protected Area	5,959 km^2	400 – 2257	100
Nakai Nam Theun National Protected Area	3710 km^2	700 - 1500	50
Laving Lavern National Protected Area	900 km^2	400 - 1000	50
Xe Sap National Protected Area	1335 km^2	700 - 1500	14
Xe Pian National Protected Area	2,400 km^2	200 - 844	60

[1] Numbers are approximate and include villages located inside and around park boundaries.

Table 2. Environmental predictors considered for log linear models of bear sign collected on line transects in eight study sites in Lao PDR, between 2000 – 2013.

Predictor	Description	Variability within study sites	degrees of freedom[1]	Include in model (Y/N)
Study site	7 study sites[2]	NA	1	Y (random effect)
Tree cover	0-100% canopy cover	High	1	Y
Forest type	3 categories[3]	Low	2	N
Human influence index	1km^2 (Sanderson et al. 2005)	Low	1	N
Road density	Within 10,000-m buffer	Low	1	N
Distance to trading post	Distance in miles to nearest known wildlife trading hub	Low	1	N
Distance to road	Meters to nearest road from middle of transect	High	1	Y
Latitude	Lao PDR ranges from 13 – 22 °N	Low	1	N
Distance to river	Meters to nearest road from middle of transect	High	1	N
Distance to village	Meters to nearest road from middle of transect	High	1	Y
Human density	Within 20,000m radius	Low	1	N

Elevation	Mean elevation within transect	High	1	Y
Slope ruggedness	Steepness and undulations of terrain	High	1	Y
Temperature	Celsius*10, Annual mean and range	Low	1	N
Precipitation	Annual mean and range	Low	1	N
Ungulate	Muntjac, Sambar and Wild pig sign	High	1	Y Local model
Food	Ripe edible fruit and acorns	High	1	Y Local model
Human disturbance	Any human sign (e.g. cutting, logging, footprints, camps)	High	1	Y Local model

[1] Number of regression parameters (coefficients, excluding intercept) needed to model each predictor as a linear effect, without interactions (table adapted from Guidice et al. 2011).

[2] Gnot Namthi Provincial Protected Area and Sam Meuang Product Forest are combined into one site as they are contiguous with similar ecological and human based conditions.

[3] Forest cover extracted from Geographic Information System land cover layer created by the Forest Inventory and Planning Division of the Department of Forestry, Lao PDR. Categories were reduced from eight categories to three, based on ecological similarity, and expected bear use; i) Primary forest (Lower dry evergreen and Lower mixed deciduous), ii) Degraded and Secondary forest (bamboo, un-stocked forest), and ii) Dry deciduous forest.

Table 3. Model coefficients from log linear generalized mixed models, relating count of bear sign collected along straight line transects in Lao PDR between 2010-2013 as a log linear function of remotely sensed predictors[1].

	Recent Bear Sign		Sign of all ages	
Predictors	β_1	95% CI	β_1	95% CI[2]
Intercept	-3.74	-4.13 – -3.34	-2.63	-2.89 – -2.37
Elevation (m)	0.90	0.42 – 1.38	0.66	0.37 – 0.95
Distance to road (m)	0.38	-0.01 – 0.77	0.28	0.06 – 0.49
Tree cover (%)	0.06	-0.51 – 0.62	0.05	0.10 – 0.85
Slope ratio	0.12	-0.39 – 0.63	0.22	-0.04 – 0.49
Distance to village (m)	-0.08	-0.52 – 0.36	-0.14	-0.36 – 0.07

Footnotes

[1] Predictors were centered using x-mean/sd. Models were offset by transect area (m^2/100)

[2] Profile confidence intervals generated by R function “confint”

Table 4. Model coefficients from log linear generalized mixed models, relating count of bear sign collected along straight line transects in Lao PDR between 2010-2013 as a log linear function of locally collected predictors[1].

	Recent Bear Sign		Sign of all ages	
Predictors	β[1]	95% CI	β[1]	95% CI[2]
Intercept	-8.9	-9.50 – -8.30	-6.57	-7.24 – -5.89
Human disturbance	-1.73	-2.69 – -0.76	-0.14	-0.23 – -0.05
Ungulate sign	0.17	-0.25 – 0.58	0.02	-0.04 – 0.07
Fruit abundance	0.55	-0.07 – 1.17	0.01	-0.05 – 0.08

Footnotes

[1] Predictors were centered using x-mean/sd. Models were offset by transect area (m^2/100)

[2] Profile confidence intervals generated by R function “confint”

Figure 1. IUCN range maps for Asiatic black bears and sun bears in Lao PDR. Range is identical for each species**.** Definite range has known bear occurrences, probably range is forested areas likely to contain bears based on habitat composition and proximity to definite range, Status Unknown is forested range which have undergone no formal surveys.

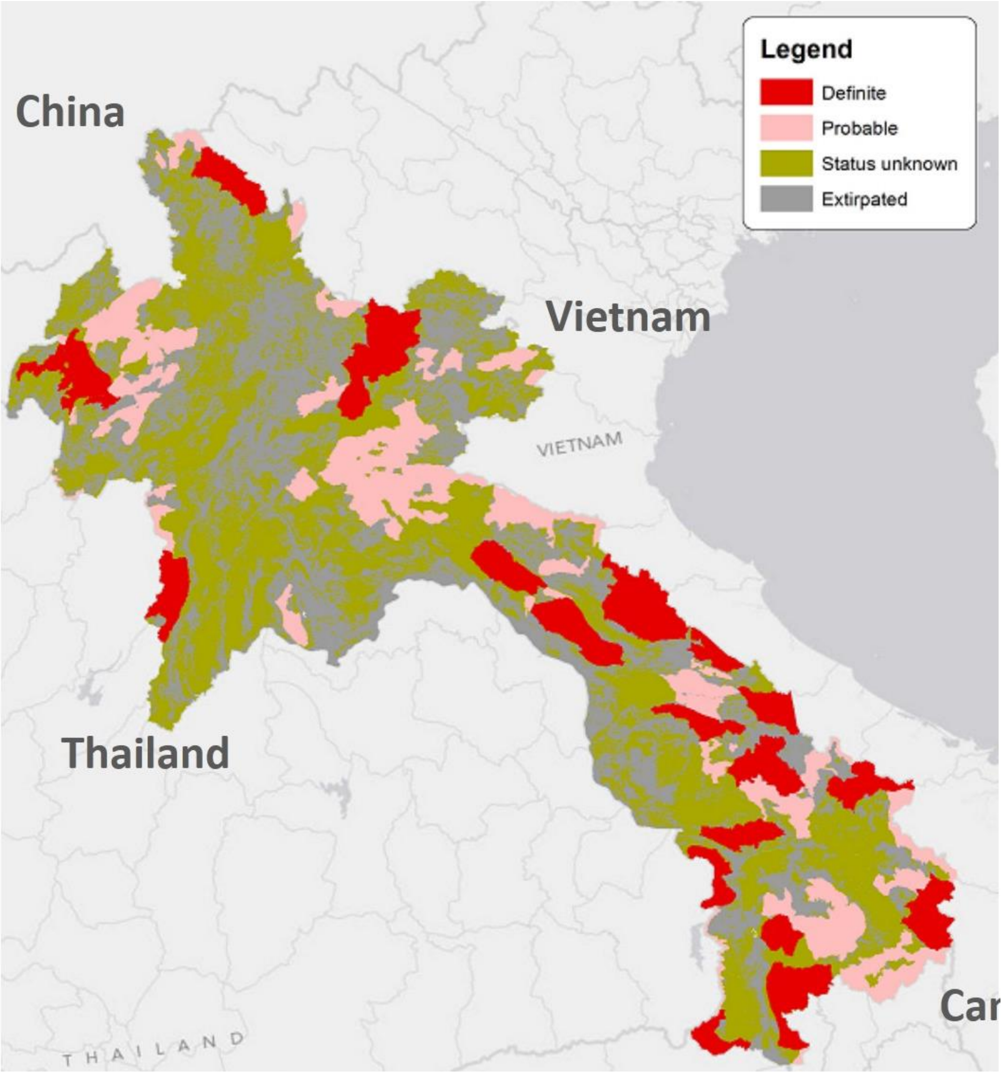


Figure 2. Eight field sites where we conducted bear sign transects in Lao PDR, between 2010 – 2013; 1) Nam Et Phou Louy National Protected Area (NPA), 2) Nam Kan NPA. Lao PDR 3) Sam Meung Product Forest and Gnot Namthi Provincial PA, 4) Laving Lavern NPA, 5) Nakai Nam Theun NPA, 6) Xe Sap NPA, 7) Xe Pian NPA. Lao PDR has three major biological subunits; A) the Northern Indochina hilly sub-tropical sector, with the country's highest point, 2820-m, B) the Annam Trung Son Mountain Chain (a.k.a. the Annamite Mountains) where elevations match those in the north, and landscape is dominated by rugged limestone terrain, and C) the Central Indochina tropical lowland plains.

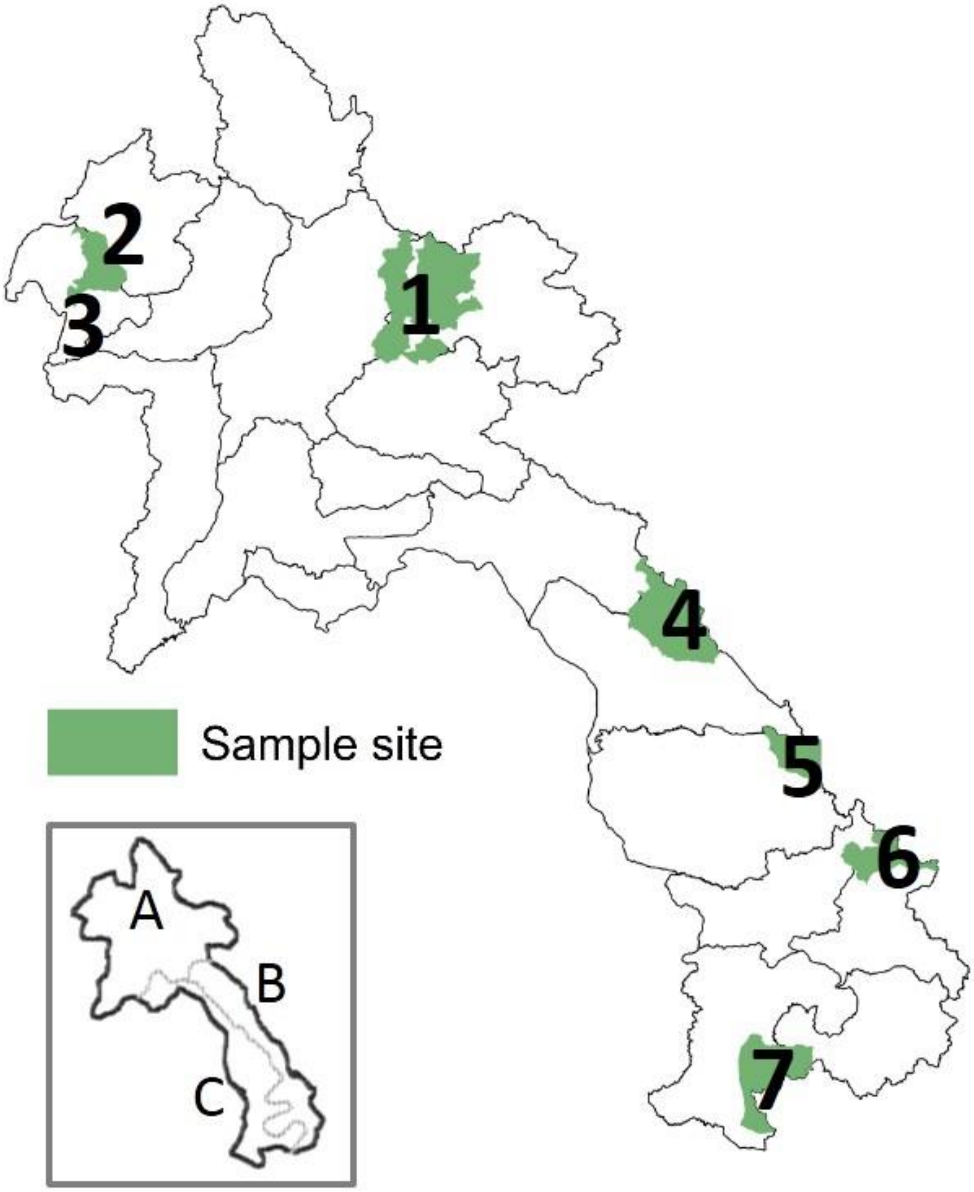


Figure 3. Density of bear sign per hectare observed within line transects walked between 2010 – 2013 in eight sites in Lao PDR. SMGN = Sam Meuang Product Forest and Gnot Namthi Provincial Protected Area, NK = Nam Kan National Protected Area (NPA), NEPL = Nam Et Phou Louey NPA, LL = Laving Lavern NPA, NKNT = Nakai Nam Theun NPA, XP = Xe Sap NPA, XP = Xe Pian NPA.

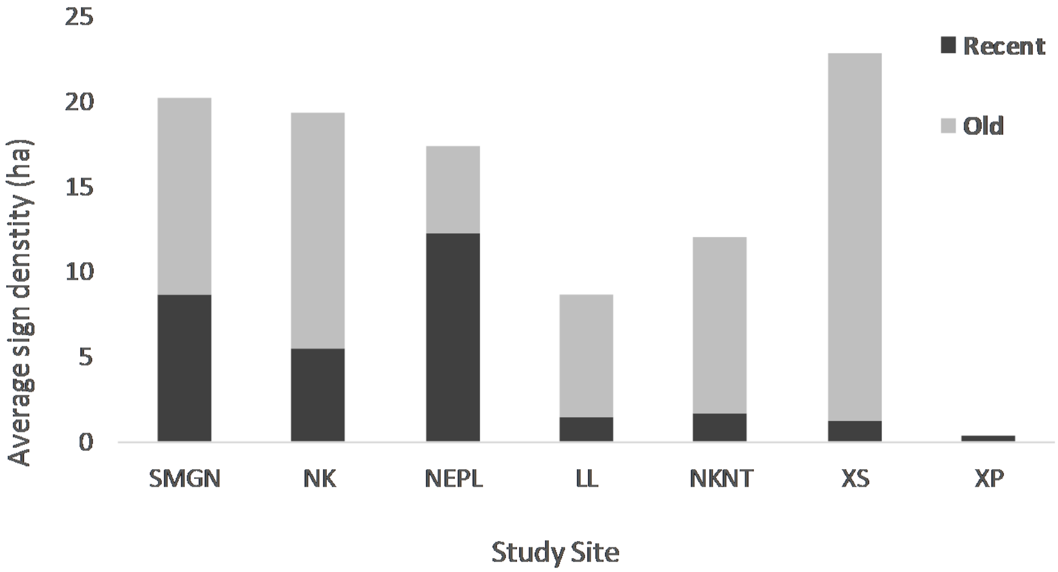


Figure 4. Modelled relationship between distance to village and % tree cover and the expected count (E[Y|X]) of bear sign on transects. Bear sign was collected within line transects in eight study sites in Lao PDR between 2010 – 2013. Models assumed that the log count of bear sign was a linear function of elevation, distance to road, slope ruggedness, % tree cover and distance to village. Covariate values were averaged within a 350-m radius of the center points of transects. The left panels display relationship from a model of recent bear sign (sign < one year old), and the right panels display relationship from a model of all bear all sign (sign of all ages). Plots are generated with values generated by the 'Predict' function in R, with values for all other covariates fixed at their means.

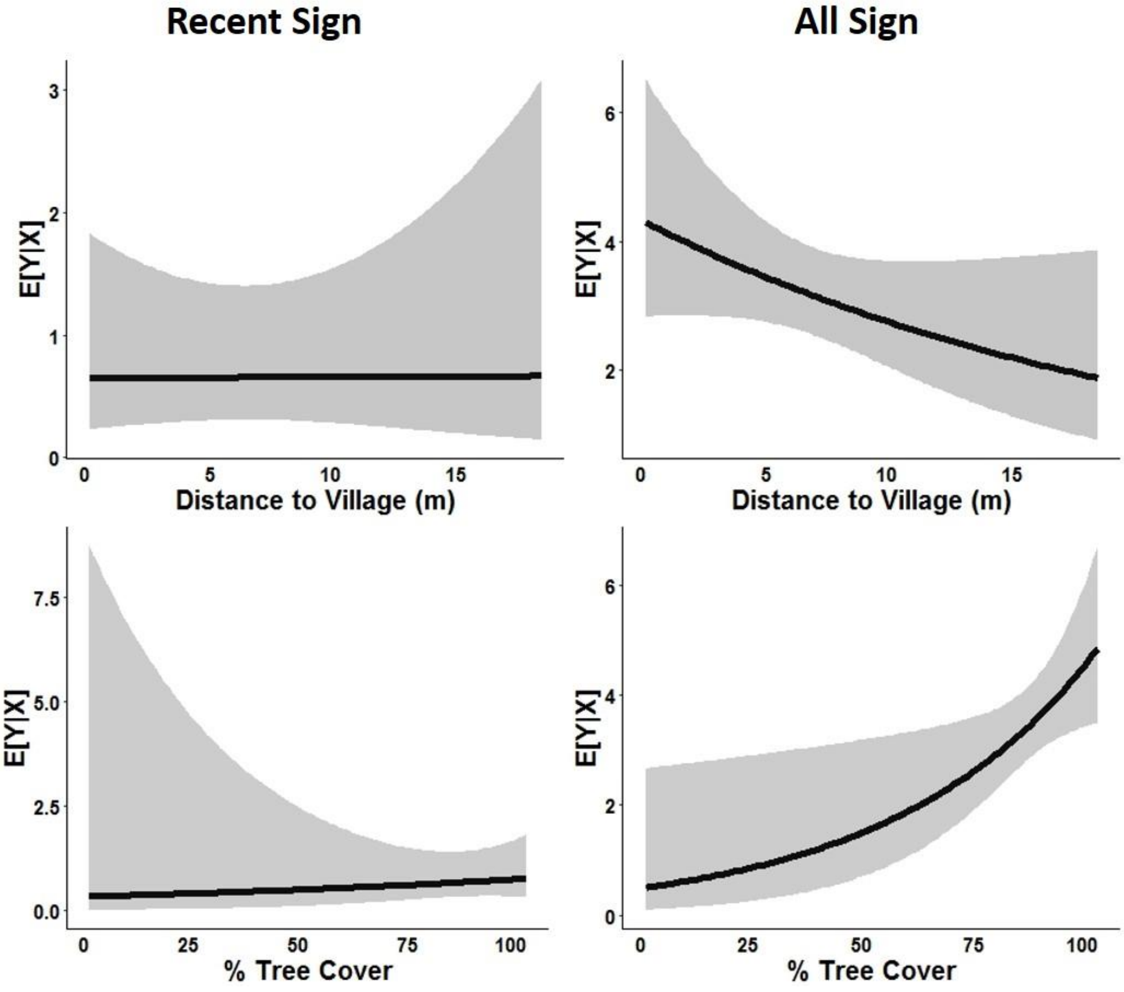
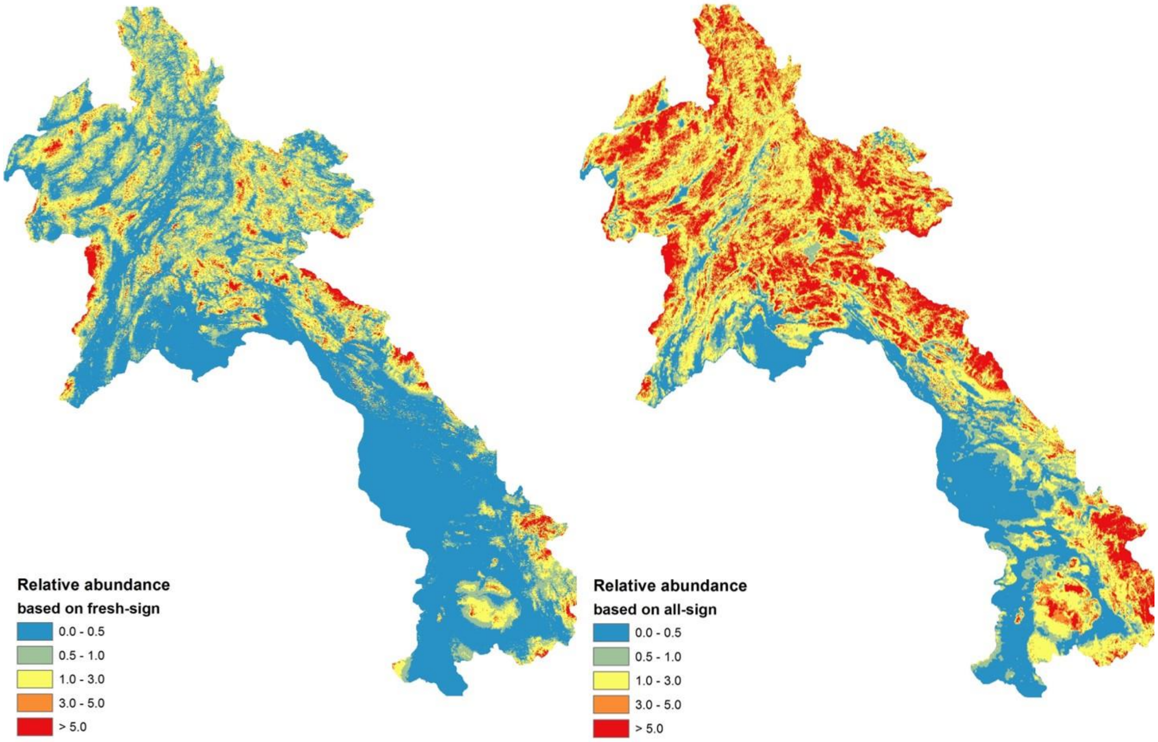


Figure 5. Predictive maps of expected count of bear sign in Lao PDR. Predictions were generated from log linear models that assumed the log count of bear sign was a linear function of elevation, distance to road, slope ruggedness, % tree cover and distance to village. Bear sign was collected within line transects in eight study sites in Lao PDR between 2010 – 2013. Left: predictions made with a model that included only sign less than one year old, reflective of relative abundance of bear populations. Right: predictions from model coefficients from a model that included sign of all ages, reflective of habitat suitability for bears.



Chapter 2

Monitoring range-wide sun bear population trends using forest cover and camera-trap bycatch data

Synopsis

Monitoring population trend of threatened species requires standardized techniques that can be applied over broad areas and repeated through time. Sun bears *Helarctos malayanus* are a forest dependent tropical bear found throughout most of Southeast Asia. We combined data from 2845 camera traps within 49 field sites across sun bear range to model the relationship between photo catch rates of sun bears and tree cover. We estimated related changes in country and global-level sun bear populations based on tree cover loss. Sun bears were detected in all levels of tree cover above 20%, and probability of presence was positively associated with areas of high tree cover. Our model-based estimates, cast over a 30-year period, predicted that sun bear populations in mainland southeast Asia have potentially declined by close to 20%, with declines highest in Cambodia and lowest in Myanmar. Insular sun bear populations were predicted to have declined at a much higher rate than the mainland (~50%), and surpassed the IUCN criteria for endangered if sun bears were listed on the population level. Indonesia and Malaysia experienced the highest country-level declines. Remote sensing tree cover data may serve as a useful proxy for monitoring population trends of sun bears and other forest dependent species over space and time with an empirical and standardized approach.

Introduction

Management and conservation of species and sub-populations threatened with extinction requires accurate and reproducible estimates of population trends. Measuring changes in the global status of a species usually requires data collected over broad spatial and temporal scales. Yet most monitoring programs tend to be restricted in scope, with data collected within a single study area, and with limited ability to extrapolate to other areas. Of the > 5000 mammalian species categorized by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species, > 800 are classed as data deficient (status unknown), and 25% are threatened with extinction. Red list assessments are usually based on a combination of anecdotal data and expert opinion [1–3]. For some species, international collaborators combine data from multiple study sites to monitor populations on regional and global scales (Ahumada et al. 2011, Linkie et al. 2013, Chutipong et al. 2014, Mathai et al. 2016). Population change is sometimes measured indirectly, by inference using a proxy measure, such as change in habitat extent (Buchanan et al. 2008, Bird et al. 2012, Tracewski et al. 2016).

Data on global population trends for sun bears *Helarctos malayanus* are deficient. Sun bears inhabit the tropical forests of Southeast Asia, and populations are threatened by rapid deforestation (Miettinen et al. 2011, Scotson et al. 2017). Sun bears' global range is contracting, and local extirpations are possible within the northern range limits of Bangladesh and China and are imminent in Vietnam (Erdbrink 1953, Islam et al. 2013, Wen, C., Wang. et al. 2013, Scotson et al. 2017). Studies that quantify the status of sun bear populations are few and limited to small areas. Density estimates are available for two national parks in Thailand (Ngoprasert et al. 2015) and population trends have been measured in a National Park in Sumatra (Wong et al. 2013*a*) and several sites in Thailand (Steinmetz et al. 2006, Kanchanasakha et al. 2010). Results of these studies cannot be readily extrapolated to other regions due to environmental variability among regions, nor are they easily compared between sites, because of differences in field methods and use of predictors that cannot be derived for areas outside those sampled. Therefore, current estimates of sun bear population trend rely on expert opinion, augmented by tree cover change estimates taken from the published literature, and by perceived levels of hunting (Scotson et al. 2017).

The IUCN classifies sun bears as vulnerable, estimating that populations have declined by ~35% in the past 30 years (Scotson et al. 2017). A lack of quantifiable data required this estimate to be generated by pooling expert representatives from 8 of 11 range countries (1 – 5 people per country). Brunei had no representative, and China and Bangladesh were both excluded from the assessment because the extent of former range in these countries is unclear. The use of expert opinion and antidotal data to forecast population trends and to estimate risk of extinction generates a semi-subjective measure, that is hard, or impossible, to replicate. Like many threatened species, sun bears would benefit from a more objective method for ongoing monitoring through time. If possible, monitoring methods should be feasible, inexpensive, and estimates of trend must be comparable between time periods (i.e. methods should stay consistent through time). As an alternative to expert opinion, changes in forest cover and rates of deforestation can be used to calculate changes in areas of occupancy and to infer population decline, by assuming that the rate of population change is equal to forest loss (Buchanan et al. 2008, Bird et al. 2012, Tracewski et al. 2016). While habitat loss is not the only driver of abundance, the IUCN Red List framework permits this measure as a viable alternative to estimating population trend in the absence of suitable field data (IUCN 2017*a*). The recent availability of online, satellite-based tree cover change data collected between 2000 and 2014, enables researches to tailor their measurements of deforestation rates (i.e. habitat change) to an area specific to a species of interest (e.g. within its' range limits; Hansen et al. 2013).

Studies that use forest loss as a surrogate for population declines have measured tree cover changes within the geographical and elevational range limits of a species, without taking into account species-specific selection for tree cover density (Buchanan et al. 2008, Bird et al. 2012, Tracewski et al. 2016). However, treatment of tree cover as a discrete value may be misleading if the density of a species varies at varying levels of tree cover. Sun bears are forest dependent, and use a broad spectrum of habitat types. Bears select habitat based on food availability and security, favoring interior forest but also using secondary, logged and regenerating burnt forests (Te Wong et al. 2004*a*, Steinmetz et al. 2011*a*, Fredriksson 2012, Nazeri et al. 2012, Cheah 2013, Wong and Linkie 2013). Sun bears also feed in, and travel through, agricultural areas close to the forest edge (Normua et al. 2004, Fredriksson 2005, Cheah 2013, Scotson et al. 2014). Sun bear populations experience steeper declines in areas of high deforestation compared with areas of low deforestation (Wong et al. 2013*a*), however the relationship between sun bear density and tree density has not yet been investigated. If sun bears select for areas of high tree density, the loss or degradation of high tree cover areas would have a greater impact on populations numbers than loss or degradation of areas of low tree density. Treating tree cover as a continuous variable and allowing estimates of population decline to be directly associated with sun bear's selection for varying levels of tree cover would generate a more biologically meaningful population decline estimate than if treating tree cover as a discrete variable.

Here we explore an alternative method to quantifying changes in sun bear populations through time that does not rely on expert opinion, and strengthens the direct inference of population decline based on forest change by treating tree cover as a continuous variable. We develop a simple, replicable univariate model, and explore the predictive power of tree cover as a variable that encompasses the underlying processes of food availability, shelter, security, human disturbance and mortality risk (factors for which data are not yet available in a uniform measure across the entire sun bear range). To test the predictive power of tree cover, we used bycatch data pooled from multiple camera trap studies within sun bear range, and integrate models using detection/non-detection data and independent count data as the response to tree cover. If sun bear presence is consistently linked to tree cover, deforestation rates could provide a standardized proximate measure of sun bear population change through time by working remotely with GIS, at least until better data become available. Data driven models have the benefit that they can be repeated, and, as these models have explicit assumptions, they can also be debated, modified and improved. To evaluate whether changing tree cover can be used to monitor sun bear populations, we asked two inter-related questions; is sun bear presence correlated with tree cover, and if so, can we use this relationship to estimate sun bear population changes through time?

Methods

We combined high resolution (30 x 30 m) tree cover data with camera trap catch rates of sun bears, pooled from multiple study sites, to model the relationship between tree cover density and sun bear detections, and to estimate population declines associated with tree cover loss between 2000 and 2014. We cast our estimates over a 30-year period, and compared our results with expert-derived estimates of sun bear decline over a similar period.

Remote sensing data

We processed Global Information System (GIS) data in ArcGIS 10.2; Arc tools referred to in the text are capitalized. We downloaded open source satellite-based tree cover rasters for the year 2000 (pixels valued from 0-100% tree cover) and tree cover loss rasters from between 2000-2012 and 2000-2014 (pixels valued 1 [100% loss of tree cover within pixel] or 0 [no loss]; www.globalforestwatch.org, accessed 14th Feb 2017). We used Extract Raster to Mask to trim all rasters to the geographic extent of historic sun bear range (Erdbrink 1953). We created a 2012 and 2014 tree cover raster with Raster Calculator by i) multiplying all loss pixels by 100 to transform pixel values to be 0 or 100, and on the same scale as the tree cover layer and ii) subtracting the transformed loss raster from the year 2000 tree cover raster. All negative values, when 100 loss was subtracted from a cell with < 100 tree cover, were transformed to zero. With the Neighborhood Function, we smoothed the tree cover rasters for all years by averaging pixel values over a 6km^2 circular area (circular radius =1.38 km), wide enough to represent the area of a core sun bear home range (home range estimates of sun bears range from 4 - 27.5 km^2; Te Wong et al. 2004, Fredriksson 2012, Cheah 2013)) and narrow enough to maintain variability in tree cover within the scale of a camera trapping site.

Sun bear detections at camera traps

We obtained sun bear detection data from 49 non-baited camera-trap studies that were conducted within sun bear range between 2000 and 2014 (Fig 1; Table 1). The primary objectives of these studies included biodiversity monitoring, and single species surveys (e.g. tiger *Panthera tigris* occupancy, Bornean orang-utan *Pongo pygmaeus morio* terrestrial behavior, sun bear occupancy), but often captured sun bears and many other species. Camera trap metadata included a GPS location, the date the camera was set, and number of nights the camera was active (trap nights). For six of the 49 sites, only an average number of trap nights (across all cameras at the site) was available. We recorded the number of independent sun bear detections per unit (independent count data) at sites where camera data included timestamps for each picture; detections were considered independent if they occurred > 1 hour apart. For all camera trap data from the mainland region (study sites=17, camera traps = 843), the number of trap nights was known but the time between sun bear detections was unknown so independent detections could not be determined. For these data, we recorded detection/non-detection within a known trapping period (data were modelled as a rate, to account for variable-length trapping periods). If cameras were set in pairs, we used the data from the second unit. We filtered the date to reduce variability in sampling intensity, removing camera units operational for < 7 days and > 3 months, and removed field sites with < 10 camera traps.

We divided the data by two regions; mainland (all countries north of Peninsular Malaysia) and insular (Peninsular Malaysia, Sumatra and Borneo). Major ecological differences between these areas (i.e. seasonal versus aseasonal forest; presence of sympatric and dominant competitor, Asiatic black bears *Ursus thibetanus*, in the mainland versus absence of this species in the insular region) may cause sun bear response to tree cover to vary by region. The mainland data were collected in Thailand, Lao and Cambodia, and these data were assumed representative of all other countries in that region (Fig 1). China and Bangladesh were excluded from the analysis; sun bears may be extirpated in these countries, and the extent of historical range is unknown

(Scotson et al. 2017). We analyzed data globally, with mainland and insular data combined, and regionally, with mainland and insular data analyzed separately (Table 2).

We recorded the number of independent sun bear detections per unit (independent count data); detections were considered independent if they occurred > 1 hour apart. For all camera trap data from the mainland region, the time-lag between sun bear detections was unknown, so we recorded detection/non-detection within a trapping period. [a]Independent sun bear detections per unit (independent count data); detections were considered independent if they occurred > 1 hour apart. [b]For all camera trap data from the mainland region, the time-lag between sun bear detections was unknown, so we recorded detection/non-detection within a trapping period.

Data analysis

Relating camera trap catch rates to tree cover

We averaged percent tree cover within a 6km^2 circular area at each camera trap location. Tree cover values were drawn from whichever raster (2000, 2012, or 2014) closest in time to when the camera was active. The 2000 raster was used for units active before 2006, 2012 for units active from 2007 – 2012, and 2014 for units that were active post 2012. For units active in 2006 we compared raster values from the year 2000 and 2012; in all cases, the values were very close or identical in value.

We examined the relationship between sun bear detections and forest cover in two ways. For most camera traps in the insular region we had catch rate data, and for all units on the mainland we had detection/non-detection data; to model both data types concurrently, and produce equivalent coefficients, we used two models. In the first, we modelled the relationship between the expected catch rate (number of independent camera detections/number of trap nights) as a log-linear function of % tree cover:

$$\log(E[Yi]/\text{trap nights}) = \beta_0 + \beta_1 \text{ \% Tree Cover} \qquad \text{(equation 1)}$$

where E[Y_i] represents the expected number of detections at site i (McCullough & Nelder, 1989). For the mainland data, for which independent catch rate was not available, we fit binary regression models to the detection/non-detection data ($Z_i = 1$ if detected at site i and 0 otherwise), using a complimentary log-log link:

$$\log(-\log(1-E[Z_i]/\text{trapnights})) = \beta_0 + \beta_1 \text{ \% Tree Cover} \qquad \text{(equation 2)}$$

The complementary log-log link usually gives similar results to models fit using a logit link, but provides a closer connection between the parameters in the two models (eq. 1 and eq. 2). Specifically, for Poisson random variables, slope coefficients in count (with log link) and presence-absence (with complementary log-log link) models will be equivalent (e.g. (Royle et al. 2009)). We fit both models using the glm function in Program R (R Development Core 2012), with family=poisson(link=”log”) when analyzing the count data and family=binomial(link=”cloglog”) when modeling the detection/non-detection data. In both cases, we included log(trap nights) as an offset to account for variable sampling effort across the different sites.

We used a cluster-level bootstrap, (resampling clusters [study sites] with replacement; sites had a minimum of 10 camera traps) to estimate uncertainty in the population-level relationship between tree cover and catch rate and detection/non-detection rate. This allowed us to relax the assumption that the counts were independent and Poisson distributed. Data collected from a single study site (or adjacent sites within a contiguous block of forest), by a single research team, were treated as a cluster of correlated observations. Observations from different field sites were treated as independent clusters. We refit models to 50,000 bootstrapped data sets. We treated the data regionally (mainland and insular separately) and globally (mainland and insular combined) to test for differences in response to tree cover between regions, and to capture uncertainty in our estimates of β_1.

Estimating sun bear population decline between 2000-2014

Camera trap data alone do not allow us to estimate the absolute abundance of animals, since the number of detections are influenced by both the density of animals and the probability of detecting individuals given they are present (Royle et al. 2014). We assume, however, that our models are adequate for modeling the relative density of sun bears as a function of tree cover. The assumption that regression parameters capture spatial variability in the relative density of individuals is common among species distribution models fit to presence-only data (e.g., (Aarts et al. 2012)). This assumption requires that the probability of detecting bears, when present, is similar across the range of tree cover values (if detection is lower in areas of dense forest, estimates would be biased low). We further assume the population distribution is in equilibrium (i.e., that the number of bears is relatively constant within the *surveyed* habitat at the time it was surveyed) and that future changes in forest tree cover will result in similar relative and absolute densities of bears for any given level of forested tree cover.

Given these assumptions, we can estimate relative changes in absolute abundance (N) using:

$$\Delta N = \exp(\beta_1[X_2 - X_1])/\exp(\beta_1 X_1), \qquad \text{(equation 3)}$$

which does not depend on any unknown parameters.

We used the estimated regression coefficient, $\hat{\beta}_1$, from the global model (mainland and insular data combined) and equation 3 to estimate the % change in the number of sun bears, range-wide and by country (excluding China and Bangladesh), between 2000 and 2014 based on change in % tree cover. We used the bootstrap distribution of regression coefficients to calculate percentile-based 95% confidence intervals for these trend estimates. We projected sun bear population decline between 2000 – 2030, assuming the annual rate of % tree cover change remained constant through time.

Results

The relationship between sun bear catch rate at camera traps and % tree cover

Sun bears were detected in all levels of tree cover above 20%, and catch rates increased with % tree cover within a 6 km^2 circular area of camera traps (Fig 2). Estimates of (β_1) were similar for the insular and mainland models, suggesting comparable responses to tree cover between regions (Fig 3). Thus, to project population trends, we used the estimated regression coefficient from the analysis of the combined (mainland and insular) data ($\hat{\beta}_1$ = 0.47; 95%
CI = 0.21 - 0.78).

Projected population declines

We predicted declines in all sun bear range countries but with varying levels of severity. Declines were predicted to be highest in Indonesia and Malaysia, and lowest in Myanmar (Fig 4). The insular region experienced a higher relative level of decline than the mainland region (Fig 5). Predicted sun bear population losses over a 14-year period, between 2000-2014, were 22% (CI = 13.4 – 28.5) in the insular region, and 8.6% (CI = 4.1 - 12.9) on the mainland. Cast over 30 years, assuming tree cover loss continues at a constant rate, loss in the insular region may exceed 50% ($\bar{x}$ = 47.7, CI = 28.7 – 61.2) and approaches 30% on the mainland ($\bar{x}$ = 18.4, CI = 8.7 – 27.7).

Discussion

Sun bear catch rate at camera traps was positively correlated with tree cover density. Changes in tree cover over time, derived from satellite imagery, therefor provided a standardized, objective and reproducible method to monitor changes in global populations through time. While tree cover alone is not expected to explain sun bear presence and population trends, its strength may be as a transcendent variable, much like greenness, a satellite derived measure of vegetation reflectance that has strong predictive power in modelling grizzly bear population dynamics (Boyce and Waller

2012). Tree cover is assumed to be related to unmeasured explanatory variables for which we do not have a measure, such as food availability, human disturbance and habitat degradation. Wide bootstrap confidence intervals reflect the unmeasured variation in local conditions, and serve as a helpful reminder that our models should not be used for fine scale interpretations, but are expected to capture broad, landscape-scale patterns. Sun bears in the mainland and insular regions face different ecosystem types (seasonal versus a-seasonal forest) and different competitive pressures (presence/absence of the dominant Asiatic black bear). Yet, the regression parameters describing the effect of tree cover on catch rate were similar for the mainland and insular models, suggesting that the data can be pooled to increase precision. Pooling the data led to narrower confidence intervals and a slightly higher estimate of β_1; the small change in estimate is attributable to the pooled data being collectively and analyzed as detection/non-detection data within a binary regression model (equation 2), where-as the mainland and insular data treated separately were modelled with log-linear-regression (equation 1) and binary regression (equation 2) respectively.

Our country-level 14-year estimates (2000-2014) predict that sun bear populations have potentially declined at the highest rates in the insular countries of Indonesia and Malaysia (including Peninsular Malaysia). Brunei is an outlier, with a low level of decline compared with the rest of the insular region. On the mainland, north of the Isthmus of Kra, rates of decline followed a longitudinal gradient, being highest in the eastern countries (Cambodia, Lao PDR, Vietnam) and lowest in the west (India, Thailand, Myanmar, Fig 4). Grouped regionally and cast over 30-years, the 95% confidence intervals of the insular estimates overlap with the IUCN expert-derived global estimates of sun bear population decline of ~ 35 % for the past 30 years, while the upper limit of our mainland estimate is slightly lower (Scotson et al. 2017). In the insular region, the upper confidence limits of our predictions meet the Red List criteria for endangered, based on a declining population trend of > 50% over a 30-year period.

Population declines associated with changes in habitat extent and habitat degradation could be driven by several cumulative and inter-related mechanisms that reduce reproductive rates and access to resources, and increase mortality and risk of extirpation (Staddon et al. 2010, N. M. Haddad et al. 2015, Riitters et al. 2016). Because sun bears are forest dependent with a broad spectrum of habitat use, tree cover may be the most appropriate proximate measure of population change. Higher tree cover may be associated with more food resources, further distance to edges, and lower accessibility to humans (e.g. hunters, gatherers, researchers, loggers). Sun bears select habitat based on food availability and security, favoring interior forest but also using secondary, logged and regenerating burnt forests (Te Wong et al. 2004*b*, Steinmetz et al. 2011*a*, Fredriksson 2012, Nazeri et al. 2012, Cheah 2013, Wong and Linkie 2013). Sun bears also feed in, and travel through, agricultural areas close to the forest edge (Normua et al. 2004, Fredriksson 2005, Cheah 2013, Scotson et al. 2014). Our data support a pattern of broad habitat use and a selection for areas of high tree cover; camera traps in our sample detected sun bears in all levels of tree cover above 20%, and within areas of highly fragmented tree cover, but catch rates were highest at sites with high levels of tree cover.

Long-term global monitoring

Sun bears and other threatened species require long term, systematic and standardized monitoring of population trends across space and time. In Europe and North America, most knowledge of population demographics of bears comes from genetic and telemetry studies (e.g. (McLellan 1989, Dahle and Swenson 2003, Kendall et al. 2008). Aside from the restrictive expense of these techniques for researchers working on low budgets in the tropics, these methods have been difficult to employ with sun bears. Researchers have had difficulty in collecting viable hair samples from sun bears due to their short pelt (Ngoprasert et al. 2015) and in collecting scats, which persist for a very short time in the rainforest, and are rarely encountered (Fredriksson et al. 2006, Steinmetz 2006). Telemetry studies of sun bears have been challenged by very low capture rates (Te Wong et al. 2004*b*, Fredriksson 2012, Cheah 2013) and data have been insufficient for estimating population density and trends.

Until now, polling field biologists (i.e., expert opinion) has been the only method used to generate estimates of regional and global population trends for sun bears (Scotson et al. 2017). Other efforts have been employed on smaller spatial scales (e.g. (Steinmetz et al. 2006, Ngoprasert et al. 2012)), and while successful in generating robust site-level estimates of population parameters, results cannot be extrapolated to other sites, and methods cannot be conducted over a large enough area to monitor regional or global bear populations. The IUCN Red List assessment of sun bears relied on a small number of people, meaning that each person had a significant influence on the global estimate, particularly when only one representative answered for a large extent of the range. The free availability of tree cover data, a uniform measure of tree density and temporal change over 14 years, between 2000 and 2014, has created new research opportunities in studies related to forest loss and fragmentation (e.g.(Donald et al. 2015, Joshi et al. 2016, Riitters et al. 2016, Tracewski et al. 2016)). Tree cover may act as a transcendent variable, and a viable substitute for causal variables (food availability, hunting pressure) that are not available on broad scales. Given the limitations associated with employing other monitoring methods over large areas, or in keeping them standardized through time, monitoring sun bears with satellite based tree cover change may be the most realistic long-term solution because these types of models can be applied repeatedly over time, as updates to tree cover data become available.

Limitations

Here we have shown a relationship between tree cover and sun bear detections. Sun bear populations respond to more than just tree cover and our estimates should be regarded as reflective of broad-scale patterns and not accurate on a finer level. Site-level variation in bear population status, and the associated threats to populations, even in dense forests (e.g. hunting, fragmentation), is unaccounted for in our models, resulting in high levels of uncertainty at finer scales. Our extrapolation to infer sun bear population decline from forest cover loss can be viewed as a hypothesis at one level. This relationship, and our results, are valid only to the extent that several important assumptions hold true.

Our primary assumption is that sun bear detection rate is related to bear density. Many studies assume detection rates are related to density, (Apps et al. 2007, 2016), including camera trap studies (Rowcliffe and Carbone 2008),and this underpins the assumptions of distance sampling methodology (Buckland et al. 2005). Nonetheless, we are aware there are caveats that influence this relationship. In particular, relative use of different habitats, and thus measures of habitat suitability or selection, will vary with both habitat availability and population density (Beyer et al. 2010, Matthiopoulos et al. 2011, 2015). Our approach also holds the equally important assumption that forest cover is related to sun bear foods, and that the quantity of sun bear foods is related to their density. The amount of camera-trap data, and the strong correlation between sun bear detection rates and tree cover (Fig 2), suggests this is a realistic assumption, even though there will be variation across forest types and within forests at different levels of canopy loss. Population dynamics within agricultural forests (palm oil and rubber plantations) will undoubtedly vary from patterns within natural forests (see below for future research considerations). Bears affected by mortality pressure in habitats below carrying capacity might not be affected by forest loss because they are heavily hunted, and already reduced below food potential. Finally, our models assumed a positive relationship between sun bear population change and tree cover density change, and that bears will not simply redistribute their numbers within the landscape when tree density changes.

Violation of these assumptions is inevitable to some degree, in some cases inflating our estimates, and in others causing underestimates of decline. Unmodeled effects from hunting and habitat fragmentation pressures may cause higher declines than we have estimated. Conversely, failure to incorporate the adaptiveness of sun bears to a changing landscape may cause inflated estimates. The declines predicted by our models are unlikely to be instantaneous, and bears presumably did redistribute themselves in the landscape in the short-term, with an unknown time-lag between when deforestation occurred and the resulting population declines bringing the food source and mortality pressure relationship to equilibrium. Our estimates are regional, and we did not combine them to create an over-all global measure of decline because densities may vary greatly between insular and mainland populations (Steinmetz et al. 2011*b*, Scotson et al. 2017) and a simple combination would be biased and/or conceal a steeper decline in a significant part of sun bear range. Sun bears population densities are thought to follow a north to south gradient, with the highest densities reported in the insular region (Steinmetz 2006). Density estimates are rare, with only one unsubstantiated figure for the insular region, 26/100km^2 (Lee 2014, unpublished data), suggesting sun bears may occur at 4-5 x the density of bears on the mainland (Scotson et al. 2017). If this is accurate for the insular range, the contribution of this region to overall global decline is much higher than if based on range size alone. Reliable density estimates of regional sun bear populations would allow an area/density weighted measure to generate more accurate decline estimates.

Conclusions

A full picture of sun bear status requires fine-scale knowledge on the status of sub-populations. Many desirable variables, including landscape, anthropogenic and biological measures were not available for inclusion. Future researchers might test, refine, and improve our analysis with the addition of a more informative suite of predictor variables, either at a small geographical scale, or across sun bear range as those data become available. Additional variables might include, human disturbance variables such as human density, road density, levels and types of land use (Griffiths and Van Schaik 1993), forest types and their relative abundance of sun bear foods, agricultural lands and their relationship to forest cover and sun bear foods, spatial variation in hunting, predation and competitive pressure. Useful landscape variables include habitat fragmentation metrics, in combination with sun bear movement parameters, to investigate the role of range connectivity (in relation to movement potential) in response to tree cover. Incorporating information about local densities of sympatric Asiatic black bears, which might suppress local sun bear populations in mainland Southeast Asia (Steinmetz et al. 2011*a*), could improve estimates by accounting for species competition. Other relationships that could be useful to explore include, compensatory responses of sun bears to partial and complete canopy loss, and mechanisms of population decline associated with forest cover loss. These factors will undoubtedly improve and refine our conclusions and better inform fine scale conservation efforts. Future analyses may also explore the utility of data collected in other ways, such as bear sign collected on line transects.

We present an alternative approach to that of expert-based estimates for monitoring the population trends of threatened species. We collected the largest catalogue of sun bear detection data to date, and made an objective estimate of global population change. Our study demonstrates the potential of using camera trap data to monitor threatened species even when most were collected on studies for which bears were not a primary focus. The conservation community would benefit greatly if more efforts were made to systematically classify and manage camera trap imagery for use on a variety of topics [56,57, Scotson et al. in review]. Our approach could be repeated for other forest dependent species for which optimal habitat may be reflected in selection for tree cover, such as Asian elephants *Elephas maximus,* Sumatran rhinoceros *Dicerorhinus sumatrensis,* Asian tapirs *Tapirus indicus* and Sumatran tigers *Panthera tigris sumatrae* (Kinnaird et al. 2003, Wibisono et al. 2011, Linkie et al. 2013).

Table 1. Camera trap field sites contributed from across Southeast Asian sun bear range.

Study Area	Date	Area (Km^2)*	No. of Units	Contributor information
Semina Protected Forest, Cambodia	2003	123	53	Wildlife Conservation Society
Phnom Prich Wildlife Sanctuary, Cambodia	2001-07	2,113	119	Thomas Gray, World Wide Fund for Nature
Siem Bok Forest, Cambodia	2001-06	826	32	Thomas Gray, World Wide Fund for Nature
Siem Pang Forest, Cambodia	2003	5	7	Thomas Gray, World Wide Fund for Nature
Virachey National Park, Cambodia	2001	566	9	Thomas Gray, World Wide Fund for Nature
Semina Protected Forest, Cambodia	2004	125	7	Thomas Gray, World Wide Fund for Nature
Belum-Temengor Forest Complex, Peninsular Malaysia*	2011-12	437	452	Reuben Clements
Kerinci Seblat Tropical Rainforest Heritage, Sumatra (8 sites)	2010-11	123	739	Wai Ming Wong
Semina Protected Forest, Cambodia	2000-02	403	92	Wildlife Conservation Society
Wehea Forest, East Kalimantan, Indonesia	2012-13	63	95	Brent Loken
Batang Hari Forest, Sumatra	2008-09	196	21	Yoan Dinata, Fauna & Flora International
Bukit Tiga Puluh National Park, Sumatra	2013-14	936	240	Alexander Moßbrucker
Xe Sap National Protected Area, Lao PDR	2013	123	38	Thomas Gray, World Wide Fund for Nature
Preah Vihear Protected Forest, Cambodia	2010-11	353	53	Wildlife Conservation Society

Kuiburi National Park, Thailand	2007-12	291	88	Rob Steinmetz
Kalabakan Forest Reserve, Sabah, Malaysia (4 sites)	2011-12	20	592	Oliver Wearn
Ulu Masen Forest, Sumatra	2013	2,702	164	Matt Linkie, Fauna & Flora International
Virachey National Park, Cambodia	2000	1,468	41	Wildlife Conservation Society
Kirirom National Park, Cambodia	2000	933	46	Wildlife Conservation Society
Kulen Promtep, Cambodia	2010-11	419	37	Wildlife Conservation Society
Hue and Quang Nam Saola Reserve, Vietnam	2012-14	210	127	Thomas Gray, World Wide Fund for Nature
Cholong Forest, Phnom Veng, Cambodia	2003-05	32	17	Thomas Gray, World Wide Fund for Nature
Khieu Forest, Prey Oso, Cambodia	2004-06	217	19	Thomas Gray, World Wide Fund for Nature
Malaysian Borneo (11 sites)	2003-15	598	209	Mohd Azlan Jayasilan b Abd Gulam Azad
Preah Vihear National Protected Forest, Cambodia	2012-13	512	51	Ai Suzuki

Forest blocks are named primarily according the IUCN World Database of Protected Areas. * Minimum Convex Polygon drawn around perimeter of camera trap units.

Table 2. Camera trap sun bear detection data, collected between 2000-2013, were combined from 49 field sites in 7 out of 11 sun bear range countries.

Region	No. Study sites	Camera traps (min/max per site)	Trap-nights (min/max per site)	Count[a]	Detections/total units[b]
Mainland	14	623 (13-126)	26,140 (8-90)	NA	379/623
Insular	17	843 (13-201)	48,752 (8-90)	524	246/843
Total	31	1,463 (13-201)	74891 (8-90)	NA	379/2,022

Figure 1. Sun bear range limits and distribution of camera trap field sites from which sun bear detection data were collected between 2000-2015. Historic (within 500 years) sun bear range extends southwards, from southeast Bangladesh, northeast India and southern China, throughout most of mainland southeast Asia, and all of Malaysia and Indonesia. Camera trap data were combined from 7 out of 11 sun bear range countries and camera traps sampled in all levels of tree cover above 3%. Sun bears were not detected below levels of 30% tree cover in the mainland, and 20% tree cover in the insular region; areas below these thresholds are blank.

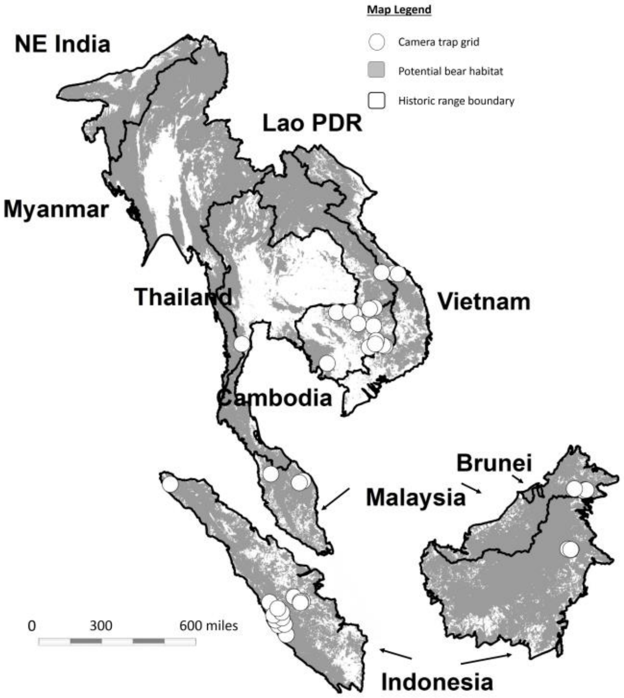


Figure 2. Relationship between catch rates of sun bear at camera traps, active between 2000-2015 across southeast Asia, and tree cover from 0-100%. Camera traps were active within all levels of tree cover, and were more active in areas of high

tree cover. Tree cover values at camera traps, taken from rasters of tree cover were averaged over a $6km^2$ area around camera traps to represent tree cover at the scale of a core sun bear range. To explore the assumption that bear detection is related to % tree cover, we calculated detection rates (detections/number of trap nights) with values pooled for camera active within 9 tree cover categories (0-20, 21–30, 31-41…etc.). In a simple linear regression, catch rates, increased by 1 (to avoid infinite values) and log transformed, were positively related with tree cover density (ln([Y+1]/Trap Nights = -8.16 + 0.03*Tree Cover, p = 0.003, R^2 = 0.7, β_1 95% CI: 0.01 – 0.04).

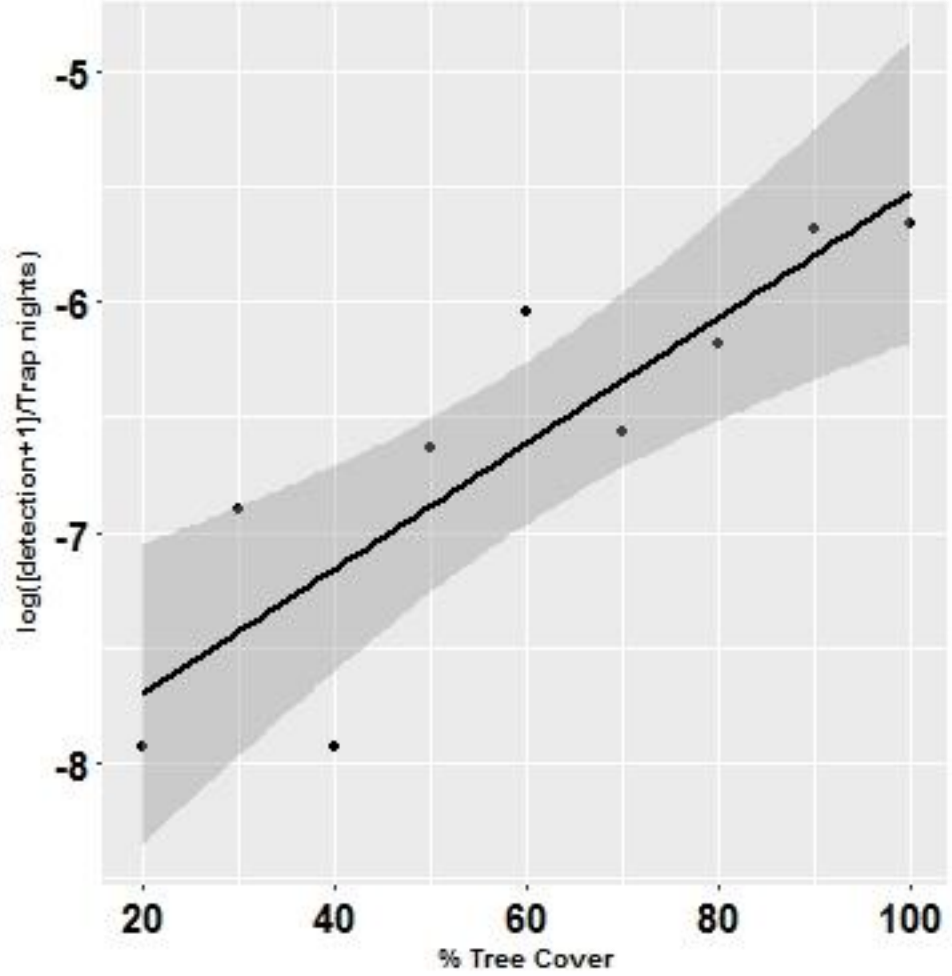


Figure 3. Estimated regression coefficients and 95% bootstrap confidence intervals for β_1, relating the log expected catch rate to % tree cover. Tree cover values at camera traps, taken from rasters of tree cover in either 2000, 2012 and 2014 (whichever was closest to the date of camera operation), were averaged over a 6 km^2 area around

camera traps to represent tree cover at the scale of a core sun bear range. Regional models were fit to data from either the insular and mainland countries, allowing the response of sun bears to tree cover to vary by region. The insular data, catch rate per camera trap, were modelled using log-linear regression (equation 1) and the mainland data, detection/non-detection per camera trap within a trapping period, were modelled using a binary regression model with complementary log-log link (equation 2). The global model pooled all data, assuming bears respond similarly to tree cover throughout the range, and modelled detection/non-detection per camera trap within a trapping period using the binary regression (equation 2). Models assumed log catch rate of sun bears at camera traps was a linear function of tree cover averaged over a 6km^2 circular area of camera traps. Data were filtered to reduce variability in sampling intensity, by removing cameras active for < 7 days and > 90 days, and study sites with < 10 cameras.

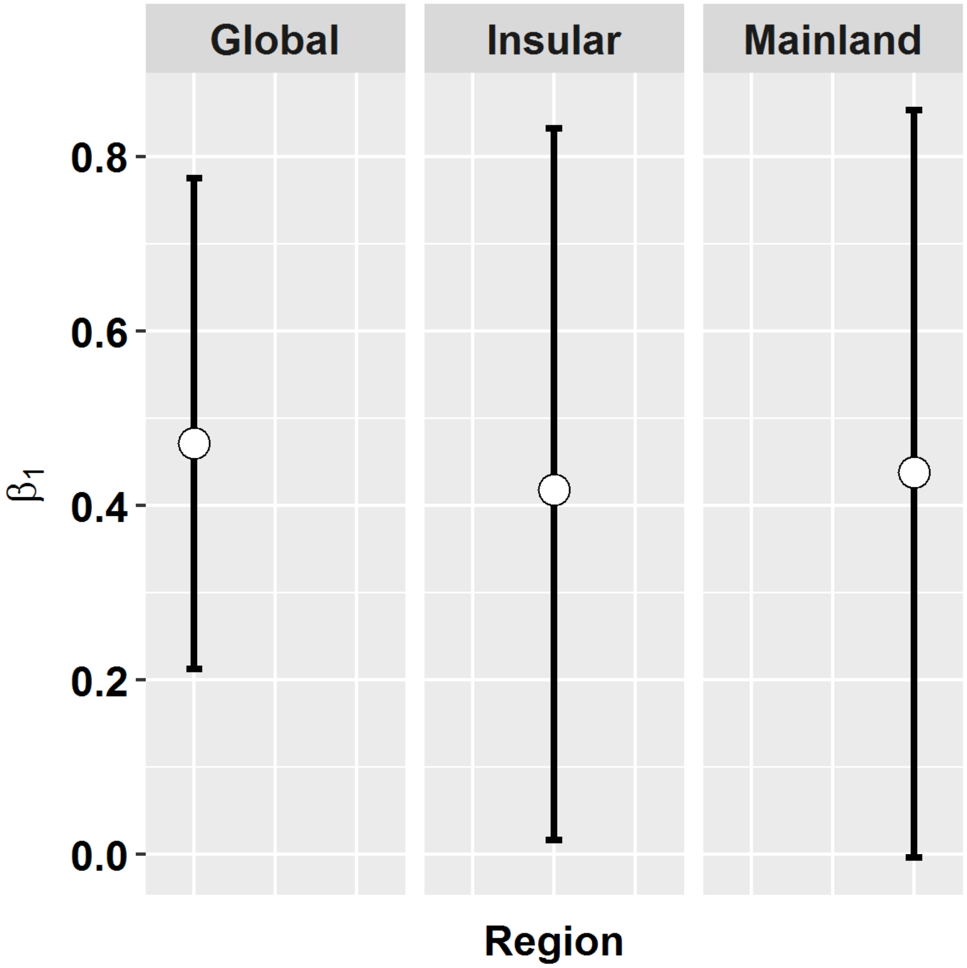


Figure 4. Model-based projections of sun bear population change across southeast Asia between 2000 – 2014. Bars, with 95% confidence intervals, show estimates generated by binary regression models (Eq 3) fit to the pooled mainland and insular data. Models assumed log catch rate of sun bears at camera traps was a linear function of % tree cover averaged over a 6 km^2 circular area around camera traps. Country-level

declines were predicted to be the most severe in Malaysia and Indonesia, which form the bulk of the insular region. On the mainland, declines roughly follow a longitudinal gradient, being highest in eastern countries (Cambodia, Lao PRD, Vietnam) and lowest in the west (India, Thailand, Myanmar).

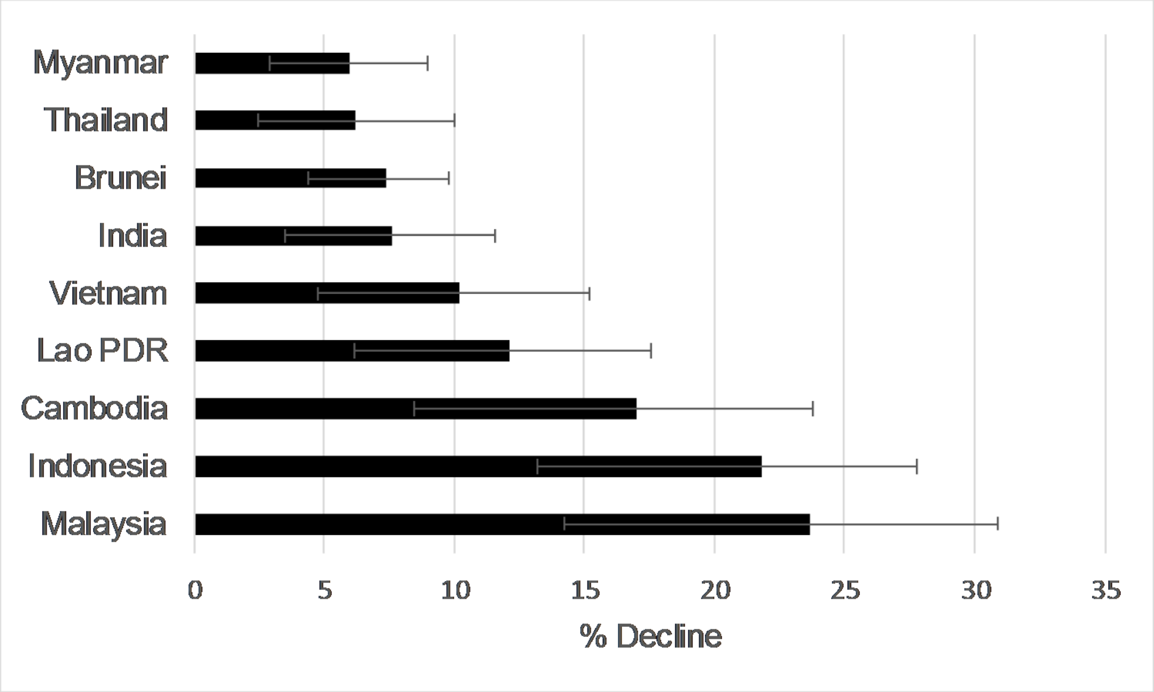
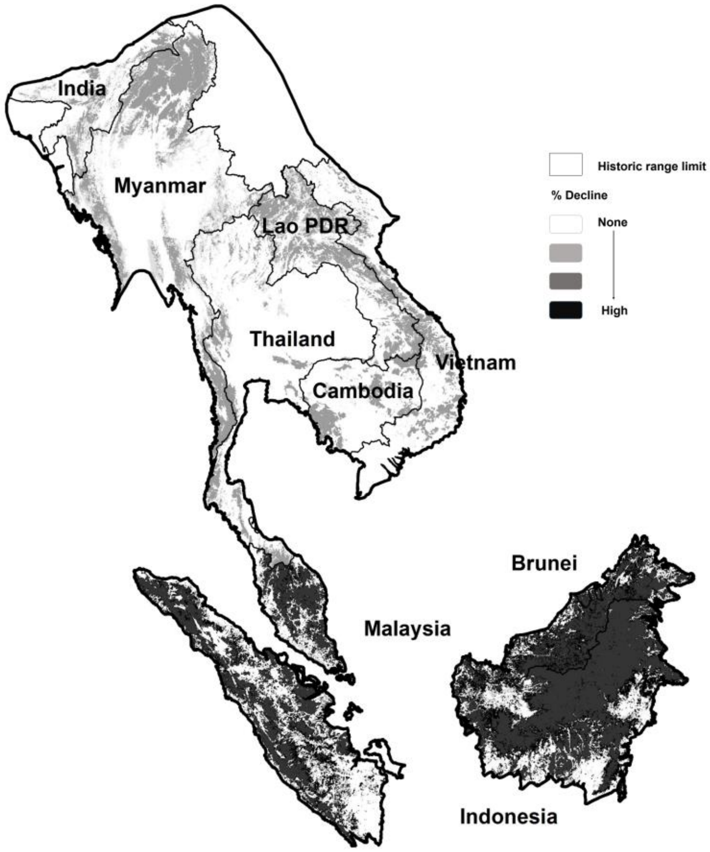


Figure 5. Location and scale of sun bear population declines between 2000-2014, based on the modelled relationship between sun bear catch rate at camera traps and % tree cover. Models assumed log catch rate of sun bears at camera traps was a linear function of % tree cover averaged over a 6 km^2 circular area around camera traps. Declines are plotted on a relative scale and are comparable at the country and regional-

levels, i.e. the insular region lost a higher % of its regional bear populations that the mainland region (north of peninsular Malaysia). Country-level decline estimates are summarized in Fig 4.



Chapter 3

Sun bear range connectivity reveals research and management priorities

Synopsis

In this modern era of rapid deforestation across human-dominated landscapes, fragmented habitat is breaking up once continuous wildlife ranges into unnatural subpopulations, which must function as some form of metapopulation to maintain sustainable population dynamics. In the tropics, where habitat is changing most rapidly, high resolution genetics and telemetry data to inform management are limited. Therefore, biologists must work with imperfect datasets in innovative ways. Here we present a novel technique, using camera trap and tree cover data, to investigate the extent of fragmented habitat within the global sun bear range, and to predict their future as modern metapopulations. To visualize sun bear range connectivity, we a created a habitat suitability index using the relationship between sun bear occurrence and tree cover derived from a separate study. To find potential fractures in range, we identified non-viable habitat (areas with < 20% tree cover, patches too small to support viable populations), and grouped the remaining habitat into a habitat quality mosaic. We visually inspected maps to identify possible subpopulations and to evaluate habitat connectivity among and within subpopulations, using habitat quality and severity of human disturbance and road network as indicators of barriers to movement. Using these methods, we identified seven potential subpopulations; two are fully isolated with no potential for inter-subpopulation movement, and in the other five, inter and intra-subpopulation habitat fragmentation occurs in a continuum of severity. We describe current day sun bear range in terms of the potential to function as human-caused metapopulations. It is clear that sun bears cannot function as their once continuous population; instead, subpopulations may require inter-area movements (exchanges of individuals), either naturally, via maintaining habitat connectivity, or through human-assisted translocation. Therefore, we used our results to list regional priorities for sun bear research and management. Studying sun bears in the context of modern metapopulations is a frontier for bear research and conservation in the tropics. Our findings advance understanding of sun bear habitat and subpopulation level

fragmentation, use landscape-scale data to investigate spatial population patterns and dynamics, and highlight locations where subpopulations are most vulnerable to isolation.

Introduction

Barriers to dispersal, created by oceans, major rivers, mountain ranges, and other geographical barriers, is a fundamental mechanism of evolution (Darwin 1859). Allopatric speciation, when geographic isolation of subpopulations leads to species divergence and increased biodiversity, is the positive side of fragmentation (Baker and Bradley 2006). Evolutionary theory suggests that historic changes in Asia's land connectivity, caused by the rise and fall of northern seaways, at the Bering Strait, once a land bridge between present day Russia and Alaska, and southern seaways, at the Java Sea, the Gulf of Siam and the Straits of Malacca, between the Indo-Malay islands of Borneo, Sumatra and Java, led to the allopatric divergence of many tropical species, including several of the Asian bears (Hughes et al. 2003, Krause et al. 2008, Kutschera et al. 2017). Human caused fragmentation, however, is recognized as one of the biggest threats to the biodiversity that natural barriers to movement once helped create (Tilman et al. 1994, Fahrig 2003). Globally, fragmentation has progressed at a rapid rate in the past few decades, with the area of interior forest declining at a greater rate than non-interior, and > 70% of the world's forest now occurring within 1 km of the forest edge (Wade et al. 2003, Nick M Haddad et al. 2015, Riitters et al. 2016).

Sun bears *Helarctos malayanus*, which occur throughout mainland and insular Southeast Asia, are classified as 'Vulnerable' on the IUCN red list, and considered to be threatened by range fragmentation (Scotson et al. 2017). However there has been no formal assessment of connectivity within global sun bear range, and the extent to which fragmentation has restricted gene flow and created unnatural subpopulations. Conserving a species requires broad understanding of population dynamics at regional and sub-continental scales. Protecting a population requires understanding at a finer scale, to combat localized extirpations and contracting range. Anthropogenic habitat fragmentation has caused many species that once occurred as spatially continuous populations to now resemble spatially disjunct metapopulations, although they might not function as such (McCullough 1996). Isolated subpopulations, and subpopulations that must spend time in low quality and non-habitat to travel between patches, face higher mortality rates, due to a variety of cumulative and interacting factors related to the short and long-term impacts of genetic and demographic isolation and often a higher overlap with human populations (Krause et al. 2008, Staddon et al. 2010, Nick M Haddad et al. 2015, Riitters et al. 2016). Global populations of the 8-extant bear species are all affected by unnatural fragmentation of habitat (including sea ice) to some degree (Scotson et al. in press., Sahanatien and Derocher 2012, Escobar et al. 2015, Dharaiya et al. 2016, Swaisgood et al. 2016). Given the cumulative threats from fragmented habitat, there is a push to recognize subpopulations as a useful entity to monitor, and monitoring authorities are moving to classify subpopulations (i.e. subsets of the global population that do not share genetic material with other subsets) into categories of extinction risk , with progress made for brown bears *Ursus arctos* and Andean bears *Tremarctos ornatus* and Polar bears *Ursus maritimus* (Kattan et al. 2004, Wiig et al. 2015, McLellan et al. 2016). An understanding of the threats posed by fragmented habitat to sun bears at the species and subpopulation level, would allow the development of specific site-level priorities for research and active management of sun bear subpopulations and habitat. Resilience to fragmented habitat is linked to several factors. Some bear species are more resilient than others, and fragmentation can restrict or filter population movement both inter- and intra-specifically. American black bears *Ursus americanus* persist in landscapes dominated by agriculture (Ditmer et al. 2015). This resilience can be explained in part by high reproductive rates, and a tolerance, and perhaps even exploitation of human food sources and , of high levels of human disturbance (Garshelis et al. 2016). Grizzly (brown) bears have comparatively low reproductive rates and appear less tolerant of human activities, with populations suffering in response to high levels of human disturbance (Craighead et al. 1974, McLellan 1995). Female grizzly bears, the primary facilitators of demographic connectivity are more easily affected by fragmented than males, being more prone to avoiding heavy traffic and settlements, and less likely to cross transportation and settlement corridors (Gibeau et al. 2002, Proctor et al. 2005, 2012). Delayed implantation in American black bear and brown bears give both species resilience to ephemeral food supplies (Mead 1989), as do their generalist omnivorous foraging strategies and ability to travel large distances to exploit varied food resources (including human foods). Fragmented habitat, however, impairs resilience by restricting dispersal in times of food shortages and can decrease productivity or increase food related mortality.

Sun bear tolerance to habitat fragmentation, and the impact fragmentation has on the global population, is not well understood. Sun bears feed in agricultural fields and plantations, use narrow corridors of habitat to transition between higher quality patches, and can cross major highways (Cheah 2013, Scotson et al. 2014, Cheema 2015, Guharajan 2016). Home range, recorded for the insular region, is small compared to other bear species (Blanchard and Knight 1991, Bertram and Vivion 2002, Hwang and Garshelis 2007). In the mainland region (i.e. all range north of the Isthmus of Kra) home range is unknown, but could be larger due to interspecific competition with the sympatric Asiatic black bear, which dominate in areas of high fruit availability (Steinmetz et al. 2011*a*). Sun bears are habitat generalists (although dependent on forest) and when food is scarce, sun bears living near human crop fields thrived while bears with no access to human food starved (Normua et al. 2004, Te Wong et al. 2004). Sun bear reproductive rates are low compared to Asiatic black bears, with usually one cub produced at a time, presumed to be at around 2 year intervals like other bears (Yamanaka et al. 2011, Frederick et al. 2012). Reproductive success is vulnerable to periodic famines induced by the El Nino weather patterns, which causes increased mortality through starvation, and greater movement through low quality habitat in search of food (Te Wong et al. 2004*a*, Fredriksson et al. 2006). Sun bears and Asiatic black bears, are heavily hunted for trade in parts (Scotson et al. *in press*; Dave Garshelis and Steinmetz 2016). When bears occupy small patches, or spend increased time moving between patches, they are more likely to encounter predators (including hunters), and are more likely to come into conflict with humans (Nielsen et al. 2004, Can et al. 2014).

Assessing range connectivity for sun bears faces several methodological problems, and requires a unique approach. Data scarcity rules out traditional methods. Few individuals have been monitored relative to north American and European bears (e.g. McLellan and Hovey 2001, Dahle and Swenson 2003, Kendall et al. 2008), with only 14 wild bears radio collared in 4 sites in Malaysia, and trapping effort high relative to success rates (Normua et al. 2004, Te Wong et al. 2004, Fredriksson 2012, Cheah 2013). Genetic samples (i.e. hair, scat) are hard to collect. The sun bear pelt is short, and hair snaring has largely been unsuccessful (Ngoprasert et al. 2015). Collecting scats has worked with bears in temperate climates (Robert A. Long, Therese M. Donovan, Paula Mackay et al. 2007, Swaisgood et al. 2016), but less so with sun bears in the tropics (Fredriksson et al. 2006, Steinmetz 2009), probably because scat degrades quickly in the tropical forest. Limited resources (i.e. time, money) and limited dedicated sun bear research means it's unlikely that such data will become available in the near to distant future. Globally available high resolution tree cover and tree cover change (Hansen et al. 2013), has advanced the spatial understanding of sun bear range extent, and on how sun bears respond to tree cover (Scotson et al. *in review*). With the rapid rate of forest cover change, loss and fragmentation, and increasing human populations, it is urgent to use what data are available and identify options for maintaining connectivity now, before those options are gone.

The goal of this study is to investigate habitat connectivity within the global range of the sun bear by addressing the following objectives; we: 1) create a habitat suitably index using the modelled relationship between sun bear occurrence and % tree cover, 2) identify areas of non-habitat and evaluate other factors that may restrict movement within sun bear range 3) assess the connectivity of global sun bear range in terms of structural connective (binary habitat/non habitat connectivity) and the potential for movement and dispersal. Finally, to improve understanding of the threats posed by fragmented habitat to sun bears at the species and subpopulation level, we translate our findings into specific site-level priorities for research and active management of sun bear subpopulations and habitat.

Methods

Overview

To create a map capturing current connectivity status of sun bear range, we began by deriving a 2014 tree cover map from tree cover available for 2000, and tree cover loss between 2000-2014. We then created a habitat suitably index using the previously modelled relationship between sun bear presence and tree cover (Scotson et al *in review*). We used standardized criteria to identify fractures in sun bear distribution and then evaluated the accuracy of our habitat/nonhabitat classes with separate land cover and human disturbance data. Next, we visually inspected maps to identify possible subpopulations and to evaluate habitat connectivity among and within subpopulations using estimates of sun bear dispersal distances. Finally, we quantified the entire spatial extent and composition of habitat, and separately calculated the extent that falls within the IUCN protected area network (a global network of IUCN designated protected area that range from Strict Nature Reserve to Protected areas with sustainable use of natural resources; IUCN 2017).

Tree cover processing

We first had to derive a 2014 tree cover layer by combing an existing 2000 tree cover layer with loss data between 2000 – 2014 (Hansen et al. 2013). We processed all GIS data in ArcGIS 10.2. We downloaded open-source satellite-based tree cover rasters for the year 2000 (pixels valued from 0-100% tree cover) and tree cover loss rasters from between 2000 - 2014 (binary pixels valued 1 [loss] or 0 [no loss]). We trimmed rasters to the geographic extent of historic sun bear range (Erdbrink, 1953). We created a 2014 tree cover raster by i) multiplying all binary loss pixels by 100 (100 = loss, 0 = no loss) and ii) subtracting the transformed pixels from the year 2000 tree cover raster. All negative values were corrected to zero. We smoothed the 2014 tree cover raster, averaging pixel values over a 6km^2 circular area to match the scale previously used to model sun bear occurrence as a function of tree cover (Scotson et al. *in review*). We excluded China, where sun bears are thought to be almost extirpated; only a tiny patch of unknown habitat remains in the western border with Myanmar (Scotson and Fredriksson, 2016).

Sun bear Habitat Suitability Index

Using the derived 2014 tree cover raster as the most recently available tree cover data, we populated cells with the relative probability of bear occurrence, first assigning all areas < 20% tree cover as zero (bears were never detected within this level of tree cover; Scotson et al. *in review).* Scotson et al (in review) fit a model relating sun bear occurrence to tree cover. We used the $\hat{\beta}_1$ from that model to calculate the relative probability of sun bear occurnace in each map pixel > 20% tree cover:

$$p[i] = \exp(\hat{\beta}_1 * \%\ \text{tree cover}) / \sum \exp(\hat{\beta}_1 * \%\text{tree cover})$$

where % tree cover is the average tree cover value within 6 km^2 circular area of a pixel in the year 2014. We used a 6 km^2 scale to match that used by Scotson et al (*in review*) to generate $\hat{\beta}_1$. To smooth out very small patches of fragmented areas that are likely to be insignificant to restricting sun bear movement, we broadened the scale to that of the mean home range size of sun bears, by averaging all relative probability values over 11km^2 (Nomura et al 2004; Fredriksson 2012; Cheah, 2013).

To examine the compositional quality of patches, we created a Habitat Suitability Index (HSI) by grouping all relative probabilities into 4 categories, non-habitat (not suitable for bears), marginal (low relative probability of use), sub-optimal (moderate relative probability of use) and core habitat (high relative probability of use). The values were grouped using Natural Jenks classification in ArcGIS 10.2. Natural Jenks minimized variability within classes and maximized variability between classes (North, 2009). We expect that in non-habitat, bears are unable to persist, except for moving through short distances between patches of habitat. We expect that marginal habitat may or may not allow bears to travel through, depending on the composition of that habitat. We expect that sub-optimal and core habitat to be largely natural forest and the most suitable habitat for bears.

Structural and potential connectivity of the sun bear landscape

We created a binary layer of habitat/non-habitat by grouping all marginal, sub-optimal and core habitat into one category (habitat), and, classified all areas outside these polygons, and within the historic range limits of sun bears, as non-habitat. We created a mosaic landscape map by extracting the Habitat Suitability Index rasters to polygons of marginal, sub-optimal and core habitat. To investigate the potential connectivity of the sun bear landscape we had to make several arbitrary decisions on viable patch size and the distance threshold for bears to move between patches of habitat through non-habitat. In making these decisions we drew from existing knowledge where ever possible. First, we removed all patches not likely to support bears, based on patch size and distance from neighboring patches. We decided that any patch smaller than 16 km^2 was not able to support a breeding population of bears and reclassified these as non-habitat. We chose 16 km^2 because this is an average male sun bear's average home range (Normua et al. 2004, Wong ST, Servheen CW 2004, Cheah 2013), and a male home range can overlap several female home ranges and so a patch this small could theoretically support a breeding population. We decided that patches from 16 - 100 km^2 were only viable if close enough to other patches for bears to move between more than one patch (i.e. connected). To identify isolated and connected patches we used the maximum recorded daily movement of sun bears - 4.5km (Fredriksson 2012) - as the most liberal measure of how far a sun bear can move in-between patches of habitat through non-habitat (not considering the composition of the non-habitat). We grouped all remaining polygons into 3 broad categories; < 100 km^2, 100-400 km^2 and > 400 km^2, and we decided that patches < 100km^2 in size and > 4.5km from the nearest patch were isolated and unable to support a viable population in the long-term. We decided that patches < 100 km^2, and < 4.5 km from the nearest patch were not isolated, being close enough to other patches for bears to move in-between. Patches 100 - 400 km^2 and > 400 km^2 were considered large enough to support a long-term breeding population of bears, regardless of distance from other patches. Finally, we compared the remaining polygons with the IUCN Sun bear range map, and removed some areas where sun bears are known not to occur. We left some patches of tree cover that IUCN classified as Extirpated, when these occurred close to, or contiguous to, known range, and could theoretically be used by bears.

Ground truthing our habitat classifications

To check if our classification of habitat into binary and mosaic habitat classifications met our expectations, we compared the resulting categories with two sets of data, on landcover, and human influence levels. We generated a set of 15,000 random points within Non-habitat, and another set of locations within Habitat, divided equally between Marginal, Sub-optimal and Core (i.e. 5000 points in each). At each random point, we calculated the percent tree cover in 2014, the relative probability of bear occurrence (based on tree cover), Human Influence Index (Sanderson et al. 2002), and Land Cover according to the Tropical Ecosystem Environment Observations by Satellites (TREES; Stibig et al. 2003). Sanderson et al. 2002 created The Human Influence Index by combining 9 global datasets related to human density, land use and infrastructure and human access to create The Human Influence Index (Sanderson et al. 2002). The TREES land cover map is at a 1km^2 resolution, with land cover classified into 13 categories, with 8 categories considered as viable bear habitat, including a range of tropical forest types and a mosaic of woodland, shrub, and croplands, and 3 categories we assumed not to be viable habitat (i.e. no data/sea, water, cropland, bare land and rock; Stibig et al. 2003). We reclassified the TREES raster, removing the No Data/Sea category, leaving classes 1 - 8 as viable or potentially viable bear habitat, and 9 – 12 as non-viable bear habitat. To correct for areas classified as viable bear habitat (categories 1-8) in the year 2000 that had since been deforested, we calculated % tree cover in 2014 to each point, and reclassified areas with no tree cover in 2014 as non-viable habitat.

We evaluated the dissimilarity of Human Disturbance Index values between our Habitat and Non-habitat categories with density plots, simple linear regression, and a Welch Two Sample t-test. We used frequency plots to compare the distribution of TREES land cover classification values within our mosaic habitat classes.

Identifying subpopulations and patches most threatened by fragmentation

To visually identify potential subpopulations of sun bears, and habitat patches at risk from becoming isolated (i.e. no connectivity with other patches), we overlaid our habitat mosaic with areas of high Human Influence Index (defined as areas with a higher than average value of Human Influence in non-habitat), and the road network (https://urs.earthdata.nasa.gov, accessed 16th Feb, 2017). To identify areas within subpopulations that are vulnerable to becoming isolated (i.e. "At Risk"), we visually inspected all core and sub-optimal habitat patches within the context of the surrounding marginal habitat, and landscape features consider to be barriers to movement (roads, human influence). We visually identified At Risk areas as having a high concentration of surrounding potential barriers to bear movement (i.e. marginal, non-habitat, high Human Influence Index and roads). We assumed that these movement barriers are related to human activity, and prone to increasing through time, thus causing patches to be progressively more vulnerable to becoming isolated. At Risk patches were either isolated already, or thought to be at imminent risk from becoming isolated. We quantified the structure of the binary (habitat/non-habitat) and the composition of mosaic (marginal, sub-optimal and core) habitat (Fig 1), by calculating the proportion of each within each potential subpopulation. We also calculated the area of habitat, and the proportion of each habitat class, that fell within the IUCN Protected Area network.
We analyzed data in Arc 10.2.4 and R Version 3.2.2 (R Core Team, 2016).

Results

Landscape metrics

Core habitat dominated just over half the sun bear range, but very little is contained within the IUCN Protected Area network. In 2014, viable habitat covered 77% of the historic range limit defined by Erdbrink 1953 (excluding China, where range limit is unclear), with 55% classified as Core, 27% as Sub-optimal, and 18% as Marginal habitat. Only 18 % of habitat classed as viable bear range falls within the IUCN Protected Area network, the bulk of which was classified as sub-optimal habitat (65%) with a smaller amount of core (12%) and the remainder marginal (6%) and non-viable habitat (16%).

Ground truthing the habitat classes

Comparing values of the Human Influence Index and TREES land classification within habitat (all classes grouped together) and non-habitat supported our assumption that habitat is different than Non-habitat. Human Influence Index values, calculated at 15,000 random points in each habitat and non-habitat areas, were on average 13.8 points higher in areas classified as non-habitat (t = -95.2, df = 29658, p < 0.001, $\bar{x}$ within non-habitat = 36.7, SD = 13.1, $\bar{x}$ within habitat = 23, SD = 11.8). When marginal habitat was grouped with non-habitat, the average Human Influence index was on average 14.2 points higher than sub-optimal and core grouped together (t= -100.3, df = 24971, p <0.001, $\bar{x}$ within non-habitat & marginal grouped = 34.6, SD = 13.5, $\bar{x}$ within sub-optimal and core grouped = 20.4, SD = 10.4,). Bear habitat was heavily skewed to lower Human Influence Index values (< ~40), however they fell to some extent within all values of Human Influence (Fig. 2). TREES land classification values within non-habitat were more often classified as areas considered as non-viable bear habitat (i.e. cropland, shrub, bare land, rock). Second to non-habitat, marginal habitat had the highest proportion of points within non-viable bear habitat categories. In sub-optimal and core habitat, land classification tended to be areas of potential bear habitat (i.e. evergreen, deciduous forest, and other forms of mosaic forest; Fig. 3).

Sun bear subpopulations and areas most at risk from isolation

The southeast Asian range of sun bears is broken up naturally, by oceanic barriers, into three natural sub-sections; mainland southeast Asia including Peninsular Malaysia, Sumatra and Borneo. A mosaic of core, sub-optimal and marginal habitat creates potential habitat connectivity throughout much of the range, However, we identified a further five potential subpopulations created by fragmentation due to diminishing tree cover, levels of human influence and road networks. With natural and un-natural fractures combined, we identified seven potential subpopulations of sun bears; i) northern Mainland, ii) Central Myanmar, iii) Central SE Asia, iv) South-central SE Asia, v) Thai-Malay peninsula, vi) Sumatra, vii) Borneo (divided by dashed lines in Fig. 4; Table 1). Within these potential subpopulations, we identified ‘At Risk’ areas where sun bears face further barriers to movement due to habitat fragmentation, human influence and roads (red ovals in Fig. 4; Table 2).

Discussion

Sun bear range can be divided into seven broad potential subpopulations; two were created naturally by the oceanic barriers among Sumatra, Borneo and mainland Southeast Asia whereas five resulted from progressive human-made fragmentation. Visualizing the landscape as a mosaic gave us a dynamic view of the compositional quality of sun bear range in 2014, allowing us to evaluate how connectivity of range affects the movement of bears across the landscape as well as potential metapopulation dynamics. Approximately 50% of the area under any level of tree cover within global range was classified as good quality habitat (core and sub-optimal), almost entirely over-lapping sun bear range depicted by the IUCN (Scotson and Fredriksson, in process), and further extending into other contiguous areas. Much of this habitat, however, appeared to be in a highly-fragmented state, a mosaic of different habitat qualities, with large areas of poor quality (marginal) and non-habitat, heavy road networks (particularly in mainland Southeast Asia), and areas of high human influence. It is noteworthy that core sun bear range is poorly represented within the IUCN protected area network, which appears to contain primarily sub-optimal bear habitat, with almost 90% of core sun bear range falling outside protected areas.

With ongoing rapid deforestation and increasing human development and limited or no management to maintain forest cover in sun bear habitat, the integrity of core sun bear range is set to degrade further. Creation of up to five subpopulations in mainland Southeast Asia and Peninsular Malaysia is a consequence of human development, deforestation, agricultural expansion, and a heavy road network. By artificially restricting movement and creating demographic and genetic isolation, these relatively recent subpopulations challenge the continued existence of sun bears and other forest dependent species (Naeem et al. 2009, Sodhi et al. 2010). In some cases, maintaining core patches is more important for the overall persistence of subpopulations; in others, subpopulations are already isolated within relative small areas, and require human intervention to maintain genetic diversity and prevent local extirpation and perhaps even restoration of corridors to other patches. Smaller isolated patches are at risk from local extirpation unless humans intervene. For patches that remain functionally connected, allowing periodic extinctions and recolonizations, further erosion of habitat into marginal and non-habitat will degrade connectivity towards a non-equilibrium metapopulation, in which long term extinction rates exceed colonization rates (McCullough 1996). The future of the potential subpopulations and ‘at risk’ areas we have identified within sun bear range depends on societies’ motivations for conserving them.

Sun bears as a form of metapopulation

Historically, sun bear populations were unlikely to have functioned naturally as metapopulations. Metapopulations occur within spatially discrete patches, interspersed with non-habitat, among which movement (physical, genetic) must occur for patches to be recolonized following periodic extirpations (Hanski and Gilpin 1997, McCullough 1996). Mountain Sheep in California are an example of a natural metapopulation, with subpopulations concentrated in mountain habitat patches, and the persistence of metapopulations dependent on the continued ability of individuals to travel between or among populations (Bleich 1999). Historically, before commercial logging, the majority of sun bear range was under continuous tree cover. Rising sea levels that reinstated ocean barriers between Sumatra, Borneo and the mainland, created natural island metapopulations that presumably left viable populations with minimal risk of excessive mortality and habitat exclusion caused by humans (Craighead and Vyse 1996). In the past 30 years, however, rapid deforestation and hunting has reduced sun bear populations in the mainland by 14% (95% CI = 9 – 28) and in the insular region by 48% (95% CI = 29 – 61; Scotson et al. *in review*). Excess fragmentation across the islands of Sumatra and Borneo, and through the mainland continental range, is creating human-fragmented island metapopulations (Craighead and Vyse 1996). Metapopulations, broadly characterized by periodic extirpation and recolonizations within discrete patches of habitat, are reliant on the demographic and genetic movement (i.e. immigration and emigration of individuals) among patches (Hanski and Gilpin 1997, L.Fahrig 2001, Proctor et al. 2015). In a review of global brown bear metapopulations, Craighead and Vyse (1996) identified three metapopulation categories that can be applied to the sun bear range; continental metapopulations, natural fragmented island populations, and human fragmented island populations, some of which may end up being unsustainable non-equilibrium metapopulations (McCullough 1996). It is the latter category that we focus our recommendations on research management and priorities.

Research and management priorities

Currently and in the future, sun bear persistence in fragmented landscapes may require active management if the species is to function as a sustainable metapopulation. We identified 17 priority areas for sun bear research and management; some are entire potential subpopulations (delineated by dotted lines in Fig. 4), and other are areas between or within potential subpopulations (red ovals, in Fig. 4, Table 2). The consequences of habitat fragmentation depend on bear movement between source populations (i.e. larger healthy breeding populations) and between source populations and adjacent smaller fragmented or isolated subunits. The number of bears within a subpopulation determines its conservation status. Population estimates of bear are rare; eventually as researchers begin to collect these data the viability and conservation needs of subpopulations will become clearer.

In small fragmented habitat patches that remain functionally connected to large areas of core habitat, periodic extinction of bears within small patches is relatively negligible to the global population’s stability, as these fragments can be recolonized by movement from core patches (Harrison and Harrison 1991, Hanski and Gilpin 1997, Frankham 2005). If small patches, however, become degraded and isolated to a degree that recolonization is impossible, downward trends will lead to permanent local extirpation, and shrinkage in total range (McCullough 1996). Applying similar criteria as Craighead and Vyse (1996) used on brown bears for sun bears, the habitat suitability index allowed us to assess the sun bear landscape, and identify where each region fits into the continuum of habitat fragmentation. For example, mainland southeast Asia fits the definition of a continental metapopulation, with potential fractures in several areas. A potential fracture in northern Myanmar and central southeast Asia might be caused by a break in core habitat, replaced by patchy sub-optimal, marginal and non-habitat, and a heavy road network. The IUCN sun bear range map supports this existence of this fracture, classifying the area directly south of the northern population limit as unknown bear range (Scotson et al. 2017). Similar habitat transitions are evident in north-eastern Vietnam, southern Thailand, southern Peninsular-Malaysia, east and west Sumatra, and around coastal Borneo, where breaks in core habitat into patchy lower quality and non-habitat are causing further sub-division of global sun bear range. Monitoring known bear movements within these areas will determine whether there is gene flow between patches. Natural island subpopulations are evident in Sumatra and Borneo. Potential human fragmented island subpopulations exist in central Thailand, northern Cambodia and southern Vietnam, where relatively small patches of core habitat are almost entirely surrounded by non-habitat, with very little potential for movement between small patches and larger neighboring blocks. In southern Cambodia, a moderate sized subpopulation is encompassed by non-habitat and roads. Several much smaller, isolated patches are located in southern Myanmar (where it is unclear if bears remain), the southern tip of Sumatra, in Way Kambas National Park, which is currently occupied by sun bears (Scotson et al. 2017), and on a tiny island of the south-west coast of Borneo (if bears are present; Fig 4).

Conclusions

We present this analysis as way to steer research priorities, and to generate baseline information on sun bear range connectivity that can be improved upon once the appropriate ecological data become available. We hope our work will lead to studies of sun bear subpopulation dynamics and response to patchy environments (Hanski and Ovaskainen 2000). Potential research questions include how habitat patch configuration influences population viability, bear susceptibility to human disturbance, and dispersal characteristics related to the viability of metapopulation dynamics (van Oort et al. 2011), however to answer such questions would require intensive population monitoring. In the absence of dispersal data for sun bears, the modelled relationship between bear occurrence and percent tree cover allowed creation of a coarse, broad overview of the global sun bear landscape. Incorporating independent land cover maps into our ground truth process allowed us to test how reliable our habitat classifications were. Using maximum recorded daily movement as an indicator for how far a bear can move between patches through non-habitat had very little effect on reducing the extent of structural connectivity. Our binary, habitat/non-habitat, map is assumed to be overly optimistic, and weakness was in being unable to distinguish between marginal habitat that bears can transit through (i.e. secondary forest, shrub, crop fields, plantations), versus that which it cannot (i.e. large highways, urban areas). Given that sun bears have been detected in marginal habitats with very low tree cover, including plantations and crop fields, it was not possible to identify a definitive edge to habitat in most areas, leaving potential connectivity interpretable through the level of human influence and road network within an area. The ability to systematically identify edge will improve as data on known bear movements and advanced land cover GIS become available.

Table 1. Potential sub-populations of sun bear identified by visually inspecting the landscape mosaic of suitable habitat in 2014, and potential barriers to bear movement.

		Landscape metrics		Habitat composition		Barriers to movement (intra-pop/inter-pop)[2]			
Subpopulation	**Countries**	**Area (km^2)[1]**	**% Range**	**% Core**	**% Sub-optimal**	**Road density**	**Human Influence[3]**	**Marginal**	**Non-Habitat**
Northern Mainland	Bangladesh, NE India, northern Myanmar	364,599	18%	27%	73%	High / High	Low / High	Low / Low	Low / Low
Central Myanmar	Myanmar	680,032	<1%	40%	60%	High / High	Low / High	Low / Low	Low / High
Central SE Asia	south Myanmar, Lao PDR, Vietnam, Thailand, north Cambodia	14,425	33%	20%	80%	High / High	High / High	Low / Low	High / High
South-central SE Asia	south Cambodia, southwest Thailand	27,941	1.30%	28%	72%	Moderate / High	Low / High	Low / Low	Low / High
Thai-Malay Peninsula	south Thailand, Malay Peninsula	126,855	6%	43%	57%	Moderate / Moderate	Moderate / Moderate	Moderate / Low	Low / Low
Sumatra	Indonesia	265,302	13%	48%	52%	High / NA	Moderate / NA	Moderate / NA	Moderate / NA
Borneo	Malaysia, Indonesia, Brunei	598,032	29%	26%	74%	Low / NA	Low / NA	Moderate / NA	Moderate / NA

Footnotes

[1] Area of core and sub-optimal habitat

[2] Visually ranked by comparing the intensity of barriers to movement among sub-populations. Interpopulation areas surrounding Sumatra and Borneo is ocean and marked as NA.

[3] Visually ranks the intensity of areas above 32.7, which is the mean value of Human Influence within Non-habitat (32.7)

Table 2. Sun bear research priorities within areas perceived to be at the most risk from un-naturally fragmented habitat in Southeast Asia in 2014.

			Research Priorities				
ID	Location	Status	Confirm presence /absence	Population viability	Inter sub-population movement	Intra sub-population movement	Possible research Methods5
1	Northern mainland sub-population	Confirmed[1]			X	X	T, G, CT
2	Sub-population divide between the northern-mainland and Central SE Asia	Unknown[1]	X			X	SS, I, G, T, CT
3	Central Myanmar Sub-population	Unknown[1,2]	X	X			SS, I, G
4	Northeast Vietnam range limit	Unknown[1,3]	X	X	X		SS, I, G, T, CT
5	Eastern Thailand	Confirmed[1]		X	X		T, G, CT
6	Central Thailand	Confirmed[1]		X	X		T, G, CT
7	Southern Thailand - northern Cambodia	Confirmed[1]		X	X		T, G, CT
8	Sub-population divide between southern Thailand and Peninsular	Confirmed[1]				X	T, G, CT

	Malaysia						
9	Southern Vietnam	Mix of confirmed & unknown1	X	X		X	SS,I,G,T,CT
10	Peninsular-Malaysia (several)	Unknown[1,4]	X	X	X		T, G, CT
11	Eastern Sumatra	Confirmed[1]		X	X		T, G, CT
12	South-west Sumatra	Confirmed[1]		X	X		T, G, CT
13	Southern Sumatra	Confirmed[1]		X	X		T, G, CT
14	West Borneo	Confirmed[1]		X	X		T, G, CT
15	South-west Borneo	Confirmed[1]		X	X		T, G, CT
16	North-east Borneo	Confirmed[1]		X	X		T, G, CT
17	Laut Island, South-east Borneo	Unknown[1]	X	X	X		SS, I, G

Footnotes:

The ID number identifies the position of each area in Figure 4.

[1] IUCN Sun bear range map, in press
[2] Classified as definite in 2006 IUCN range map edition
[3] Rural interviews reported bear presence in 74% of interviews, but there is no distinction between Asiatic black bear and sun bear (Crudge et al. 2016)
[4] Maxent habitat suitability models predicted that the only highly suitable habitat in the south of Peninsular Malaysia occurs within Endau Rompin National Park (Nazeri et al. 2012). The IUCN 2016 range map marks several patches in this region as definite.
[5]T = radio telemetry, G = genetics, CT = camera traps, SS = Sign surveys, I = rural interviews

Figure 1. An example of a binary (A) and mosaic (B) habitat raster of Sabah, Borneo. The binary raster has values of 1 and 0; habitat and non-habitat, and represents the structural connectivity of the landscape. The mosaic raster has pixel values 0 (no habitat), 1 (marginal), 2 (sub-optimal) and 3 (core), and represents the varying habitat quality of the landscape. The outer line is the country border and the area beyond is the ocean.

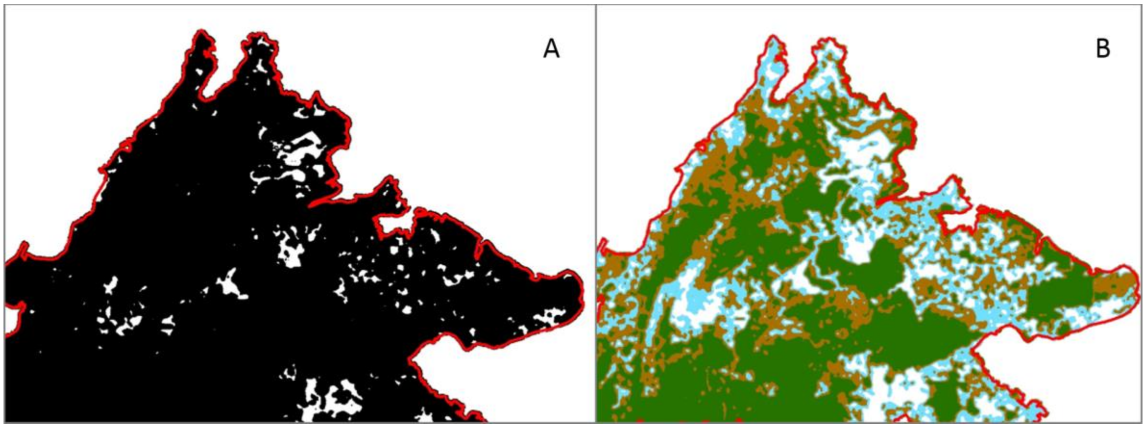


Figure 2. Density plots of Human Influence Index values within areas classified as Habitat and Non-habitat within sun bear range. Human Influence Index values (Sanderson et al. 2002) were calculated to 30,000 random points generated equally within areas of non-habitat and habitat. Human influence Index values were on average 13.8 points higher in areas classified as non-Habitat (*t* = -95.2, *df* = 29658, $p < 0.001$, x̄ within non-habitat = 36.7, SD = 13.1, x̄ within habitat = 23, SD = 11.8) supporting our assumption that habitat is different than non-habitat.

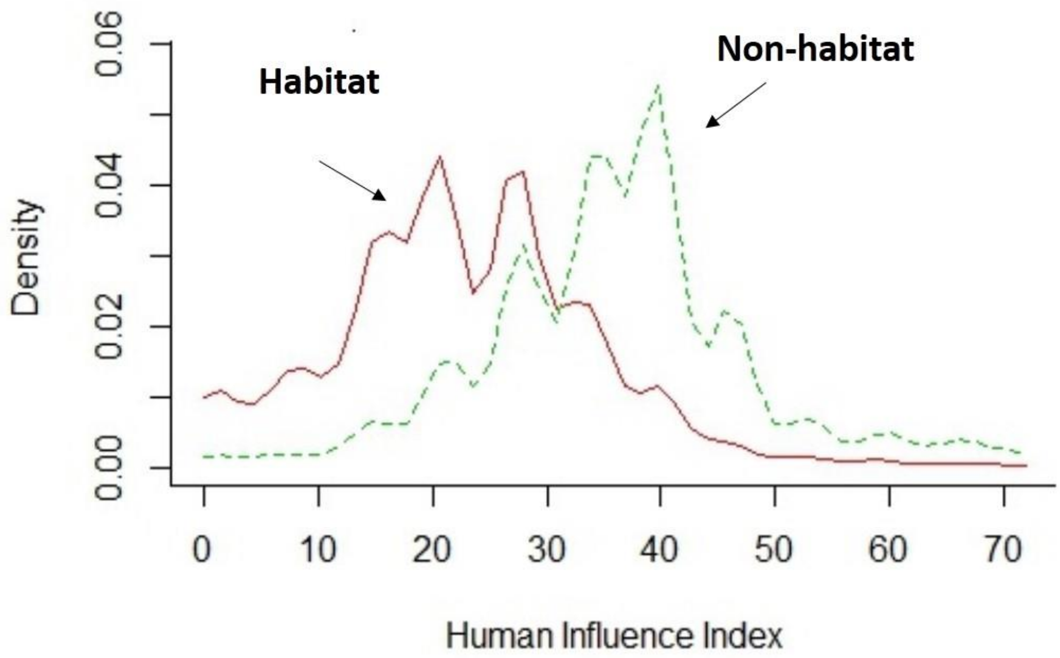


Figure 3. Frequency plots of land type values from the Terrestrial Ecosystem Environment Observation by Satellites (TREES; Stigbig & Beuchle 2003). TREES land type values were calculated to 20,000 random points generated equally between Non-habitat, Marginal, Sub-optimal and Core habitat. We reclassified land type into 12 categories; 1-8 are categories in which bear use has been previously detected (1-3 = evergreen, 4 = deciduous, woodland, 5 = mangrove, 6 = swamp, woodland, 7-8 = Mosaic of woodland, secondary, evergreen and cropland), and 9-12 are considered non-habitat (9 = Cropland, shrub, 10 = cropland, bare land, 11 = rock, limestone, 12 = water). TREES land classification values within Non-habitat were more often classified as areas considered as non-viable bear habitat (i.e. cropland, shrub, bare land, rock). Second to Non-habitat, Marginal habitat had the highest proportion of points within non-viable bear habitat categories. In Sub-optimal and Core habitat, land classification tended to be areas of potential bear habitat (i.e. evergreen, deciduous forest, and other forms of mosaic forest).

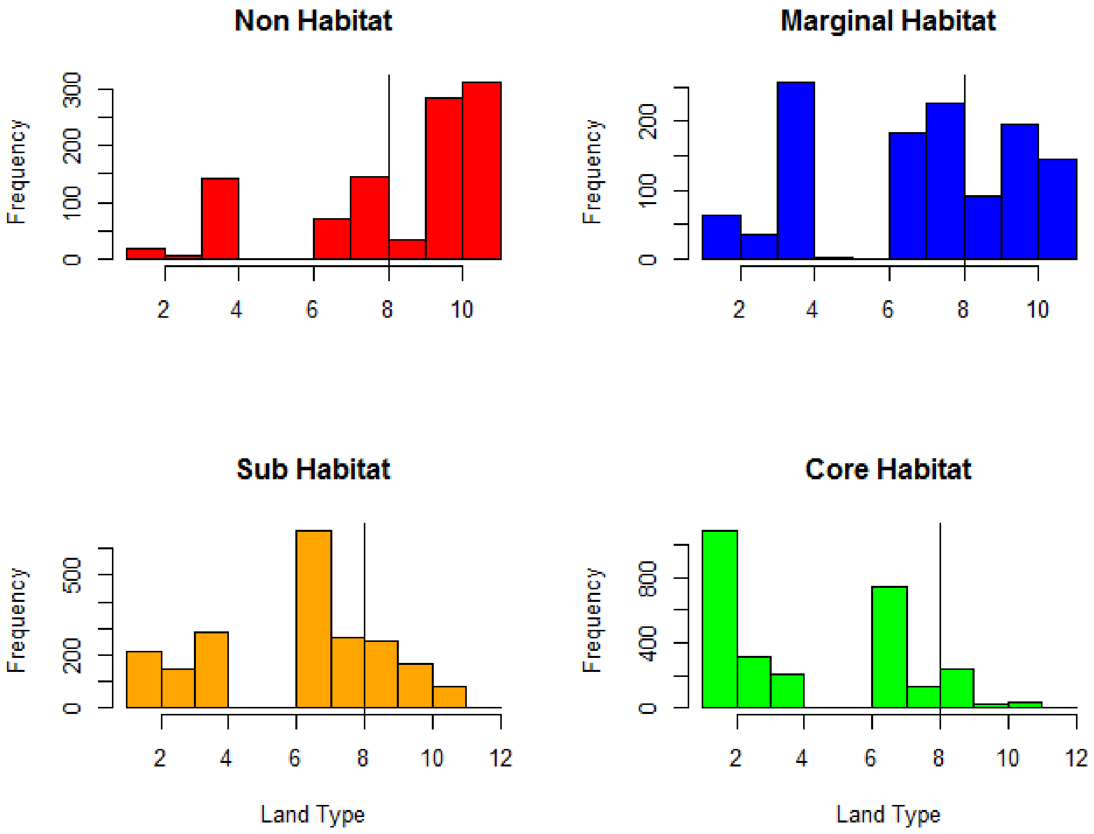
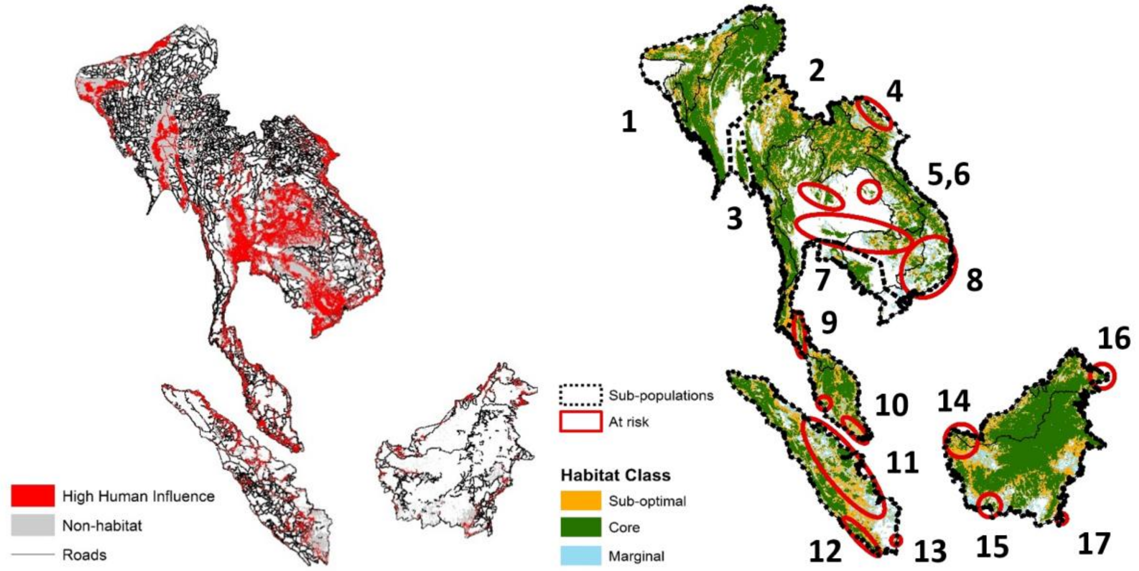


Figure 4. Sun bear landscape fragmentation and connectivity in Southeast Asia. Left: High human influence and road network are assumed to be significant barriers to bear movement (i.e. fragmentation) across the landscape. Right: Core and sub-optimal contiguous range is assumed to positively impact bear movement (i.e. connectivity), although dependent on associated levels of human influence and roads. We visually identified 7 subpopulations of sun bears; i) northern Mainland, ii) Central Myanmar, iii) Central SE Asia, iv) South-central SE Asia, v) Thai-Malay peninsula, vi) Sumatra, vii) Borneo (divided by dashed lines). Within these subpopulations, we identified 'At Risk' areas where sun bears face further barriers to movement due to habitat fragmentation, human influence and roads (identified by solid line ovals).



Chapter 4

Best practices and software for the management and sharing of camera trap data for small and large scales studies

Synopsis

Camera traps typically generate large amounts of bycatch data of non-target species that are secondary to the study's objectives. Bycatch data pooled from multiple studies can answer secondary research questions; however, variation in field and data management techniques creates problems when pooling data from multiple sources. Multi-collaborator projects that use standardized methods to answer broad-scale research questions are rare and limited in geographical scope. Many small, fixed-term independent camera trap studies operate in poorly represented regions, often using field and data management methods tailored to their own objectives. Inconsistent data management practices lead to loss of bycatch data, or an inability to share it easily. As a case study to illustrate common problems that limit use of bycatch data, we discuss our experiences processing bycatch data obtained by multiple research groups during a range-wide assessment of sun bears *Helarctos malayanus* in Southeast Asia. We found that the most significant barrier to using bycatch data for secondary research was the time required, by the owners of the data and by the secondary researchers (us), to retrieve, interpret and process data into a form suitable for secondary analyses. Furthermore, large quantities of data were lost due to incompleteness and ambiguities in data entry. From our experiences, and from a review of the published literature and online resources, we generated nine recommendations on data management best practices for field site metadata, camera trap deployment metadata, image classification data, and derived data products. We cover simple techniques that can be employed without training, special software and internet access, to options for more advanced users, including a review of data management software and platforms. From the range of solutions provided here, researchers can employ those that best suit their needs and

capacity. Doing so will enhance the usefulness of their camera trap bycatch data by improving the ease of data sharing, enabling collaborations, and expanding the scope of research.

Introduction

Use of camera traps to obtain self-triggered photographs of wildlife for ecological research is widespread, with a 10% annual growth in scientific publications since the early 1990s (Mccallum 2013, Burton et al. 2015). Camera traps typically collect data on a diverse array of terrestrial animals, with a wide range of study objectives (Cutler and Don 1999, Thorn et al. 2009, Rowcliffe et al. 2014). Camera traps are widely used for small fixed-term surveys in areas of conservation significance to collect baseline data, often with loose or undefined objectives. Parallel to the increase in camera trap studies, the volume of 'bycatch' data (i.e. images collected incidentally, and unrelated to the study's objectives) has increased steadily. When combined over multiple sites, bycatch data can reveal landscape scale macro-ecological patterns across space and time, and can aid in the research of understudied threatened species (Heffernan et al. 2014, McShea et al. 2016).

There is a data gap in global monitoring programs, with fewest data available for areas highest in biodiversity (Collen et al. 2008). Managing species threatened with extinction requires research into species occurrence, population trends, and on population responses to changes in the environment, particularly those caused by humans (Balmford et al. 2003, Maxwell et al. 2016). These research topics cannot be addressed by data collected from a single study site, and require combining data from multiple sites across large areas. Such datasets, from small fixed-term studies, are extensive in the tropics and provide considerable, often under utilised, information (e.g. Gray et al. 2012). In the absence of primary data, bycatch data could be key to monitoring progress towards the targets of the Convention on Biological Diversity (CBD, (Balmford 2005, Dobson and Nowak 2010, O'Brien 2010). Likewise, bycatch data can inform assessments of mammals considered as threatened with extinction, or data deficient, by the World Conservation Union (IUCN) Red List of Threatened Species, many of which are outside the scope of primary research (Schipper et al. 2008).

To increase use of bycatch data, many challenges need to be overcome. For example, varied study objectives, field methods, and data management standards (including data sharing policies and restrictions) of research groups create logistical and statistical challenges in pooling bycatch data over multiple sites (Olsen et al. 1999, Sanderson and Trolle 2005). Large volumes of data can accumulate quickly, and data managers may lack motivation to record and classify all images, due to limited time, funding, staff and other resources. Project resources (e.g. time, money, personnel) are often used for fund raising, training, field work, reporting and administration, with limited resources allocated to tasks that are perceived as less urgent, such as data management. Furthermore, researchers may under-estimate the expense and time required for effective data management. Bycatch images have been likened to the fisheries bycatch; data are either left unclassified, or are filed away and never used or made publicly available (O'Brien 2010). Identification errors are also widespread within such datasets. Limitations are strongest in small studies working within low-income regions, which have fixed budgets and short time frames (e.g. Non-Government Organizations [NGO's], graduate student projects).

Camera trap studies that are ongoing (i.e. not fixed term) accumulate massive amounts of data over time. Such studies optimize their efficacy by using standardized sampling designs and data management protocols. The Tropical Ecology Assessment and Monitoring Network (TEAM), for example, operates in 17 sites globally, in Africa, Asia and Latin America. Their use of standard methods on a global scale allows combining and analysing data over multiple sites, and enables monitoring of global patterns in ecosystems and biodiversity (www.teamnetwork.org). Another ongoing study is The Serengeti Lion project, which maintains a fixed grid of 225 camera traps in the Serengeti National Park, Tanzania, with a strict protocol used to determine camera placement and data processing. These camera traps are used to monitor temporal trends and patterns in wildlife communities within the National Park. The camera traps operate continuously, accumulating massive numbers of primary and bycatch images. The Serengeti Lion project operates an innovative crowdsourced citizen science online platform, Snapshot Serengeti, to quickly classify their ever-growing catalogue of images (www.snapshotserengeti.org ; Swanson et al. 2016).

Data management is an essential, yet often-neglected skill for wildlife ecologists. A survey of 48 American research institutions found that lack of time and teaching resources limited student training on management and preservation of data (Strasser and Hampton 2012). Researchers who are not part of an academic institution, and those from undeveloped regions, may not have access to technology, software, training and materials to facilitate good data management. Skilled data management, however, is critical for camera traps studies; poor data management systems, lack of standardization, and failure to use automated management tools, can result in the loss of significant amounts of data, especially bycatch data (Harris et al. 2010). There are multiple resources on data management online, in text books, and in the grey and published literature (e.g. Borer et al. 2009, Briney 2015, McGill 2016), with several peer-reviewed publications focused on the management of camera trap data (e.g. (Tobler et al. 2008, Harris et al. 2010, Fegraus et al. 2011, Sundaresan et al. 2011, Sunarto et al. 2013, Meek and Fleming 2014, Burton et al. 2015, Niedballa et al. 2016). We attempted to develop a succinct set of recommendations and to review related resources on data management best practices, ranging from very simple techniques that can be employed with minimal resources (e.g. without need for training, special software and internet access), to options for more advanced users, including a review of data management software and platforms. By publishing in an open access journal, our guidelines will reach researchers without institutional journal access.

We begin with a case study that reports our experiences assembling and processing bycatch camera trap data from multiple datasets in a study measuring global population trends of sun bears. We use these experiences to identify common data management malpractices that create difficulties in using bycatch data for secondary research. Subsequently, we make recommendations on data management best practices that are focused on enhancing the quality and efficiency of data management, highlighting critical information to include within data, and improving the ease of data sharing and preservation, and we identify relevant resources available to help researchers follow our recommendations. We review currently available camera trap management software and platforms for those with more advanced needs, including Wild.ID, Camera Base, CPW Photo Warehouse, eMammal, Aardwolf, CamtrapR, and TRAPPER. Finally, we discuss the value of good data management practices for enabling sharing and secondary research.

Combining camera trap data from multiple sources: a case study

In our case study, like typical data sharing mechanisms reported in the literature (e.g. Kratz and Strasser 2015), we obtained data from external studies via email requests. We combined data from twelve research groups working in 49 field sites. The primary objectives of these studies, which were conducted by NGO's and graduate students (i.e. Dinata 2008, Clements 2013), included species inventories (Mohd-Azlan and Engkamat 2013), occupancy modelling (Wong and Linkie 2013), understanding habitat use and activity patterns (Gray and Phan 2011, Gray et al. 2012), primate terrestrial behaviour (Loken et al. 2013) and investigating response to altered habitats (Wong et al. 2013*b*, Spehar et al. 2015). The data consisted of 43 sets of data in several formats (collectively referred to here as datasets), including raw camera trap images, pdf tables, GIS shapefiles, and (in most cases) single and multi-tab Excel spreadsheets. Data contributors commonly expressed difficulties in locating and preparing our requests, and communications usually spanned several months. The time it took to process the data was the most significant problem we encountered (Table 1). Manipulating the data into our desired format (i.e. one standardized dataset) often required substantial manual editing and many follow-up questions and requests to contributors. Each dataset took between 2 – 8 hours to process. Many data points (i.e. sun bear records) and three entire datasets were discarded due to one or more ambiguities (see Fig 1 for an exaggerated example of a ‘problem’ dataset). Missing or ambiguous latitude and longitude data was the most persistent issue leading to loss of data; this problem was encountered in all but one dataset (Table 1). Data were also lost due to missing or ambiguous dates, gaps in trapping effort records, and other unclear entries (e.g. Fig. 1). Of 43 datasets, three were unusable (representing data collected from > 400 camera traps), and portions of data were lost from 80% of other datasets (Fig. 2).

Contributors to our case study were asked to complete a brief web-based survey of the data management protocols used by their group. Respondents (n=8) expressed that they were mostly satisfied by their data collection methods, but cited problems associated with lack of standard data management protocols and a high turnover in staff responsible for data management. In handling metadata, no group used an industry standard method (e.g. Ecological Metadata Language); 75% of respondents created a custom organizational structure, and 25% used a standard developed exclusively for their organization. Data entry and management was the responsibility of a combination of field technicians (88%), administrative staff (25%) and research coordinators (75%). In 50% of cases, data quality was maintained by a process of re-checking by multiple people. In 25% of cases, research groups followed a standard protocol for data entry intended to minimize risk of human error. In 25% of cases, maintaining data entry quality was the responsibility of one person. No respondents reported using automated camera trap data entry software. A repeated sentiment in the survey responses was that data management practices could be improved by increased standardization, and by access to online platforms, which allow storage and sharing of data. Main obstacles to data management were a lack of capacity, high turnover of expatriate and local staff, and a failure to use pre-developed standardized protocols. Specific ideas expressed by data contributors in our case study are incorporated into our list of recommendations below.

Recommendations for managing camera trap data

We generated nine key recommendations related to data management practices of the four main data types collected by camera trap studies; field site metadata (e.g. forest type, season, weather conditions), camera trap deployment metadata (e.g. date, time, location, camera trap settings, position, trap nights), image classification data (e.g. species identification, behaviour, number of animals), and derived data products (e.g. species occurrence, count of detections/non detections per unit/per site, detection rates relative to sampling effort). We incorporated recommended best practices from the scientific literature, field manuals, online forums and blogs, and have embedded links to some of these resources within our recommendations.

1. Adopt a standardized, non-proprietary and transferrable data storage format to store all camera trap data.

In our case study, most of the data contributors used Microsoft Excel to store data. Without requiring significant training in relational database design, this tool is preferred by many researchers (Herold 2015). A major drawback, however, is that Excel is a proprietary, non-transferable format, notoriously unreliable as this tool can invisibly interpret and change entered data (e.g. drop leading "0's and change character strings to Julian dates). Propriety software, such as Excel and Microsoft Access, may be superseded in the future by incompatible formats, so data stored in these formats could become unusable in the same way that external hard drives, CD-ROMs and DVDs may one day become outdated and unusable, like the floppy disk. If using Excel, Borer et al (2009) recommend storing all data in non-proprietary software formats, such as comma separated value (.csv) files, which can be viewed and manipulated in Excel. There are several advantages to storing data in open source non-proprietary relational database systems such as PostgreSQL or SGLite, or ecology specific tools such as ECOLOG (www.ecolog.sourceforge.net/index_e.htm). These formats are available without license fees, are not controlled by developers (e.g. Microsoft), and have wide online communities of users which collectively serve as a crowdsourced online help forum. These formats work across many different operating platforms, are operated with Structured Query Language (SQL), a standard language for relational database management systems, and store data in a format that is transferable to a new system or software.

2. Accompany all spreadsheets with structured metadata.

Good management of field and camera trap deployment metadata, regardless of image classification, is crucial for long-term preservation and sharing of data. In our case study, only two research groups included metadata within their datasheets; lack of metadata reduced the interpretability of the datasheets and increased the length of time it took to process the data. Metadata, which give descriptive information about the content, context and structure of data, should accompany all raw data. When possible, use a standard metadata format, such as the Ecological Metadata Language (EML), a metadata standard, developed by the ecology discipline for the ecology discipline. EML is a pre-designed method that can facilitate efficient data sharing. EML works so that the data created in, for example, the software Morpho, a free program for storing, cataloguing, querying and editing metadata, can be easily ingested into other platforms that are programmed to anticipate the EML data structure (https://knb.ecoinformatics.org/#tools/morpho). Forrester et al. (2016) describe a metadata standard specific to camera trap data, which is compatible with EML and other industry standards. At a minimum, researchers should create and provide a 'ReadMe' file that describes why the data were collected, including objectives, methodology, database metadata, definitions of all co-variates, codes and acronyms, point of contact, ownership, rules of use and instructions for acknowledgement. A freely available template, developed by the University of Minnesota Libraries, can be found here: https://z.umn.edu/readme. For detailed descriptions of desirable metadata refer to Michener and Jones (2012), Sunarto et al. (2013), Meek and Fleming (2014), and Meek et al. (2014). Much of the metadata associated with camera-trap data (e.g., date and time) can be gleaned directly from the image metadata tags if users process their data using camera trap data management software (e.g. eMammal, Wild.ID, Camera Base, Aardwolf; Table 2), but it is important to make sure that labels and formats for GPS coordinates and date and time stamps are consistent across cameras.

3. Record data at the highest possible resolution

Researchers should use a structure for raw data that minimizes entry errors and promotes error checking. All raw data and accompanying metadata should be recorded at the highest possible resolution, with other data products derived from these raw data ideally using well-documented computer code that facilitates transparency and reproducibility (Sandve et al. 2013). McGill (2016) suggests using an instance-row/variable-column format, in which each measurement has one row, and each column is a different variable or attribute. At minimum, researchers should record the start and end time and date each camera trap was active. This information will allow users to determine camera-specific measures of sampling effort (i.e. number of trap nights), which is preferable to an average measure of effort across all cameras on a site. Ideally, researchers should also provide unique times and dates of individual photos, allowing secondary users to implement their own criteria for what constitutes an independent detection event. Alternatively, it is important to define how data were filtered whenever it is not practical to record individual photographs (e.g. 500 photos of a pig-tailed macaque *Macaca sp*. group are recorded over a 60-minute period). TEAM provide a list of data quality control measures for camera trap data, which includes recommendations on sampling effort (i.e. number of units, trapping periods) and maintaining data quality (access here: www.teamnetwork.org/files/protocols/terrestrial-vertebrate/TEAM_Terrestrial_Vertebrates_Data_Quality_Standards.pdf).

4. Use a clearly documented and consistent geographic coordinate system.

Providing accurate and identifiable Global Positioning System (GPS) locations with your data is critical. In our case study, missing or ambiguous latitude and longitude data was the most persistent issue leading to loss of data – this problem was encountered in all but one dataset (Table 1). Camera trap deployment metadata should be relatable to an exact geographic location. The large number of geographical and projected coordinate systems available within Global Information Systems (GIS), (i.e. GPS units and mapping software) makes it critical to record the coordinate datum that points are collected in in the field (e.g. Indian Thailand Datum). Data collected without an accurate geographic location are of limited use, and may require significant time to process by secondary researchers. A single coordinate system (e.g. Geographic Coordinate WGS 1984) should be used consistently within each stage of collection, entry and processing of data. If changes to the coordinate system are required, they should be carefully documented. Store GPS coordinates in a format easily read and transformed by a GIS (i.e. numbers only; avoid placing letters or symbols within the same cell as geographic coordinates: doing so requires manual editing. See Fig. 1. for an example of this problem). Whatever system is used, also report locations in decimal degrees out to 5 decimal places, placing the location within 1-metre accuracy, and avoiding ambiguities with incomplete UTM coordinates and studies that straddle more than one UTM zone. Include information on map datums, UTM Zones and geographic coordinate systems within the field metadata. If possible, researchers should label and store each camera trap location in GPS units (keeping hand written locations as a backup), rather than record and transcribe GPS locations from datasheets. Camera trap management software, such as those reviewed below and in Table 2, can import labelled waypoint files from a GPS unit as text or shapefiles, allowing automated data handling and minimizing data entry errors.

5. Maintain a consistent date-time format.

In our case study, many data were lost due to missing or ambiguous dates. When dates are missing, trapping effort become ambiguous, or impossible to calculate manually. Researchers should include dates of camera operation (start date, end date), and date and time of individual pictures in the deployment metadata. Regional differences in date-time systems (e.g. UK versus USA) can lead to confusion in data entry and interpretation. Data managers should choose a date system, specify it clearly in the column heading and/or metadata and stick to it consistently within a dataset. An example of a well-defined date system is 2011-09-14 00:23:33 (YYYY-MM-DD hh:mm:ss). Camera trap management software, such as those reviewed below and in Table 2, can automate handing of time and date data and minimizing errors.

6. Record covariate data that might be used to assess detection probability.

An inability to account for differences in detection probability can lower the value of bycatch data. Therefore, researchers should record factors that influence detection probability (e.g. season, habitat type, height of vegetation and tree density) in the field metadata (Rowcliffe and Carbone 2008, Nichols 2010). Likewise, in the deployment metadata, include factors that influence species-specific detection probability (e.g. camera trap model, settings, position, date, and time of day). Variables that influence detection probability are useful to both primary and secondary researchers. However, given the multiple factors that can influence detection probability from camera-trap data, it is unlikely that researches using by-catch data, particularly from many small fixed-term studies, will be able to collect sufficient and consistent information for accurately modelling detection probability. Nevertheless, it is important to clearly state assumptions necessary for drawing valid conclusions from camera-trap data (e.g. constant detection probabilities), particularly when analysing data pooled across multiple studies.

7. Plan for the eventual identification of all bycatch data on non-target species and non-animals.

Image classification should ideally include all bycatch data as well as target species. This effort will allow researchers to later ask different questions of their data (e.g. plant phenology, weather patterns, animals’ behaviours) and increase opportunities for data sharing and collaborative efforts with other research groups. Classification of all images, however, can be unrealistic when vast quantities of data are collected. As cameras become more affordable, with greater memory capacities and battery life, data processing has become increasingly limited by human processing capacity. At a minimum, researchers can manage field and metadata, and upload images into an online storage system, such as Camera Base (www.atrium-biodiversity.org/tools/camerabase/) so that images can be classified later. Alternatively, engaging citizen scientists to catalogue images is an emerging technique that can significantly increase the amount of information researchers can extract from large datasets (Swanson et al. 2015). Snapshot Serengeti (University of Minnesota Lion Project) and Camera CATalogue (Panthera) are examples of citizen science platforms, both hosted by the Zooniverse (www.zooniverse.org). Readers seeking more efficient methods to process raw data are directed to guidelines included in Harris et al. (2010) and Niedballa et al. (2016), and a variety of platforms and software are reviewed below (Table 2).

8. Manage data as one authoritative set, which can be acted on by multiple users consistently and simultaneously.

Store a single, raw, unedited, and ‘read-only’ copy of image classification and derived data products in a central location with regulated access. Data replication and confusion can arise when re-editing and renaming multiple file versions (e.g. Raw_data_FINAL_FINAL_v3). Multiple downloads by different users can introduce errors or unclear versioning in the data being analysed. Create new copies of edited raw data, with a record of who made edits and why. Free web-based tools like Open Science Framework (http://osf.io/) and GitHub (https://github.com/) capture and record changes to files, and log and facilitate version control.

9. Archive data, and make it available to other researchers with defined conditions for reuse.

This final step allows well-managed data to be discovered and reused by other researchers. Consider sharing data on a project page, with clear terms and conditions for use. The TEAM Network does this (e.g. www.teamnetwork.org/data/use), and they developed software, Wild.ID, that facilitates data management and long-term storage (www.teamnetwork.org/solution) in the Wildlife Insight web warehouse. Researchers can register on Wildlife Insights (previously The Camera Trap Federation) for open access, citation and preservation of data (www.wildlifeinsights.org/WMS/#/shareData). Alternatively, eMammal provides a paid online platform for project pages (www.emammal.si.edu/participate/science-and-management) with an option for long-term storage on the Smithsonian Data Repository. A researcher's local institutional repository may provide free services for publicly archiving data, including minting Digital Object Identifiers (DOI's), for better citation of the data collection, and preservation of data after the project is complete (e.g. Harvard University's DataVerse or the Data Repository for the University of Minnesota, DRUM). Readers are directed to Whitlock (2011), who outline a set of data archiving best practices.

Camera trap data management platforms

Our recommendations highlight the steps researchers can take to improve data quality when using non-standardized, custom designed data handling methods. We encourage where possible, however, the use of data management software and/or web-based platforms that are designed specifically for camera trap data management. Use of these programs can reduce data entry errors and data loss, increase efficiency in data management, and improve ease of data re-use and sharing. The applications we reviewed include Wild.ID, Camera Base, CPW Photo Warehouse, eMammal, Aardwolf, CamtrapR, TRAPPER, and Agouti. These systems range from stand-alone desktop applications, to extensions of Microsoft Access and R (R Core Team 2016) and web-based platforms. We found a wide range of overlapping general features, summarized in Table 2, and some unique features, described below, all of which users can consider when selecting the system most appropriate for their research needs.

Wild.ID, developed by the TEAM network, is a desktop application designed for protected area managers and wildlife professionals. Described as an 'easy interface' information management platform, Wild.ID can export data to be shared with other Wild.ID users. Users can store data in the Wildlife Insights data repository, a long-term cloud-based storage system with additional analytic capability (e.g. Wildlife Picture

Index; www.wildlifeinsights.org). There is a plug in for TEAM Network members (Wild.ID.TEAMPlugin), and multi-language options including English, Chinese, Spanish, and Portuguese.

Camera Base and CPW Photo Warehouse are free desktop extensions of Microsoft Access. Both are limited to handling tens of thousands of images and therefore are suitable for small projects. Unique features of Camera Base include the ability to calculate Mean Maximum Distance Moved (MMDM), and to automatically classify photos as taken during the day, night, dusk or dawn, based on sunrise and sunset calculated for the survey location for each specific date. Camera Base has an interface for direct comparison of images from paired cameras (Tobler 2007). Unique features of CPW Photo Warehouse include; a capacity for multi-observer species identification and user-customized functions via Access query modifications or via VBA and SQL code modifications for advanced user (Ivan and Newkirk 2016).

Aardwolf desktop application and camtrapR R package are both free, open source, extendable, multi-platform systems suitable for projects with large volumes of data (> 1 million images). Both systems can handle the complete workflow associated with processing camera trap data, from image organization and annotation, identification of species and individuals, image data extraction, tabulation and visualization of results, and export for other analyses. Aardwolf is designed for small research teams and independent researcher's, boasting minimalistic data management, built for use on personal computers, and works with SQlite, MySQL and PostgreSQL (Krishnappa and Turner 2014). Aardworlf includes an option to store added metadata (species, etc) as .XMP files. CamtrapR R package was designed for flexible and efficient management of camera trap data, with a streamlined, reproducible process, including multiple analysis options and the possibility to export data to GIS software (Niedballa et al. 2016). Species and individual identification is performed outside the package, via custom metadata tags assigned in image management software or by moving images into species directories.

TRAPPER and Agouti are a web-based platform for managing, classifying, sharing and re-use of camera trap data, designed for researchers working alone or within collaborators. TRAPPER handles videos and still images, and features spatial filtering and web-mapping. TRAPPER is open source, allowing flexible data collection protocols, and multiple role-based users to facilitate collaborative projects (Bubnicki et al. 2016). TRAPPER has an Application Programming Interface (API), allowing direct access to raw and classified data from a range of software (e.g. QGIS, R, PYTHON, KEPLER or VISTRAILS). TRAPPER allows export of metadata in EML standard. Advanced users can customize functionalities via Python language; Python scripts for some functionalities (e.g., video conversion) are already provided with the software. Agouti, at the time of writing, was available, by request, to scientists and non-profit organizations, with plans to make it publicly available in the near future (Y. Liefting, Personal Communication, May 2017). Agouti is aimed at structured projects, with projects set up according to user needs on a per-project basis. Project assess will be handled per user by a project administration manager, a single user can manage multiple projects, and projects accommodate different user roles within projects (e.g. volunteer, professional). There will be a fee for hosting and support costs, although use for academic reasons (e.g. MSc thesis) is typically free of charge. Agouti supports both photo (most camera trap models and regular cameras) and video (currently .avi, .mov, and .mp4). Agouti will include an online data storage solution and follows a metadata protocol compatible with the Smithsonian eMammal and Wildlife Insight repositories.

eMammal is designed for landscape scale projects that use citizen science volunteers to set cameras and collect and upload data. eMammal includes four main components: i) Leopold, a desktop application for viewing, tagging and uploading camera trap photos, ii) an expert review tool, iii) a curated data repository for archiving approved data, and iv) a web-based platform for managing studies and accessing and analyzing data (McShea et al. 2016). Images are stored for free in the Smithsonian Data Repository, and are publicly available, with options for 1-3-year embargo, or a permanent embargo on data of species of concern and threatened species. Users can tag their favorite pictures and share them on their website and via social media. The desktop app, Leopold, facilitates citizen scientist and multiple researcher participation in species-ID, with a mandatory expert review/quality control process for species-ID through the web-based Expert Review Tool (ERT). Users can decide whether to open the project to the public and take advantage of the citizen scientist option, or to split the images to be identified among a set of researchers. There is a one-time set up cost for creation of a custom-made home page and project structure, based on information supplied by project managers. There is a per-deployment upload cost, to keep the images in a cloud service during the citizen scientist and expert review process for species identification. The monthly cost is calculated per month of camera activation, and ranges from $3.87 - $4.19, depending on number of camera-months (the more you have, the less you pay for each unit; www.emammal.si.edu/about/FAQ).

For large-scale long-term projects that produce millions of images each year an option is to utilize the recently developed resources provide by the Zooniverse web-platform (www.zooniverse.org). Besides online photo storage, Zooniverse offers researchers the chance to increase public visibility of projects and to take advantage of citizen science. Two of the earliest and widely known camera trap-based Zooniverse projects are Snapshot Serengeti (Serengeti Lion Project; Swanson et al. 2015) and Camera CATalogue. Camera CATalouge currently engages more than 8,000 volunteers, processing approximately 20,000 images per day. Volunteers are presented with an image and asked to tag the species present, using a predefined list of existing species in the area, and to record the number of individuals, and what side of the animal is visible. Volunteers can confirm the species by comparing it with a preexisting photograph and species description. Algorithms identify uncertain images that require expert review by selecting those that do not reach a consensus during citizen scientist classification. Accuracy ratings calculated for Camera CATalogue and Snapshot Serengeti are 96% and 97.9% respectively (Swanson et al. 2016; R. Pitman pers. comm). These platforms produce outputs that can be paired with R packages such as CamtrapR to create a holistic camera trap data management and analytical tool.

The value of sharing data

This paper seeks to convince readers of the benefits of creating a data management plan, maximizing the quality and usability of secondary data, sharing data, and preserving it for the long term. Likewise, we hope that our set of recommendations and resources therein make this considerable task more achievable to researchers at all levels of skill and capacity. Data sharing within the scientific community is widely encouraged (Hampton et al. 2013); according to the Committee on Responsibilities of Authorship in the Biological Sciences, scientists are obligated to make their data available to others in a format that other scientists can use in future research (Corrado 2014). Some suggest making data sharing a mandatory condition of funders and publishers, and to increase the value of sharing by making datasets publishable and citable (Balmford 2005, Reichman 2011, Whitlock 2011, Goring et al. 2014). Indeed, many journals now require that data are publicly available, including PlosOne, Scientific Reports and all British ecology journals. Some opponents to data sharing are cautious of sharing sensitive data on threatened species, when illegal hunting is a primary threat. Engaging the public in “citizen science” has great potential to raise interest in conservation, while expanding the scope and scale of research (Swanson et al. 2015).

Data are the currency of research and are payoff for all effort invested in planning, fundraising and undertaking research activities. Collection of bycatch data represents a significant portion of that time and effort. Sharing and combining data over multiple sites harnesses the power of bycatch data, broadens the scope of research, creates multi-collaborator studies, and leads to valuable scientific publications. The TEAM network, for example, has published several multi-collaborator research papers on community structure and population trends of threatened tropical species (Ahumada et al. 2011, Jansen and al et 2014, Beaudrot et al. 2016). Likewise, The Serengeti Lion Project has studied the distribution and community interactions of over 30 species across the Serengeti landscape (Swanson et al. 2015), and their bycatch data have led to multiple collaborations (A. Swanson, pers.comm 2017). Bycatch data pooled across multiple smaller studies have led to publications on regional and range-wide studies of many threatened mammals in Southeast Asia, including Asian tapir *Tapirus indicus,* gaur *Bos gaurus*, sambar *Rusa unicolor*, red muntjac *Muntiacus muntjak*, wild pig *Sus scrofa* (Lynam et al. 2012), small carnivores in Thailand (Chutipong et al. 2014)and almost all the carnivore species occurring on the island of Borneo (Mathai et al. 2016). Bycatch data for the Asian tapir, collected mainly on tiger *Panthera tigris* surveys, led to an extension of the known tapir range in Southeast Asia (Linkie et al. 2013). Collaborations can allow researchers to estimate population densities of hard-to-detect species, such as clouded leopards *Neofelis nebulosa*; data from one site are often of limited use, but it is possible to analyse detections across multiple sites using techniques such as Spatially Explicit Capture Recapture (e.g. Gardner et al. 2010). Open and efficient sharing of camera trap bycatch data has the potential to create endless research opportunities, improving ecological understanding of poorly-studied species, from accessing basic information on species distribution and abundance, to allowing the development of complex hypotheses related to habitat preferences, lifecycles, behaviour and response to human disturbance and management interventions.

Table 1. Data problems frequently encountered whilst processing 43 datasheets submitted by 12 different research groups.

Data Problem	Examples encountered	Consequence
Datasheet structure in format difficult to manipulate (n=9)	Merged and double header rows do not allow easy sorting. Databases with camera trap location and operation information on a separate worksheet than detection data, with no obvious link	Reformatting data for secondary use is time intensive.
Locational information ambiguous, inconsistent or incomplete (n=12)	Geographic coordinates missing. Lack of accompanying information on map datum or UTM zones. Order of X and Y coordinates muddled within a datasheet. Coordinates recorded in a format that cannot be read by GIS software. Coordinates recorded in format that cannot be automatically transformed to another system.	Transforming and projecting points can be time intensive. Data with no location information are usually meaningless.
Date information ambiguous, inconsistent or incomplete (n=7)	Dates missing or incomplete (e.g. start date but no end date); date format not specified (e.g. UK or USA); date format used interchangeably within a datasheet.	Data with no date information are usually meaningless.
Number of trap nights averaged across units, unclear or missing (n=6)	Manual calculation of trap nights often problematic due to ambiguous date information (see above). Trapping effort sometimes not available for individual units, and instead averaged over all cameras.	Data without trapping effort are usually meaningless. Using average number of trap nights reduces data resolution.
Ambiguous/unintelligible cell entry and formatting (n=4)	Ambiguous use of comments and colour coding cells and rows suggests some problem with data	Discard affected data or costly follow up communication required.
Missing or incomplete metadata (n=6*)	No definitions given for co-variates (i.e. land use type, forest cover). No metadata provided.	Undefined covariates are meaningless to secondary researchers.

Table 2 – Part 1. A comparison of camera trap data management software in April 2017. The current features of each system were evaluated manually, and by review of user manuals and published literature.

	Wild.ID	**Camera Base**	**CPW Photo Warehouse**	**eMammal**
General features				
Platform	Desktop	Desktop	Desktop	Desktop plus web-warehouse
Cost (US$)	Free	Free (GNU General Public License)	Free (CPW Reciprocal Open Source License Agreement)	Project setup cost of $150, and a monthly per-camera cost of between $3.87 - $4.19 for image upload and species id
Data Capacity	100,000's	~2,000,000[1]	~800,000 (double observer) or ~2,000,000[1] (single observer); expandable using SQL Server	Unlimited
Operating System	Windows, MacOS	Windows	Windows, MacOS[2], Linux[2]	-
Software requirements	Java (free version available)	Microsoft Access 2010 (tested with MS Office XP 2002, 2003, 2007 and 2010; known issues with Office 2013), or free Microsoft Access 2010 Runtime. Windows Media Player, or VLC Player for videos.	Microsoft Access, or free Microsoft Access Runtime (2007 or newer).	-
Internet access required	No[3] (online registration required)	No[3]	No[3]	Yes (image upload/download)/ No[3] (species ID; processed images unloadable later)
Skill requirements	Low	Medium (requires familiarity with MS Access)	Low/High[4]	Low

	Wild.ID	**Camera Base**	**CPW Photo Warehouse**	**eMammal**
Functionality				
Automatic metadata import	EXIF and camera custom tags	EXIF	EXIF	EXIF
Customize event intervals	Yes	Yes	Yes	No (1-min sequence)
Identification at individual level[7]	No	Yes	Yes	No
Classification by multiple observers	Yes	Yes	Yes	Yes
Visualize/filter images by tag or species	Yes	Yes	Yes	Yes
Verify Taxonomic name	Yes	No	No	Yes
Video	No	Yes	No	No
Output				
Comma separated values (.csv)	Yes	Yes	Yes	Yes
Summaries[6]	No	Yes	Yes	Yes, as online resources
Data export for occupancy model analysis	No	Yes, MARK, PRESENCE	Yes, MARK, PRESENCE	No
Data export for capture-recapture analysis	No	Yes, CAPTURE, MARK, DENSITY, EstimateS	Yes, MARK, DENSITY,‘secr’ R package	No

	Wild.ID	**Camera Base**	**CPW Photo Warehouse**	**eMammal**
Support and/or data export for activity patterns analysis	No	Yes	Yes, 'overlap' R package	Yes, as online resources
Mapping	No	Yes, exporting to GIS	Yes, spatial queries to view data in Google Earth or ArcMap	Yes, as online resources
Photo Reports	No	Yes, suggested 30-50 images per report	No	No
Documentation	http://wildid.teamnetwork.org/help.jsp	Tobler 2007 http://www.atrium-biodiversity.org/tools/camerabase/files/CameraBaseDoc1.7.pdf	Ivan and Newkirk 2016 http://cpw.state.co.us/Documents/Research/Mammals/Software/CPW-Photo-Warehouse-4.0-User-Guide.pdf	McShea et al 2015 https://emammal.si.edu/participate/science-and-management

Footnotes:

[1] Limited by Microsoft Access (Ivan and Newkirk 2016)

[2] By installing Windows in a virtual machine environment

[3] After downloading the installer software or package

[4] Medium (through Access) and high (VBA and SQL code modifications) for advanced user

[5] Low for basic use; high (python and/or R) for advanced use. Good IT knowledge to be installed (including server configuration) and maintained (e.g. updating the source code)

[6] Includes everything between simple counts of trap-nights per camera, to detection rates, to species-specific detection counts

[7] Recording of individuals uniquely identifiable by natural or artificial marks

[8] Based on the information available at the time of writing (May 2017)

Table 2 – Part 2. A comparison of camera trap data management software in April 2017. The current features of each system were evaluated manually, and by review of user manuals and published literature.

	Aardwolf	**camtrapR**	**TRAPPER**	**Agouti**[8]
General features				
Platform	Desktop (web browser: Google Chrome suggested)	R software (R Core Team, 2016)	Web-warehouse	Web-warehouse
Cost (US$)	Free (GNU General Public License 3.0)	Free	Free (GNU General Public License 2.0)	Operating costs shared by users
Data Capacity	Unlimited (limited by user's computer memory)	Unlimited	Unlimited	Unlimited
Operating System	Windows, Ubuntu, Mac OS, Linux	Windows, MacOS, Linux	Windows, Ubuntu	-
Software requirements	Freely available: - Node.js, - SQLite; - ImageMagick; - GraphicsMagick; - Exiftool	Freely available: - R; - ExifTool	-	-
Internet access required	No[3]	No[3]	Yes	Yes (possible to run locally, and local system acts as 'server')
Skill requirements	Low	Medium (requires familiarity with R)	Low/High[5]	Low

	Aardwolf	**camtrapR**	**TRAPPER**	**Agouti**[8]
Functionality				
Automatic metadata import	EXIF	EXIF and user-customized tags	EXIF	EXIF
Customize event intervals	No	Yes	Yes	Yes
Identification at individual level[7]	Yes	Yes	Yes	Yes
Classification by multiple observers	Yes	Yes	Yes	Yes
Visualize/filter images by tag or species	Yes	Yes	Yes	Yes
Verify Taxonomic name	No	Yes	No	No
Video	No	No	Yes	No
Output				
Comma separated values (.csv)	Yes	Yes	Yes	Yes
Summaries[6]	Yes	Yes	No	No
Data export for occupancy model analysis	No	Yes, PRESENCE, ‘unmarked’ R package	No	No
Data export for capture-recapture analysis	No	Yes ‘secr’ R package	No	No

	Aardwolf	camtrapR	TRAPPER	Agouti[8]
Support and/or data export for activity patterns analysis	No	Yes, for single-species: histograms of hourly activity, activity kernel density estimations and radial plots; for two-species: activity overlaps	No	Yes
Mapping	No	Yes, in R or export to GIS Shapefile	Yes, online and in GIS	Yes, online
Photo Reports	No	Yes	No	No
Documentation	Krishnappa and Turner 2014 https://github.com/yathin/aardwolf2/blob/master/README	Niedballa et al 2016 https://cran.r-project.org/web/packages/camtrapR/index.html	Bubnicki et al 2016 https://bitbucket.org/trapper-project/	http://cameratraplab.org/agouti/ https://www.agouti.eu

Footnotes:

[1] Limited by Microsoft Access (Ivan and Newkirk 2016)

[2] By installing Windows in a virtual machine environment

[3] After downloading the installer software or package

[4] Medium (through Access) and high (VBA and SQL code modifications) for advanced user

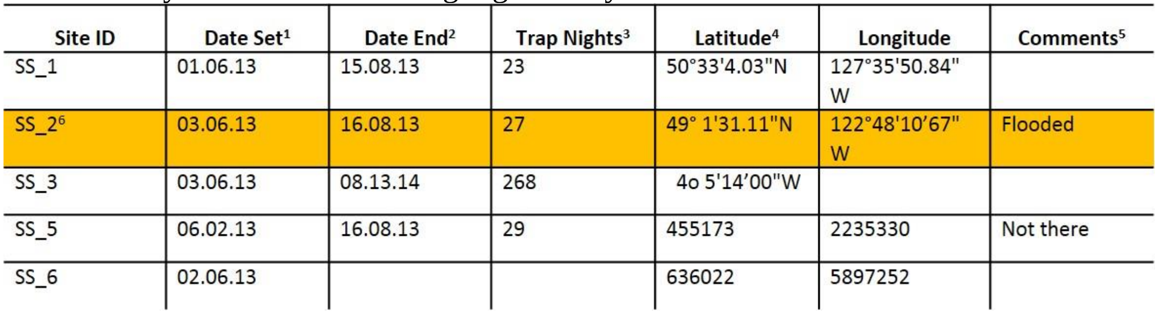
[5] Low for basic use; high (python and/or R) for advanced use. Good IT knowledge to be installed (including server configuration) and maintained (e.g. updating the source code)

[6] Includes everything between simple counts of trap-nights per camera, to detection rates, to species-specific detection counts

[7] Recording of individuals uniquely identifiable by natural or artificial marks

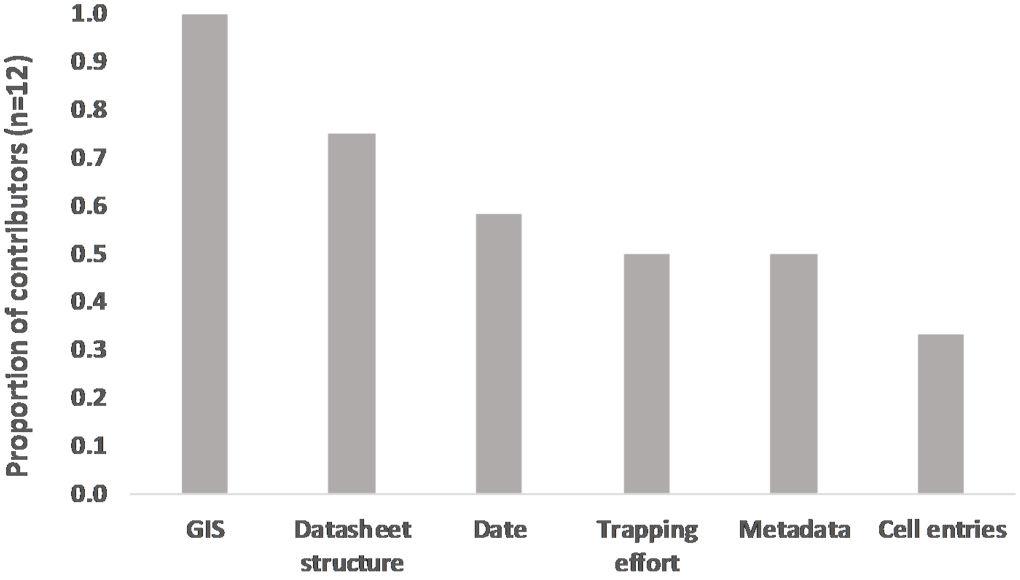
[8] Based on the information available at the time of writing (May 2017)

Figure 1: This example problem data sheet includes a collection of errors and ambiguous cell entries that we commonly encountered on data sheets contributed to a global assessment of sun bears. Data system is undefined, and could be in either UK or US system. [1]Dates all similar except for SS_5; either this unit was set in a different month, or the date is entered incorrectly. [2]End date for SS_3 is clearly the US date system (mm/dd/yy); system is unclear for all other dates. [3]SS_3 has an unusually high number of trap nights, and it is unclear if this is an error or real value. [4]Coordinates are inconsistently formatted and switch between Lat/Long and UTM systems. GIS software cannot read Lat/Longs in this format, and inclusion of symbols prevents easy transformation. UTM coordinates are missing zone and map datum information (i.e. WGS 1984 47N). Longitude for SS_3 is missing so point cannot be projected. [5]Comments are ambiguous – unclear if row of data should be disregarded or not. [6]Unclear why this row has been highlighted in yellow.



Site ID	Date Set[1]	Date End[2]	Trap Nights[3]	Latitude[4]	Longitude	Comments[5]
SS_1	01.06.13	15.08.13	23	50°33'4.03"N	127°35'50.84" W	
SS_2[6]	03.06.13	16.08.13	27	49° 1'31.11"N	122°48'10'67" W	Flooded
SS_3	03.06.13	08.13.14	268	4o 5'14'00"W		
SS_5	06.02.13	16.08.13	29	455173	2235330	Not there
SS_6	02.06.13			636022	5897252	

Figure 2: Proportion of common data entry errors encountered in camera trap datasheets. Multiple datasheets were contributed by 12 research groups to aid in a range-wide assessment of sun bears *Helarctos malayanus* in Southeast Asia; we used this as an example case study to illustrate the common errors that occurred in datasheets that led to loss of data. Data entry errors were combined into six categories, described in Table 1, and occurrence of errors that led to loss of data was calculated as a proportion of the number of research groups.



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