The occupancy-abundance relationship and sampling designs using occupancy to monitor populations of Asian bears

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ABSTRACT

Designing a population monitoring program for Asian bears presents challenges associated with their low densities and detectability, generally large home ranges, and logistical or resource constraints. The use of an occupancy-based method to monitor bear populations can be appropriate under certain conditions given the mechanistic relationship between occupancy and abundance. The form of the occupancy–abundance relationship is dependent on species-specific characteristics such as home range size and population density, as well as study area size. To assess the statistical power of tests to detect population change of Asian bears, we conducted a study using a range of scenarios by simulating spatially explicit individual-based capture-recapture data from a demographically open model. Simulations assessed the power to detect changes in population density via changes in site-level occupancy or abundance through time, estimated using a standard occupancy model or a Royle-Nichols model, both with point detectors (representing camera traps). We used IUCN Red List criteria as a guide in selection of two population decline scenarios (20% and 50%), but we chose a shorter time horizon (10 years = 1 bear generation), meaning that declines were steeper than used for IUCN criteria (3 generations). Our simulations detected population declines of 50% with high power ($>$0.80) and low false positive rates (FPR: incorrectly detecting a decline) ($<$0.10) when detectors were spaced at $>$ 0.67 times the home range diameter (home-range spacing ratio: HRSR, a measure of spatial correlation), such that bears would tend to overlap no more than two detectors. There was high (0.85) correlation between realized occupancy and N in these scenarios. The FPR increased as the HRSR decreased because of spatial correlation in the occupancy process induced when individual home ranges overlap multiple detectors. The mean statistical power to detect more gradual population

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declines (20% in 10 years) with HRSR > 0.67 was low for occupancy models 0.22 (maximum power 0.67) and Royle-Nichols models (0.24; maximum power 0.67), suggesting that declines of this magnitude may not be described reliably with 10 years of monitoring. Our results demonstrated that under many realistic scenarios that we explored, false positive rates were unacceptably high. We highlight that when designing occupancy studies, the spacing between point detectors be at least 0.67 times the diameter of the home range size of the larger sex (e.g., males) when the assumptions of the spatial capture-recapture model used for simulation are met.

1. Introduction

Habitat loss and poaching have been implicated in the decline of most populations of Asian bears including the Asiatic black bear (*Ursus thibetanus)*, sun bear (*Helarctos malayanus*), and sloth bear (*Melursus ursinus)* (Harrison et al., 2016; Scotson et al., 2017; Dharaiya et al., 2020; Garshelis and Steinmetz, 2020)*,* all of which are listed as globally threatened (vulnerable) on the IUCN Red List. Giant pandas (*Ailuropoda melanoleuca*) are threatened (vulnerable) due to small population size (Swaisgood et al., 2016). The brown bear (*U. arctos*) is not globally threatened, with a worldwide distribution that includes increasing populations in North America and Europe, but includes many populations that are vulnerable, endangered or critically endangered in Asia (McLellan et al., 2017). Accelerating declines and small population size among Asian bear populations necessitate survey methods that can achieve objectives of monitoring programs, including assessing the status of populations (system state), and providing information on system response to management actions (Yoccoz et al., 2001). Ultimately, the goal is to implement conservation or management actions to help recover the species, but an evaluation of the effectiveness of those actions is also of interest. The IUCN Species Survival Commission describes an "assess, plan, act" species conservation cycle for effective conservation (Rodríguez, 2021). The process requires identifying areas most in need of conservation actions, designing actions to reduce threats, implementing conservation actions, and evaluating if the actions result in population recovery. System-state variables of interest may include population size, occupancy rate, or area of available habitat; understanding the system state is necessary prior to taking action, and monitoring is necessary to evaluate the effectiveness of management actions in achieving objectives (Lyons et al., 2008). The future of Asian bear populations would benefit from survey methods that allow for reliable conservation decisions to be made using study designs, data collection methods, and statistical analyses that allow for tracking populations through time.

1.1. Occupancy for monitoring population trends

Occupancy has been used in large-scale monitoring programs of mammals, birds, and anurans, serving as an alternative to monitoring abundance (MacKenzie et al., 2004; Weir et al., 2009; O'Brien et al., 2010; Karanth et al., 2011; Pavlacky et al., 2012; Fuller et al., 2016). Occupancy is useful to monitor populations across large spatial extents to understand how a species is distributed in space, resulting in an estimate of the true probability that a site is occupied by the species (MacKenzie et al., 2002, 2006). A site is considered occupied with the presence of ≥ 1 individual (MacKenzie et al., 2006), with a site being defined by the investigator (e.g., patch of habitat, length of trail, a discrete island, or some area around a device used to detect the species). Occupancy models allow for imperfect detection: instead of assuming that non-detections represent true absence, occupancy models use repeat sampling, yielding detections or non-detections at each site on each survey, to jointly estimate the occupancy and detection probability (*p*) (MacKenzie et al., 2002). The most basic occupancy model estimates the expected site-level occupancy probability (ψ) and the probability of detecting the species given that the species occupies a site (*p*).

Royle and Nichols (2003) developed an extension of occupancy models (Royle-Nichols model: R-N) that incorporate abundance-induced heterogeneity to estimate the expected site-level abundance (λ) from the same detection-nondetection data used for occupancy analyses. Site-level abundances are difficult to interpret when the effective sampling area is unknown or when detection of individuals is not independent (MacKenzie et al., 2017); with unknown sampling area, total abundance cannot be derived. The R-N model explicitly deals with site-level heterogeneity in detection induced by variation in site-level abundance; the probability of detection is modeled as a function of the number of animals available for detection at a site and the probability of detecting an individual animal. As such, the abundance information is derived from the observed level of heterogeneity among sites in the probability of detecting the species.

Several advantages of occupancy as a monitoring method are that it does not require capture or marking animals, it allows for the incorporation of indirect observation data (e.g., tracks, scat, photographs), and it is less costly, logistically efficient, and requires less effort than methods that require individual identification (i.e., capture–recapture). Additionally, it has an advantage over presence-only methods that rely on strong assumptions such as random or representative sampling and constant detection probability across sites (MacKenzie et al., 2017). Several monitoring objectives can be addressed with occupancy modeling, including geographic range, rate of change in occupancy over time, habitat relationships, and multiple species interactions (MacKenzie et al., 2006, 2017). Further, the IUCN Red List of Threatened species includes declines in area of occupancy as part of criteria A, B and D for classifying species as threatened (IUCN, 2019).

1.2. Occupancy-abundance relationship and grain size

Under particular circumstances, trends in occupancy can be strongly and positively related to abundance (Gaston and Blackburn, 2003). Using occupancy as an index for abundance relies on the mechanistic relationship between occupancy and abundance and that the combination of sample unit definition and variation in abundance leads to variation in occupancy (Efford and Dawson, 2012; Linden et al., 2017; Steenweg et al., 2018). The occupancy–abundance relationship can depend on the sampling method employed (e. g., areal sampling, point sampling, patch sampling; Steenweg et al., 2018). Areal sampling utilizes a grid cell as the sampling unit (i.e., with grain size describing the dimension of each grid cell) and includes areal sampling of individuals (e.g., Atlas data) or areal sampling of use (e.g., sign surveys on transects). Conversely, when the sampling unit is a point (and the associated detection area around the point), cells are relevant only to space sampling units sufficiently far apart to achieve independence between sites. Grain size can be an important consideration when using occupancy as an index of abundance (He and Gaston, 2000), but is dependent on whether the sampling method uses areal or point sampling. When sites are defined as areal units (as opposed to point detectors), the relationship between occupancy and abundance is positive when the combination of animal density, home range size, and spatial grain size lead to occupancy values not near 0 or 1. When sites are defined as points in continuous space (Efford and Dawson, 2012), the occupancy-–abundance relationship is unaffected by spatial grain/cell size since occupancy is defined by the presence of one or more individuals at a point and is not dependent on the density of sampling points (Steenweg et al., 2018).

With areal sampling, a key assumption is that each sampled cell is either occupied or not occupied during the entire sampling period (O'Connell and Bailey, 2011). Even if individual animals move among grid cells, the overall occupancy state of each individual grid cell remains the same over the course of the survey: that is, if an animal leaves a cell, others remain there (MacKenzie et al., 2017). For low densities and grid cells smaller than the home range size, it is clear that this closure assumption would often be violated. For that reason, it is common for investigators to choose grid cells approximately equal to home range size (Karanth et al., 2011). If the closure assumption is violated, then instead of measuring occupancy, the survey would measure accumulated 'use' (MacKenzie and Royle, 2005). When grain size is small relative to home range size using areal sampling, 'use' (i.e., proportion of area occupied) should not be used as an index of abundance (MacKenzie and Royle, 2005).

In continuous space with point detectors, Efford and Dawson (2012) suggest that when ψ is redefined as proportion of area occupied or the proportion of area used ('use' sensu MacKenzie and Royle, 2005), ψ is independent of the spatial grain used to space point detectors, but it still is a function of the home range size of the species and the abundance of the species. The effect of home range size on estimates of occupancy are not confounding with very large plot sizes on the order of 10x home-range area for a low density species (Efford and Dawson, 2012). A trade-off associated with selecting a large grain is that fewer sampling sites can fit within a pre-defined survey area than if grain size was smaller. Investigators often use point detectors (e.g., camera traps), which have an effective sampling (detection) area much smaller than the spatial grain size chosen to approximate the home range of the species; in

Table 1
We reviewed the 15 studies that used an occupancy model on Asian bear species identified in the literature review conducted by Garshelis et al., 2022 to highlight the decisions made regarding choice of the spatial unit of analysis/spatial grain (site size) and associated justification for the site size chosen as well as the method of data collection to produce the estimate of occupancy.

Species	Method	Site Size	Justification for Site Size	Region	Author
Sun bear	Camera	4 km^2	4–16 km^2 home range size	Sumatra & Borneo	Augeri (2005)
Sun bear	Camera and Sign	2 km^2	Average daily bear movements (1.45 km) and average home range 14.8 km^2	Myanmar	Bisi et al. (2019)
Sun bear	Camera	1.22 km between cameras	Survey designed for clouded leopards	Borneo	Guharajan et al. (2018)
Sun bear	Camera	1.5–4 km between cameras	None	Sumatra	Linkie et al. (2007)
Sun bear	Camera	14.8 km^{2}4 km min distance between cameras	Home range size of 14.8 km^2	Sumatra	Wong et al. (2013)
Asiatic black bear	Camera	4 km^2	None	India	Bashir et al. (2018)
Asiatic black bear	Camera	6.25 km^2	Home range size of 3.55 km^2	Bhutan	Letro et al. (2020)
Sloth bear	Sign	4 km^2	12 km^2 home range size	India	Babu et al. (2015)
Sloth bear	Sign	2 km^2	Survey estimate of 1 bear/1.5 km^2	India	Das et al. (2014)
Sloth bear	Camera	10 km^2, 18 km^2, 25 km^2, 50 km^2	Home range sizes of 10–25 km^2	India	Gopalaswamy (2006)
Sloth bear	Sign	188 km^2	Larger than 3–15 km^2 home range size to represent "landscape scale"	India	Puri et al. (2015)
Sloth bear	Camera and sign	13 km^2	Home range of 10 km^2	India	Srivathsa et al. (2018)
Sloth bear	Camera	1.8 km between cameras	Design for tiger, leopard, dhole	India	Ramesh et al. (2012)
Brown bear	Camera, hair rub station	25 km^2	"intended to roughly approximate the annual home range size of a female bear"	Armenia	Burton et al. (2018)
Brown bear	Camera, sign	100 km^2	"representing the home range of brown bear size"	India	Sharief et al. (2020)

these instances, grain size is used to control spacing between sites (Tucker et al., 2021). Home range size is used as a means to control spacing between detectors when point sampling, but it is not related to the occupancy-abundance relationship and the potential for bias in estimates of occupancy. Rather, the importance of home range size to control spacing is related to bias in the standard errors if the independence of occupancy status assumption (e.g., sites are closed to changes in the state of occupancy for the duration of sampling) is violated. Investigators choose grain size, yet many studies fail to report justification for the selected grain size (Devarajan et al., 2020), and frequently use grid cell size to space traps/detectors under aerial sampling in discrete space and point sampling in continuous space.

A final concern related to the site grain size and assumption that the occupancy states across sites are independent relates to spatial correlation in the occupancy process. If individual home ranges overlap more than one point detector (e.g., point sampling of use), there is potential for spatial correlation in neighboring site occupancy states that could lead to false positives in testing hypotheses about ψ, as for example, in incorrectly concluding that occupancy changed (increased or decreased) over time. The outcome of spatial correlation in the occupancy process is that measures of precision will be overestimated (MacKenzie et al., 2017). To our knowledge, these types of false positive errors have not been formally investigated in occupancy models. The choice of grain is therefore an important consideration in occupancy studies since that choice will affect model assumptions and interpretation and is dependent on whether the study involves areal or point sampling (Efford and Dawson, 2012). Finally, point sampling in continuous space may result in unmodeled site-level heterogeneity in detection, resulting in underestimates in both ψ in occupancy models and site-level abundance in Royle-Nichols models (Efford and Dawson, 2012). This form of heterogeneity may arise because the probability of detecting an individual should increase with increasing overlap of its home range and a detector, and the number of individuals varies among occupied sites; the probability of detecting the species given presence may therefore be heterogeneous due to both variation in home-range overlap with sites and abundance at sites, while Royle-Nichols models only account for variation in abundance across sites.

1.3. Occupancy studies of Asian bears

We reviewed 15 published studies on Asian bear species that used an occupancy-based model as a possible surrogate for abundance (i.e., not just for examining habitat covariates important to occupancy). We evaluated how they chose their site size (i.e., grain size, sampling unit) and sought to understand variability across different studies (Table 1). These studies include all the species of Asian bears except giant pandas (methods for monitoring giant pandas differ from the other Asian bear species); eight employed camera traps, three used sign surveys (e.g., a tangible alteration of the environment that remains as a trace of an animal's presence such as tracks scats, claw marks, foraging evidence), and four sampled with both camera traps and sign surveys. The most frequent justification for site size was the assumed home range size of the species, regardless of whether studies employed areal sampling of sign or point sampling with cameras, highlighting a basic source of confusion regarding spatial grain in occupancy studies, which our simulations intend to address in the context of point sampling.

1.4. Simulation studies for optimal study design

Several studies have evaluated occupancy study designs, exploring factors such as number of sites sampled, number of sampling visits per site, and survey duration (MacKenzie and Royle, 2005; Bailey et al., 2007; Guillera-Arroita et al., 2010; Sewell et al., 2012; Ellis et al., 2014; Barata et al., 2017; Latif et al., 2018). Given fixed resources, there is a trade-off between sampling more sites and applying more effort per site (MacKenzie and Royle, 2005; Bailey et al., 2007; Guillera-Arroita et al., 2010) and the general guidance for rare species, which would apply to Asian bears, is to survey more sites less intensively. However, in some instances, even intensive sampling may not provide adequate power to detect population declines (Ellis et al., 2014; Latif et al., 2018). Authors have also conducted simulations to explore plot size relative to home range size used to measure occupancy (Efford and Dawson, 2012), and similarly, to evaluate how effective sampling area affects the ability to detect trends in occupancy (Tucker et al., 2021). Steenweg et al. (2018) evaluated how survey conditions affect the occupancy-density relationship, but they did not focus on conditions that lead to reliable inference for changes in population density. No simulation studies that we are aware of have investigated the possibility of false positives, i.e., detecting a change when none has occurred, when evaluating power to detect trends in occupancy estimates.

1.5. Aims of our simulation study

In the context of monitoring threatened species, simulations are important in designing a survey to achieve the desired power to detect a particular effect size (e.g., decline in occupancy between survey periods given an actual proportional decline in abundance). We conducted a simulation study to evaluate if occupancy or Royle-Nichols models are a suitable method for monitoring Asian bear populations, in which the objective is to detect a 20% or 50% decline in a population over 10 years (one generation). We evaluated power to detect population declines under different study area sizes, home range sizes, population densities, number of detectors (e.g., camera traps), and number of sampling occasions. In addition to power, we investigated the false positive rates in detecting population declines across all simulation settings, and from these we discuss options for monitoring Asian bears using occupancy.

2. Methods

We simulated populations of Asian bears to assess the statistical power to detect population declines using the kind of occupancy

data that would be obtained from camera trapping (site-level detections and non-detections); camera trap studies are now common in Asia, either focused on bears or generating by-catch data on bears (Garshelis et al., 2022). We simulated data from an open population spatial capture-recapture (OPSCR) model, converted it to occupancy data, and assessed our ability to detect trends across years using two state variables: site-level occupancy and abundance. We used regular occupancy models for the occupancy state variable and the Royle-Nichols model (Royle and Nichols, 2003) for the site-level abundance state variable. The Royle-Nichols occupancy model allows for abundance-induced heterogeneity in detection probability where probability of detection is modeled as a function of the number of animals available for detection. This approach is similar to Steenweg et al. (2018) who simulated data from closed population SCR models and estimated occupancy probabilities for the resulting data sets to characterize the relationship between population density and occupancy probability. Here, we were interested in open populations and our ability to make inferences about changes in abundance inferred from occupancy models that are misspecified. Specifically, of particular concern is that (1) the simulated SCR ecological process produces occupancy and site-level abundance states that are not independent across time and space, and (2) the SCR observation process implies that the detection probability for the set of individuals occupying a site is spatially heterogeneous. These situations violate the assumptions of the occupancy and Royle-Nichols models, which should inflate the false positive rate (FPR; e.g., a "false alarm" in detecting a population decline) under the scenario of no population change. Specifically, the assumption of site in-dependence and the assumption of homogenous detection probabilities (when appropriate covariates explaining the heterogeneity are not available) will be violated. For the occupancy model, site-level detection probability, p, is assumed to be homogenous across sites and for the Royle-Nichols model, individual detection probability, r, is assumed to be homogenous across sites with the detection probability of site j being a function of the site-level abundance, $p_j = 1 - (1 - r)^{N_j}$.

2.1. Population dynamics and detection simulation

We evaluated occupancy designs by simulating spatially explicit individual-based population data from an open population model with individuals subjected to a typical spatial capture-recapture (SCR) process (Royle et al., 2013). We used an exponential population growth model to determine the number of individuals alive in each year. The exponential model was chosen based on IUCN guidance (IUCN, 2019) on patterns of exploitation of the species whereby any exploitation of the species does not change as the population size declines (e.g., hunting/poaching mortality or the proportion of individuals taken does not change as the population size declines). Given a starting population size, N_1, a time duration for population simulation in years ($T = 10$), and a designated total population change over the time duration (λ^T), we calculated the final population size, $N_T = N_1 + N_1 \lambda^T$. Then, we calculated the yearly population growth rate that yields the desired total population growth rate, $\lambda^y = \left(\frac{N_T}{N_1}\right)^{1/(T-1)}$. The yearly population sizes for years $t = 2, ..., T-1$ are then $N_t = \lambda^y N_{t-1}$ rounded to the nearest integer. This deterministic rather than stochastic population growth model allowed us to assess the power to detect *realized* rather than *expected* population changes which is the problem confronted by wildlife managers.

Individuals in year $t + 1$ consist of individuals that survived after year t as well as new recruits which were handled as follows. Given a desired individual survival probability, φ, we assumed the number of survivors in year t follows $S_{t+1} \sim Bin(\phi, N_t)$ with pop-ulation growth parameters chosen so that the number of survivors in year $t + 1$ is never greater than the number of individuals alive in year $t + 1$. Then, the difference between N_{t+1} and S_{t+1} was made up of new recruits. The individual by year inclusion status in the population is the *M x T* matrix *Z*, where $z_{it} = 1$ if individual i was in the population in year t and 0 otherwise, and *M* is the maximum number of individuals that can be simulated, used to fix the size of *Z* and other data structures during simulation (following Chandler and Clark, 2014). Associated with each individual is an activity center s_i, and we assumed individual activity centers are distributed uniformly across a 2-dimensional state space, $\mathscr{S}$, following $s_i \sim Uniform(S)$. We assumed that individual activity centers do not move through time. Density was then simulated based on the number of bears in the set state space with demographic processes modeled by random deletion/addition of the home range centers.

For the detection process, we assumed individual detection probability declined as a function of the distance d_{ij} between the in-dividual activity center s_i and each detector, j with location of detector x_j, following a hazard-half-normal detection function. We assume the expected number of detections for individual i at detector j is $\lambda_{ij} = \lambda_0 \times \exp(\frac{-d_{ij}^2}{2\sigma^2})$ where λ_0 is the baseline detection rate, σ is the spatial scale parameter, and d_{ij} is the distance between individual activity center s_i and detector j. Then, we converted the

Table 2
Parameter values for simulation scenarios to detect population change in Asian bears of 20% or 50% across 10 years. Combinations resulted in 3024 scenarios. Population change of -0.2 is a 20% decline and -0.5 is a 50% decline.

Simulation parameter	Values
Study area size	300, 600, 900, 1200 km^2
Initial population density (*D*)	6, 16.5, 27 bears/100 km^2
Number of detectors (*J*)	36, 49, 64, 81, 100, 121, 144
95% home range area	7.5, 30.75, 54 km^2
Individual survival probability (φ)	0.6, 0.8
No. capture occasions/year (*K*)	6, 12
Total population change (λ^T)	0, -0.2, -0.5
Single detector sampling area (a_0)	0.925, 1.85, 5.65

individual by detector detection rate to the individual by detector (e.g., camera trap) detection probability following $p_{ij} = 1 - \exp(-\lambda_{ij})$. The individual by detector by occasion by year detection process is then $y_{ijkt} \sim Binomial(z_{it}p_{ij})$, where k is the occasion index.

2.1.1. Simulation parameters

The parameters we varied (Table 2) were the study area size, population density (D), number of detectors (*J*), 95% home range area, individual survival probability (φ), number of capture occasions per year (K), total population change (λ^T), and single-detector sampling area (a_0; Efford and Mowat, 2014).

We considered three initial population densities (6, 16.5, and 27 bears/100 km^2) and used a range of population densities representing a low of 6 bears/100 km^2 representative of sun bears (Ngoprasert et al., 2012) to 27 bears/100 km^2 for sloth bears in good habitat (Garshelis et al., 1999). The four study area sizes (300, 600, 900, and 1200 km^2) were chosen to represent approximate sizes of reserves occupied by Asian bears: 300 km^2 (e.g., Pench Tiger Reserve, India), 600 km^2 (e.g., Parsa National Park, Nepal), 900 km^2 (e. g., Bardia National Park, Nepal, Gunung Palung National Park, West Kalimantan, Indonesia) and 1200 km^2 (e.g., Yushan National Park, Taiwan). We included two values for the number of capture occasions (6, 12). Individual survival probabilities of 0.6 and 0.8 were chosen since they are within the range of typical of pooled-sex bear survival estimates of bear populations with human-caused mortality (Harris et al., 2011). We chose three home range sizes (7.5, 30.75, and 54 km^2), with the low of 7.5 km^2 representing sloth bears (Ratnayeke et al., 2007; Joshi et al., 1995) while also reflective of giant pandas (Hull et al., 2015) and the lower end of the 6–20 km^2 range for sun bears (Wong et al., 2014), the largest 54 km^2 representing Asiatic black bears (Hwang et al., 2010), and mid of 30.75 km^2 representing halfway between these home range sizes. We did not simulate the very large home ranges in some populations of Asian brown bears. The number of detectors (e.g., camera traps) in our simulation ranged from 36 to 144 (36, 49, 64, 81, 100, 121, 144), within the range of previous studies on Asian bear species (Srivathsa et al., 2018; Ramesh et al., 2012; Babu et al., 2015). These detector numbers were chosen to produce square sampling arrays with equal spacing and we used a 3σ buffer around the maximal trap extent to produce the state space. The detection spatial scale parameter was calculated from the 95% home range area values assuming a bivariate normal utilization distribution (Royle et al., 2013) according to $\sigma = radius/\sqrt{5.99}$, where radius is the 95% home range radius. Then, λ_0 was calculated from a_0 and σ following $\lambda_0 = a_0/2\pi\sigma^2$ (Efford and Mowat, 2014). We included 3 a_0 levels (0.925, 1.85, 5.65). Data for single detector effective sampling area (a_0) were obtained by calculating a_0 from the male and female λ and σ estimates from Whittington et al. (2018), a camera-based spatial mark-resight study of brown bears, and the same estimates for pooled-sex American black bears (*U. americanus*) from Sun et al. (2019), an integrated DNA and camera survey. The female a_0 estimate of 1.91 from Whittington et al. (2018) was very similar to the pooled-sex estimate of 1.79 from Sun et al. (2019), so we used the male estimate of 5.65 from Whittington et al. (2018) and the average of the female estimate from Whittington et al. (2018) and Sun et al. (2019), which was 1.85. We created a third, lower detectability scenario by reducing the 1.85 scenario 50% to 0.925. Finally, we considered a time period of $T = 10$ years and population changes of 0, − 0.2 and − 0.5, representing no change, a 20% decline, and a 50% decline. The 50% decline scenario was conducted only for the occupancy models. The IUCN uses one or more of five criteria to evaluate the category of each species on the Red List (IUCN, 2019). Three species of Asian bears (Asiatic black bear, sun bear, sloth bear) are classified under Criteria A, which looks at the rate of decline over 30 years (3 bear generations). Under this criterion, Vulnerable is a 30% decline, Endangered a 50% decline and Critically Endangered an 80% decline. Our decline scenarios of 20% and 50% over 10 years were chosen to evaluate if there would be sufficient power to detect a significant decline with enough time to employ conservation actions, but recognizing that the rate of decline in this shorter time horizon would be steeper than if it occurred over 30 years.

The combination of three starting population densities, three home range sizes, four study area sizes, seven different levels of detectors, two occasion numbers, three detection levels, and two survival levels produced 3024 different simulation scenarios.

2.2. Occupancy and Royle-Nichols models

For each simulated data set, we fit single season occupancy models in the R package unmarked (Fiske and Chandler, 2011). We formatted the multi-year simulated data sets as single season occupancy data sets by treating the same detectors across years as independent sites with site and site by occasion covariates for the year of deployment (i.e., a "stacked data" structure). Specifically, we converted the individual detection data to site-level detection data and then concatenated the yearly *J* x *K* occupancy data sets to create a *JT* x *K* data set. We assumed $logit(\psi_j) = \beta_0 + \beta_1 year_j$ where ψ_j is the occupancy probability of site j operated in year $year_j$ Then, we assumed the occupancy state of detector j in year $year_j$, z_j, follows $z_j \sim Bern(\psi_j)$. For the detection model, we also assumed a time trend because site-level detection probability declines as the local density around a detector declines, at least in certain regions of the simulation parameter space. For detection, we assume $logit(p_{jk}) = \gamma_0 + \gamma_1 year_j$. For the Royle-Nichols model, we assumed $log(\lambda_j) = \beta_0 + \beta_1 year_j$, where λ_j is the abundance of site j operated in year $year_j$. Because the Royle-Nichols model has a defined relationship between site-level abundance and individual detection probability, we modeled *r*, the individual detection probability, as fixed across time.

2.3. Simulation evaluation

For each of the 3024 simulation scenarios, we simulated data from an open population SCR model, converted the individually-referenced detections to simple (non-individually referenced) detection/non-detection data, and fit occupancy and Royle-Nichols

models to the resulting data sets across 200 replications. We used an α level of 0.05 to infer a population change with power (in true decline scenarios) and FPR (in no decline scenarios) being the proportion of 200 replications where the p-value for the occupancy time trend beta_1 was < 0.05. We considered all possible combinations of the simulation parameter values for population changes of 0 and -0.2. For the population change of -0.5, we considered all possible combinations excluding the two largest reserve sizes of 900 and 1200 km^2 and only considered occupancy models because the purpose of the large decline scenario was to evaluate if we can achieve sufficient statistical power in small reserves with occupancy models, which was not the case (see results below) for the more modest population decline. The no change scenario allowed us to assess the false positive rate for detecting a population change and identify scenarios that are likely to lead to erroneous conclusions of a population change when no change occurred.

Preliminary investigation of the simulation results raised two issues that informed further analyses. First, many scenarios showed a high FPR and we hypothesized that the inflated FPRs were largely related to within-year spatial correlation in the state processes (site-level occupancy and abundance) due to individual bears occupying more than one detector/site. To quantify this effect, we calculated a measure of spatial correlation as the ratio of the detector spacing to the 95% home range diameter (HRSR; home-range spacing ratio). Because we assumed home ranges were circular and detector spacing was uniform, a HRSR of 1.0 is when the diameter of the home range equals the spacing of detectors, or in other words, the point where a single individual's 95% home range just overlaps a second detector (Fig. 1). A HRSR of 0.5 is where an individual's 95% home range may overlap a maximum of 5 detectors (Fig. 1). These thresholds are not exact because individuals may be detected beyond the boundaries of their 95% home range radius and the total area over which an individual is detected is a function of their overall detectability (K and a_0). These effects illustrated in Fig. 2 led us to hypothesize that total detectability modulates the effect of spatial correlation on the FPR. Second, many of the scenarios for occupancy models led to all sites being occupied across all years. All such scenarios had closely-spaced traps, where we expect spatial correlation in the occupancy process; however, there can be no measurable spatial correlation when all occupancy states are 1. Therefore, we used the mean occupancy rate across the 10 years and 200 replications to exclude scenarios with a mean occupancy rate > 0.999 from the false positive analysis only.

To formally investigate the potential causes of the inflated FPR, we fit a generalized additive model (GAM, Hastie and Tibshirani, 1990) using the Binomial response of the number of false positive events out of 200 events (1 per simulated data set) for each scenario and each model (occupancy, Royle-Nichols). We used a logit link and a quasibinomial family to accommodate extra-Binomial dispersion. To investigate the spatial correlation effect and how it may be modulated by overall detectability, we used a spline for HRSR, stratified by detection level. We define the detection levels to be all combinations of K and a_0, yielding six levels; however, the product of a_0 and K yielded the same value for two scenarios (the products of a_0 =1.85, K=6 and a_0 =0.925, K=12 both equal 11.1), so we expected them to have similar relationships. We also included additive effects for a_0, K, D, and φ, as well as interaction effects between K and a_0. The effect for φ was included to assess the effect of temporal correlation due to the same individuals occupying the same detectors across years.

Because the FPR was high for scenarios where home ranges overlapped many detectors (small HRSR ratios; Fig. 2), we assigned a HRSR threshold to rule out scenarios likely to lead to a high FPR from the power analysis. The relationship between the FPR and HRSR (Fig. 2) indicated that the FPR stabilized when HRSR≈0.67, yielding an FPR consistently < 0.1 for the occupancy results, though not
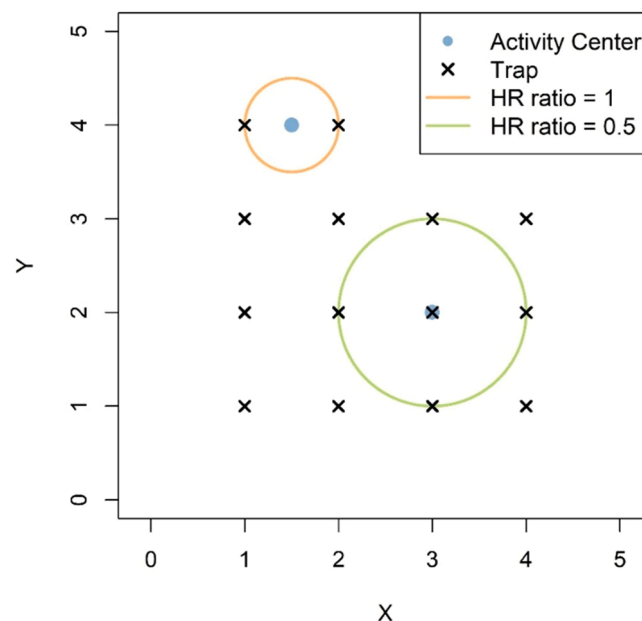

Fig. 1. Depiction of the maximum number of sites occupied by a single 95% home range with home-range spacing ratios of 1.0 (2 sites) and 0.5 (5 sites).
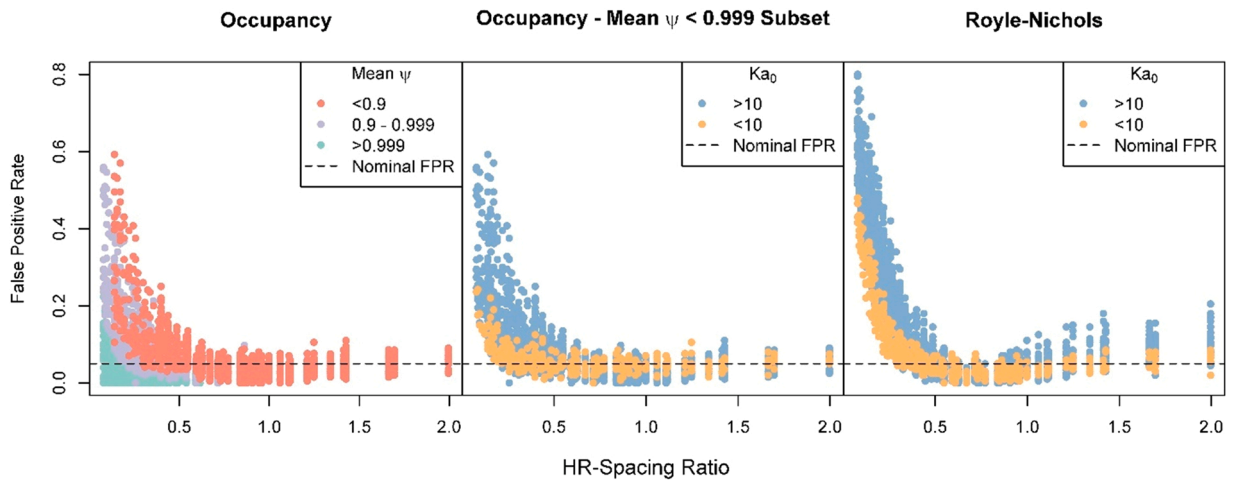
Fig. 2. The false positive rate (FPR) of the no population change scenarios as a function of home-range spacing ratio (HR-Spacing Ratio: HRSR) for occupancy and Royle-Nichols models. The first pane is further stratified by the mean occupancy and the second two panes are further stratified by overall detectability, Ka_0, for occupancy (middle) and Royle-Nichols (right) estimates. The dotted line indicates the nominal FPR (0.05).

consistently below the nominal value of 0.05. A HRSR of 0.67 also appeared appropriate for the Royle-Nichols results, though the false positive rate increases again at higher HRSRs (above ~1.0).

Using the HRSR of 0.67 as an exclusion threshold ruled out all scenarios with a 54 km² home range area (Table 3). There were three combinations of study area size and number of detectors that yielded a home-range spacing ratio > 0.67 using a 30.75 km² home range size and there were 22 combinations with a home range area of 7.5 km². These 25 combinations of home range area, study area size, and number of detectors that yielded a home-range spacing ratio > 0.67 included 900 scenarios of the total 3024 scenarios possible (Table 3). Finally, for the Royle-Nichols power analysis, we also excluded the highest detectability scenarios (the combination of $a_0 = 5.85$ and K=12) (Fig. 3), which showed higher FPRs for the higher HRSR scenarios where spatial correlation was unlikely to be present (see Results).

After screening out 2124 scenarios with HRSR< 0.67, we used the reduced data sets (900 scenarios) and investigated the effects of each simulation parameter on the 20% decline scenarios using logistic regression with a quasibinomial distribution. We also excluded the highest detectability scenarios (the combination of $a_0 = 5.85$ and K=12) for the Royle-Nichols model (Fig. 3), which showed higher FPRs for the higher HRSR scenarios where spatial correlation was unlikely to be present (see Results), resulting in 750 scenarios retained. The response was the number of data sets for which the p-value for the state variable trend parameter was less than 0.05 out of the total 200 data sets. Reference classes were the smallest values for each setting (e.g., study area size of 300 km² and density of 6 bears/100 km²).

3. Results

The false positive rate declined as the home-range spacing ratio increased for both occupancy and Royle-Nichols models (Figs. 2 and 3), with the effect being stronger for populations with higher overall detectability. For occupancy models, the FPR stabilized

Table 3

Number of scenarios (of 3024) that had a home range-spacing ratio > 0.67 (detectors are spaced at greater than 0.67 times the home range diameter: HRSR) by study area size, home range size, and number of detectors. Scenarios with a zero were excluded from power analyses.

95% Home range area (km²)	Study area size (km²)	Number of detectors						
		36	49	64	81	100	121	144
7.5	300	36	36	0	0	0	0	0
	600	36	36	36	36	36	36	0
	900	36	36	36	36	36	36	36
	1200	36	36	36	36	36	36	36
30.75	300	0	0	0	0	0	0	0
	600	0	0	0	0	0	0	0
	900	36	0	0	0	0	0	0
	1200	36	36	0	0	0	0	0
54	300	0	0	0	0	0	0	0
	600	0	0	0	0	0	0	0
	900	0	0	0	0	0	0	0
	1200	0	0	0	0	0	0	0

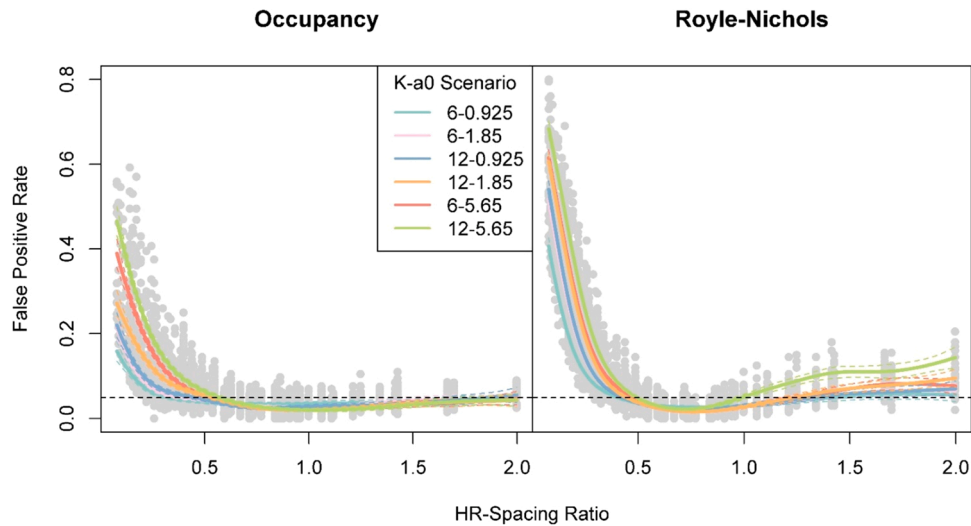**Occupancy**　　　　　　**Royle-Nichols**

Fig. 3. Predicted relationships between the false positive rate (FPR) and home-range spacing ratio (HR-Spacing Ratio: HRSR) for each level of overall detectability for both occupancy and Royle-Nichols models. Occupancy scenarios exclude those with a mean occupancy rate greater than 0.999. Overall detectability, the combination of K (number of capture occasions per year) and a_0 (single detector sampling area) is ordered from lowest to highest in the legend. Mean relationships are solid lines and 95% prediction intervals are dotted lines. The horizontal dotted line indicates the nominal FPR (0.05).

around a home-range spacing ratio of 0.67 (detectors are spaced at 0.67 times the home range diameter or larger). Royle-Nichols models appeared to reach a minimum FPR of around 0.67, but the FPR then increased again at higher HRSRs, with more of an increase for higher detectability scenarios (those with K-a_0 >10: the combination of $a_0 = 5.85$ and K=12). False positive rate increased with increased detectability for R-N models (Table 4). The FPR was also influenced by population density (Table 4), with higher densities reducing the FPR for R-N models and inconsistent effects for occupancy models. Increased individual survival increased the FPR in both models.

The mean statistical power for the occupancy models with home-range spacing ratios > 0.67 (and excluding scenarios with mean occupancy rate >0.999) was 0.22 and the maximum power was 0.67 for detecting a real decline of 20% (Fig. 4). The analogous results for the Royle-Nichols models (excluding scenarios with high detection, K-a_0 >10 and HRSR <0.67) were a mean of 0.24 and maximum of 0.67. For the 50% decline scenarios, occupancy models had a mean power of 0.82 with 18% of scenarios yielding a power of 1.0 (Appendix A1). Sub-setting the 50% population decline scenario by only those occupancy scenarios that achieved power ≥ 0.80, 31.7% had FPR > 0.10. Under the 20% population decline case, none of the scenarios maintained a FPR < 0.10 with power ≥ 0.80 whereas under the 50% decline case, 22.6% of the scenarios met these criteria for what may be considered "acceptable" for a monitoring program.

The statistical power was positively correlated with the mean correlation between realized ψ or λ (in occupancy and Royle-Nichols models, respectively) and N across the 200 replicate data sets within a scenario (Fig. 5), with a less variable relationship for scenarios with a HRSR > 0.67. For the occupancy models, the mean correlation for scenarios with an HRSR less than and greater than 0.67 was 0.19 and 0.45, respectively. Mean correlation for scenarios with mean occupancy > 0.999 was only 0.04. When removing scenarios with mean occupancy > 0.999 (and retaining scenarios with HRSR >0.67), the mean correlation was 0.47. For the Royle-Nichols

Table 4
Parameter estimates (excluding splines, see Fig. 3) for factors influencing the false positive rate in no change scenarios for the occupancy and Royle-Nichols models. All variables are factors with reference levels $a_0 = 0.925$, K = 6, φ = 0.6, and D = 6. The quasibinomial scale parameter estimates were 2.44 and 1.77 for occupancy and Royle-Nichols models, respectively.

Parameter	Occupancy		Royle-Nichols	
	Est	p-value	Est	p-value
Intercept	-2.94	< 0.0001	-2.60	< 0.0001
K = 12	0.04	0.33	0.12	< 0.0001
$a_0 = 1.85$	0.02	0.61	0.10	0.0001
$a_0 = 5.65$	0.24	< 0.0001	0.35	< 0.0001
φ = 0.8	0.19	< 0.0001	0.19	< 0.0001
D = 16.5	-0.11	< 0.0001	-0.07	< 0.0001
D = 27	0.28	< 0.0001	-0.15	< 0.0001
K=12:a_0=1.85	0.09	0.11	0.03	0.32
K=12:a_0=5.65	0.09	0.08	0.17	< 0.0001

a_0 = detectability, K = number of capture occasions per year, φ = individual survival probability, D = starting population density
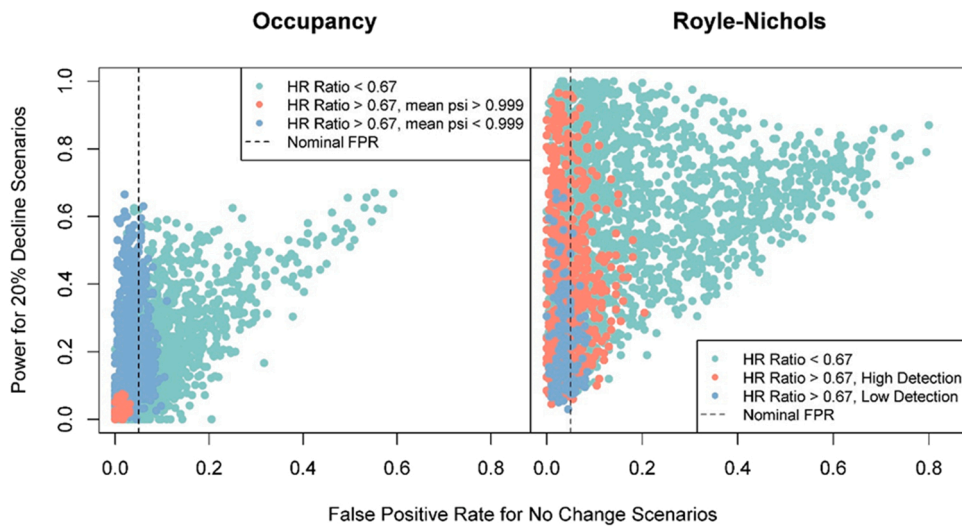
Fig. 4. The relationship between the false positive rate for the no change scenarios and the statistical power for the 20% decline scenarios, showing the differences between scenarios with home-range spacing ratios (HR Ratio) above and below 0.67 for occupancy and Royle-Nichols models. The Royle-Nichols models are further stratified by overall detection, low detection = $Ka_0 < 10$ where $K = 6$ and $a_0 = 0.925$) and all other K- a_0 combinations are high detection scenarios. The occupancy models are stratified by scenarios with mean realized occupancy above and below 0.999. The vertical dotted line indicates the nominal false positive rate (FPR, 0.05).
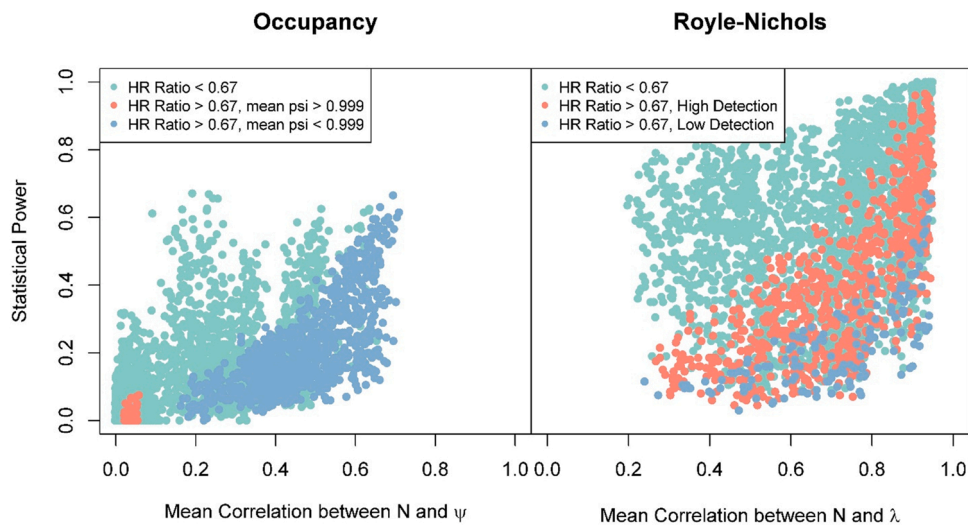
Fig. 5. Statistical power as a function of the mean correlation between realized N and ψ (occupancy) or N and λ (Royle-Nichols) across replications of each scenario for the 20% decline scenarios, showing the differences between scenarios with home-range spacing ratios above and below 0.67.

models, the mean correlations were stronger at 0.68 and 0.72 for scenarios below and above a HRSR of 0.67, respectively. Mean correlation with HRSR > 0.67 for both low and high detection scenarios was 0.72. For the occupancy models with the 50% decline scenario, the mean correlation for scenarios with a HRSR less than and greater than 0.67 was 0.46 and 0.85, respectively (Appendix A1). In the occupancy models, the mean correlation for scenarios with a HRSR less than 0.67 was lower, in part, because these scenarios were more likely to lead to fully saturated detectors with $\psi = 1$ across the full N gradient (Fig. 6). The variability in the relationship between the mean correlation of the state variable with N and the HRSR was larger for scenarios with a HRSR less than 0.67, in part, because of the lack of independence falsely inflating the statistical power.

All parameters except for survival influenced the statistical power for the 20% decline scenarios that were not excluded for higher FPR rates. Survival was significant for Royle-Nichols models, but not for occupancy models (Table 5). Power increased with study area size, density, detectability, occasion number, and detector number. Power decreased for a home range size of 30.75 vs. 7.5 for occupancy models and increased for Royle-Nichols models (note no home range areas of 54 km^2 exceeded the HR ratio threshold).

Factors that influenced the occupancy-abundance relationship were density, home range size, and study area size, as depicted in

Table 5

Parameter estimates for factors influencing statistical power for the 20% decline scenarios with a home-range spacing ratio > 0.67. Occupancy models were further screened to only include those scenarios with an expected mean occupancy < 0.999 and Royle-Nichols models were further screened to exclude the highest detectability scenario (the combination of $K = 12$ and $a_0 = 5.65$). All variables are treated as factors except for J (detector), which was treated as a continuous predictor. Reference levels are Area = 300, D = 6, HR area = 7.5, a_0 = 0.925, K = 6, and φ = 0.6. The quasibinomial scale parameter estimates were 3.15 and 2.79 for occupancy and Royle-Nichols models, respectively.

Parameter	Occupancy		Royle-Nichols	
	Est	p-value	Est	p-value
Intercept	-4.00	< 0.0001	-3.59	< 0.0001
D = 16.5	1.27	< 0.0001	0.78	< 0.0001
D = 27	1.83	< 0.0001	0.84	< 0.0001
HR area = 30.75	0.44	< 0.0001	-1.08	< 0.0001
Area = 600	0.30	< 0.0001	0.09	0.07
Area = 900	0.38	< 0.0001	0.17	0.0007
Area = 1200	0.40	< 0.0001	0.19	0.0003
K = 12	0.50	< 0.0001	0.28	< 0.0001
a_0 = 1.85	0.44	< 0.0001	0.40	< 0.0001
a_0 = 5.65	1.03	< 0.0001	0.7	< 0.0001
J	0.02	< 0.0001	0.01	< 0.0001
φ = 0.8	-0.01	0.78	0.06	0.004

Area = study area size in km^2, D = density of bears/100 km^2, HR area = 95% home range area, a_0 = detectability, K = number of capture occasions per year, φ = individual survival probability, J = number of detectors.

Fig. 6 for the 20% decline scenario under an occupancy model and in Appendix A2 for the 50% decline scenario. Power was greater under the 20% decline scenarios when home range area was smallest (7.5 km^2), and density was higher (16.5 or 27 bears/100 km^2), and the number of detectors was greatest (121 or 144) (Fig. 6). The 50% decline scenarios only achieved power > 0.80 when home range area was smallest (7.5 km^2) (Appendix A2). Power was greater under the 20% decline scenarios for the Royle-Nichols models at the smallest home range size (7.5 km^2) with initial population densities of 16.5 and 27 bears/100 km^2 and with the largest study area sizes (900 or 1200 km^2) (Fig. 7).

4. Discussion

Our occupancy simulation study suggests that if detectors are spaced such that individuals overlap multiple sites, inducing high spatial correlation in the state process, the likelihood of falsely detecting population declines can become unacceptably high. Not accounting for false positive rates can lead to overly optimistic statistical power estimates since there were many scenarios that had high power to detect real declines, but also a high incidence of detecting declines that were not real. In computing our home-range spacing ratio (detector spacing relative to home range diameter), we assigned an individual as occupying a site (being in range of a detector) or being part of a site's abundance if its 95% home range overlapped the site's detector. Defining occupancy or site use in this manner does not provide insights into which home range area isopleth (core or total HR extent) the estimated occupancy or site-level abundance corresponds to. We believe the most appropriate home range area isopleth to define these states depends on the overall detectability. Similar to there being an effective sampling area for abundance models that is a function of the spatially variable individual detection probability and number of occasions (Royle et al., 2013, p. 167), there should be an analogous "effective home range area" for these types of occupancy and site use evaluations. This hypothesis is supported by the different slopes in the FPR – HRSR relationships across the detectability levels at very low HRSR levels (Fig. 3). Also, the stabilization of the FPR around a HRSR of 0.67 suggests the effective home range area for these scenarios is less than the 95% home range area used to calculate the HRSR—the spatial correlation using the 95% home range definition for site-level state definition does not disappear until a HRSR of 1.0 (Appendix A3). Regardless of the magnitude of spatial correlation depending on overall detectability, it appears that the 0.67 threshold using a 95% home range definition is sufficient to minimize the effect of spatial correlation when fitting occupancy and Royle-Nichols models when the data generating process is well approximated by an SCR model. For instance, using a sloth bear home range size of 7.5 km^2, detectors would be spaced no closer than 2.1 km apart. For Asiatic black bears with a home range size of 54 km^2, detectors would be spaced no closer than 5.6 km apart. For an intermediate home range size of ~30 km^2, detectors would be spaced no closer than 4.1 km apart. The practical problem is that investigators are unlikely to know the actual home range size and would need to extract it from the literature, but home range sizes can vary enormously among areas. For example, home range size of a female radio-collared sloth bear in Panna National Park in central India was 23 km^2, and a male was 129 km^2 (Yoganand 2005 cited in Seidensticker et al., 2011). Home ranges of male bears are often much (>3x) larger than that of females, and since the sexes cannot be distinguished by camera trapping, and occupancy is thus pooled for the sexes, avoiding false positives requires using the home range size of males, which is often more than the examples that we used in our simulations.

The optimal spacing for occupancy studies is larger than that for spatial capture-recapture (SCR) studies. The minimum HRSR of 0.67 for detector spacing in occupancy studies translates to 3.28 times the SCR spatial scale parameter (σ) used for density estimation. The 3.28σ value is greater than the 1σ to 3σ suggested for detector spacing in SCR studies (Sun et al., 2014; Efford and Boulanger, 2019). Efford and Boulanger (2019) suggest that optimal detector spacing for SCR studies should be where the number of unique bears detected equals the cumulative number of recaptures (including spatial recaptures within sessions). A companion density paper (Morin
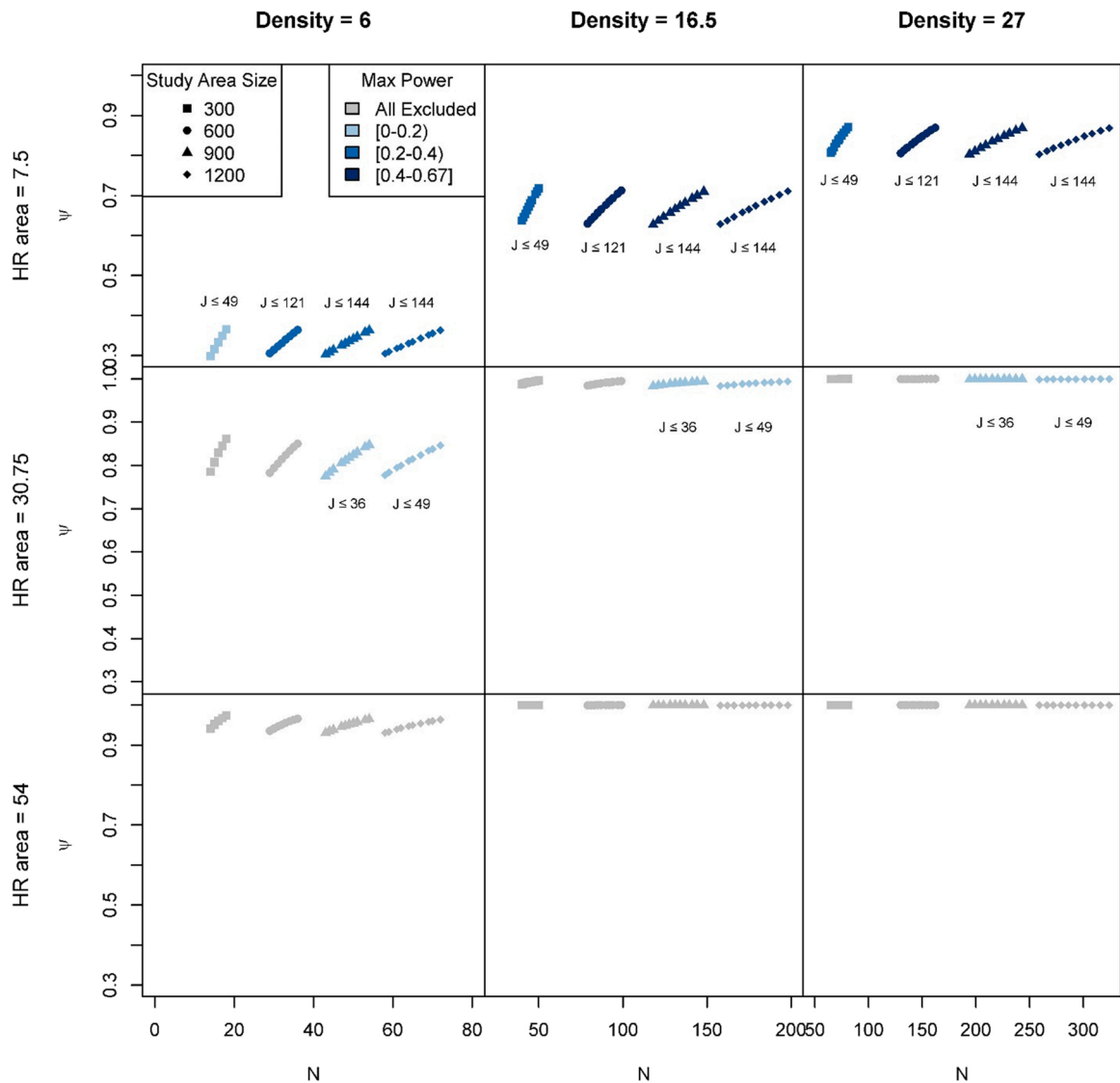
Fig. 6. Effects of home range area (km^2), initial population density (bears/100 km^2), study area size (km^2), and the number of detectors (J) on the occupancy-abundance (N) relationship from simulations to detect a 20% decline in Asian bear populations under an occupancy model. Each color represents the statistical power for the given simulation scenarios. Scenarios in gray were excluded based on home-range spacing ratio < 0.67.

et al., 2022) estimated optimal detector spacing for sun bears at 3.6 km which equates to 1.6 times σ (σ = 2.27 km; Ngoprasert et al., 2012, sampled for 5 sessions in a 6 ×6 grid with an assumed density of 5 bears per 100 km^2). At farther detector spacings, the number of bears detected exceeded recaptures, and at closer spacings the number of recaptures exceeded bears detected (Fig. 2 in Morin et al., 2022). Using the results of our occupancy simulations where we report optimal spacing of 3.28σ, we calculate that this would equate to a trap spacing of 7.44 km for the sun bear example explored by Morin et al., 2022. Minimizing detections of bears at multiple detectors in occupancy studies is at odds with maximizing recaptures of the same individual at different detectors in SCR studies. Thus, optimal designs for occupancy studies at 3.28σ are not optimal designs for SCR studies at closer detector spacing of 1–3σ.

Although the Royle-Nichols models had higher power than the occupancy models for many of the scenarios, once screened for scenarios with acceptable false positive rates (<0.05), there was little difference in statistical power between the two models. An unanticipated pattern was that the FPR for the Royle-Nichols models declined to < 0.05 at a HRSR of around 0.67, but increased again above 0.05 as the HRSR increased beyond 1.0 (Fig. 3). Because spatial correlation should no longer be a factor in this range, we hypothesize that the inflated FPR is associated with individual by trap heterogeneity in detection probability. Under the SCR model that we simulated from, individual by trap detection probability is a function of the distance between an individual's activity center and the detector, whereas this information cannot be included in the Royle-Nichols model and we assumed the individual detection probability was homogenous across individuals and detectors. The FPR in this higher range of the HRSR was also modified by the overall detectability, with the highest detectability having the highest FPR (Fig. 3; non-overlapping prediction intervals).
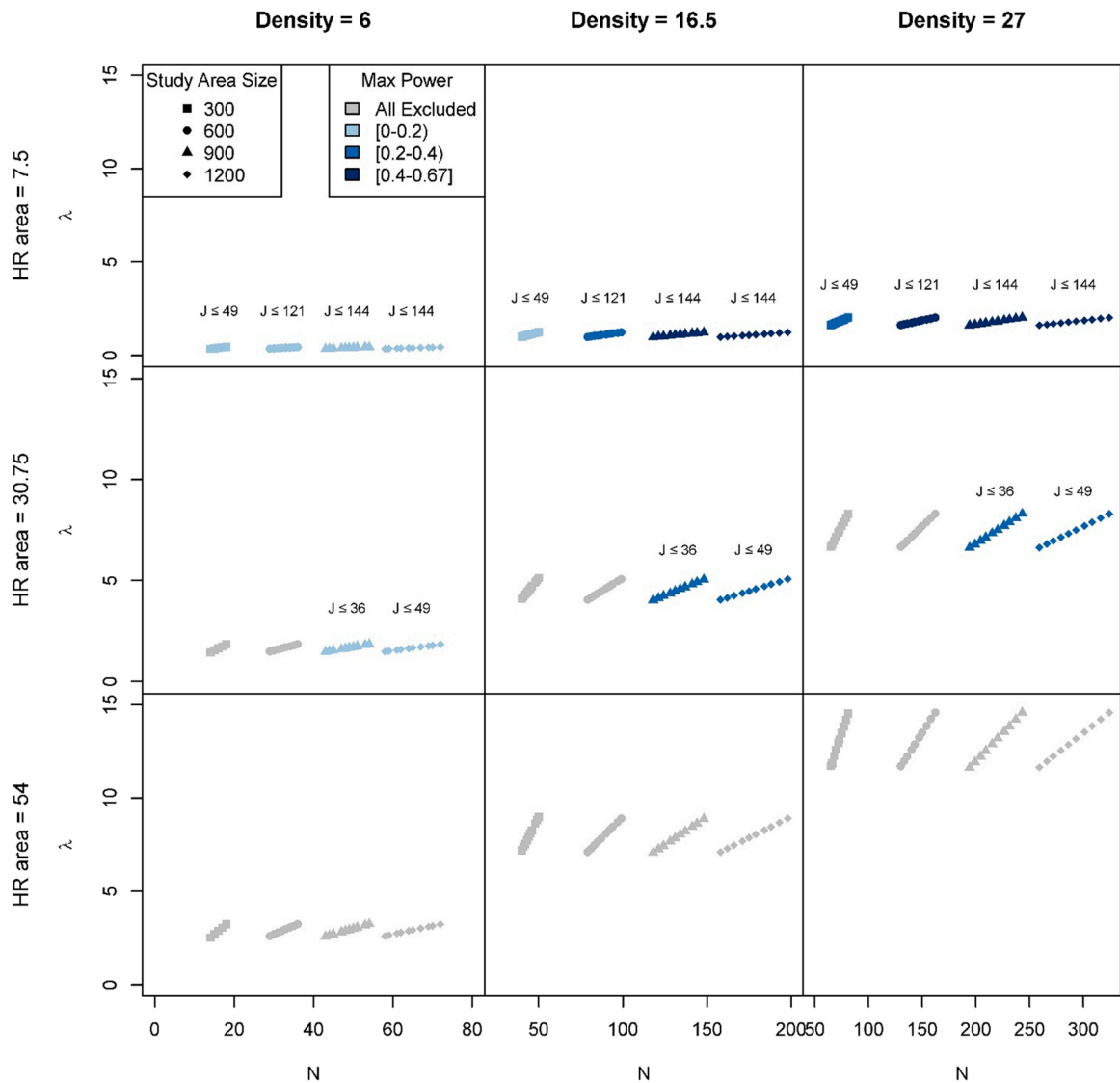
Fig. 7. Effects of home range area (km^2), initial population density (bears/100 km^2), study area size (km^2), and the number of detectors (J) on the occupancy-abundance (N) relationship from simulations to detect a 20% decline in Asian bear populations using the Royle-Nichols model. Each color represents the statistical power for the given simulation scenarios.

Heterogeneity in detection probability can be abundance-induced and bias occupancy estimates (Dorazio, 2007).

False positive rate was especially high for low density Asian bear populations (6 and 16.5 bears/100 km^2) when bears are detected at more than one site (ratio of home range diameter to detector spacing, or home range-spacing ratios, ≤1). False positive rates become acceptable (<0.05) under most scenarios when Asian bear population density is high (27 bears/100 km^2), regardless of the home-range spacing ratio. However, densities this high have only been reported for sloth bears, and possibly giant pandas. We chose study area sizes that were representative of a range of reserves in countries with Asian bear populations. Small reserves or survey areas limit the number of independent sampling sites that can fit within the defined area. As the number of sites within a small reserve increase, trap spacing decreases, and this will induce more spatial correlation in the occupancy process. Increasing the number of sites beyond a certain point relative to home range size (when the ratio of home range diameter to detector spacing is ≤1), will not generate more independent data. When using occupancy as a monitoring approach to detect trends in population size for species that occur at low densities, it is important to recognize the possibility of false positives, not only for declines, but also for increases that we hope to occur after conservation actions are implemented. Yet, to our knowledge, this is the first study to evaluate false positives in identifying trends in monitoring via occupancy.

Spatial correlation in the occupancy process occurs when nearby spatial units are more likely to have a similar occupancy status than units farther away, thus violating the assumption that the occupancy states are independent. In the presence of spatial correlation, the regular binomial proportion estimator will provide an unbiased point estimate, but the standard error will overestimate the

precision (MacKenzie et al., 2017). If spatial correlation is induced by missing spatial occupancy covariates, including these covariates in the model will remove the spatial correlation. However, in this case, the spatial correlation is in the covariance of the nearby occupancy states, not their expected values, so occupancy covariates will not be useful. Explicit models for spatial correlation, including conditional auto-regressive models (Magoun et al., 2007), kriging (Pacifici et al., 2016), and restricted spatial regression (Johnson et al., 2013), should reduce the FPR, but they may not perform well with fewer detectors within a single year (i.e., sample size of detectors may be too small to accurately quantify spatial correlation). The most appropriate model to deal with this form of spatial dependence may be unmarked SCR (Chandler and Royle, 2013), though this model often produces biased and/or very imprecise density estimates (Morin et al. 2022) and are therefore unlikely to detect population declines with reasonable power.

We demonstrated increased power and reduced false positive rates when spatial grain (commonly referred to as grid cell size in camera trapping studies) was approximately the size of home ranges or larger (when detectors were spaced at 0.67 times the home range diameter or larger). Our review of previous studies estimating occupancy of Asian bears suggests that most researchers select grid cells approximating home range size of the target species, but several did not (Table 1). MacKenzie et al. (2017) suggest that selection of sample unit size should be based on the objective of the monitoring program and the desired interpretation of 'occupancy'; they do not advocate for or against using home range size of the species to guide selection of sample unit size, saying "there is no clear theoretical advantage to defining sample units at the approximate size of a home range or territory, and believe it is perfectly acceptable to define units at a scale that may be much smaller, or larger". However, when the objective of a monitoring study is to detect population declines using an occupancy modeling framework with point detectors in continuous space, one statistical advantage of selecting a grain size approximately the size of a home range or larger is that it will reduce the rate of detecting population changes that have not actually occurred, in either direction (increase or decrease). Falsely concluding that a small, still-threatened population is recovering is particularly concerning. The costs of this type of false positive population change can be extremely consequential for species that already occur at low abundance and may face many external threats since models with high false positive rates would not trigger conservation or management action. The monitoring efforts would therefore not provide the intended early warning needed for species that may truly be in decline. False positives in the other direction, where a population decline is registered when there is in fact no change, is also consequential since this may trigger management action and unnecessary spending of limited conservation funds, or may prompt a government or conservation organization to give up on a successful strategy that was thought not to be working.

The factors that influence the relationship between occupancy and abundance include population density, home range size, and study area size. Similar to simulations conducted by Steenweg et al. (2018), our occupancy-abundance relationship was positive for low density populations (6 or 16.5 bears/100 km^2) with low to moderate occupancy ($\psi < 0.9$) in both decline scenarios regardless of spatial grain. While grid cell size does not affect the occupancy-abundance relationship when sampling points in continuous space, we found that the selected spatial grain dictates the distance between detectors, which can induce spatial dependence in the occupancy process. Similar to our results, regardless of differences in spatial grain, the functional form of the relationship between occupancy and abundance remained the same (Steenweg et al., 2018). As occupancy approaches one as population density increases, increases in density no longer have an effect because all sites are already occupied and thus the positive and linear relationship between occupancy and abundance begins to attenuate due to sites being saturated and additional individuals at sites can no longer be reflected using presence/non-detection data when using occupancy as an index to abundance. Consistent with our results, home range size (Efford and Dawson, 2012) can affect the relationship between occupancy and abundance, suggesting that species-specific occupancy-abundance relationships may be necessary (Steenweg et al., 2018). Further, some studies have reported density-dependent changes in home range size (Efford et al., 2016), but we do not have insights into whether home range sizes of Asian bears are affected by local density.

Our simulation results were discouraging insofar as being able to detect changes relative to IUCN guidelines. Our simulations using a normal occupancy model and Royle-Nichols model showed that we had low (<0.67) power to detect a 20% population decline in 10 years, which is a steeper population decline than most IUCN criteria (since these criteria span three generations, or 30 years for bears). The low power to detect change is a result of not being able to fit enough detectors into any of the four study area sizes we evaluated. However, when the grid cell size was adequate in relation to home range size, we observed high power (>0.8) to detect 50% population declines with low (<0.05) false positive rates. Under the sampling conditions that we examined, these results suggest that occupancy or Royle-Nichols models are not good choices for monitoring when population changes are likely to be modest, but could be useful for detecting very dramatic changes.

Because we were simulating from a spatially-explicit population and detection model, several assumptions of typical occupancy models were violated, particularly that the occupancy states of sites within and between years are independent. Within years, our simulated site occupancy states will not be independent when single home ranges overlap multiple detectors. Then between years, our simulated occupancy states will not be independent due to the individual survival process and the assumption that individuals do not relocate activity centers between years. Both sources of dependence will be stronger at lower population densities where it is more likely that a single individual determines the occupancy states of multiple detectors across space and single detectors across time. Models to account for this spatio-temporal dependence exist, such as dynamic occupancy models (Banner et al., 2019) and/or occupancy models with spatial correlation in the occupancy process (Johnson et al., 2013). However, because we were interested in using realistic reserve sizes and realistically low population densities of Asian bears, we assumed the data sets for these populations will be too sparse to reliably fit the more complex models that can account for spatial correlation. We investigated violations to the occupancy model assumption of no unmodeled heterogeneity in site-level detection probability by evaluating false positive rate for the subset of scenarios not subject to spatial correlation. The false positive rate was affected by unmodeled site-level heterogeneity in detection, with false positive rate declining as detection increased, as the number of occasions increased, and as survival increased. We also found support that occupancy increases the false positive rate because it causes temporal dependence. Therefore, spatial correlation is the major cause of the inflated false positive rate, with site-level heterogeneity in detection and temporal correlation being more minor

causes.

5. Future directions

Well-articulated objectives are important at the forefront of a monitoring program and will help guide the data needed to achieve the stated objectives (Yoccoz et al., 2001). A values-focused approach (Keeney, 1992) allows for monitoring programs to be designed to best achieve stated objectives and inform conservation and management action (Nichols and Williams, 2006; Lyons et al., 2008; Lindenmayer et al., 2013). The focus on objectives helps ensure that monitoring programs are designed with adequate power to detect the desired trend (Legg and Nagy, 2006). Indeed, a shift to a more systematic approach to decision making may present challenges to managers, but those challenges can be overcome (Fuller et al., 2020). Clearly stated objectives and an accompanying set of simulations in advance of implementing fieldwork will help to avoid later misconceptions about what the monitoring program can achieve. We are hopeful that the simulations conducted here are a good guide as to practical expectations, and we summarize our findings as a distillation of the study design considerations for assessing trends in occupancy (Fig. 8).

Much data on Asian bears is now being obtained from large-scale, non-species-specific camera trapping, which allows for efficient monitoring of multiple species simultaneously (Sanderlin et al., 2014; Banner et al., 2019; Emmet et al., 2021), or as by-catch data on surveys designed for another focal species (Guillera-Arroita, 2017). For example, various national tiger (*Panthera tigris*) surveys (DNPWC and DFSC, 2018), optimized for this species, can be a rich source of data for other species, including sloth bears and Asiatic
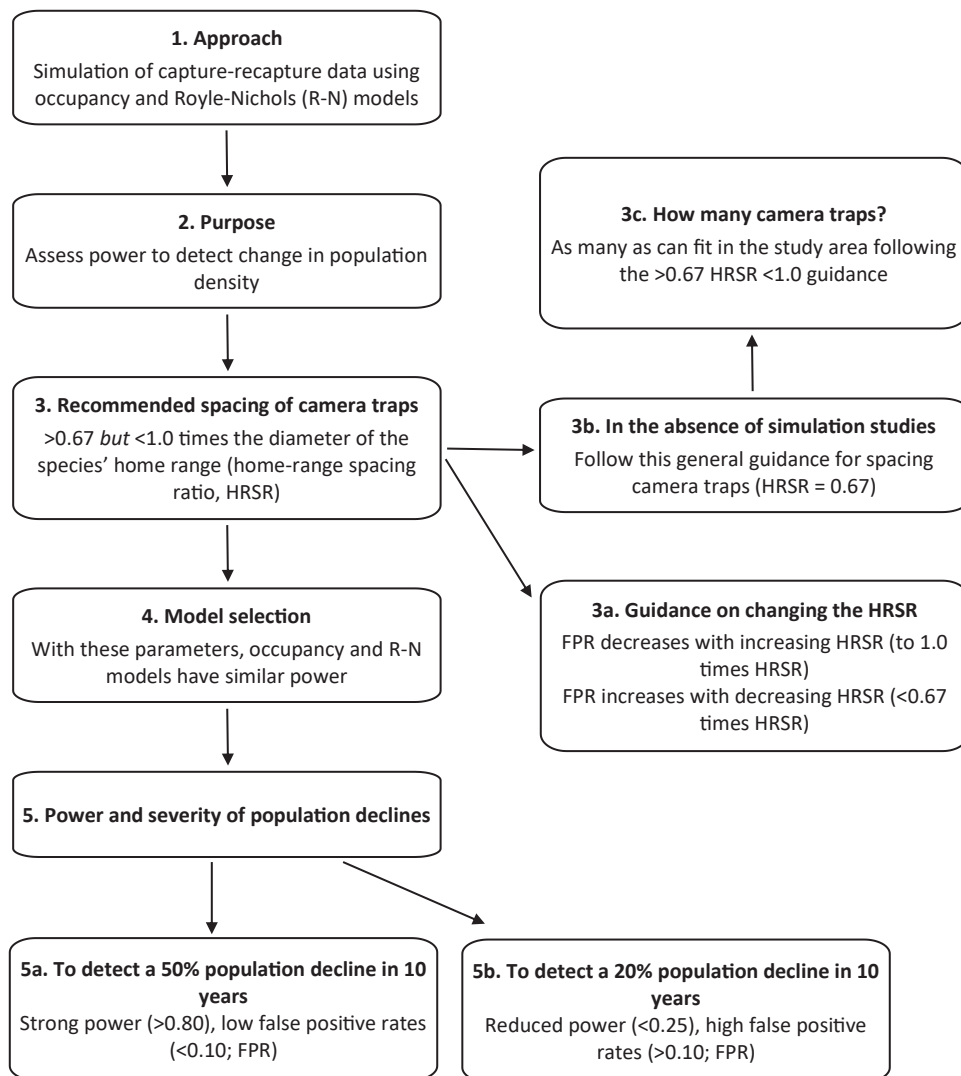

Fig. 8. Flowchart outlining results of the simulation study that could be used in the decision-making process associated with designing an occupancy study to detect population declines in Asian bears. Guidance uses mean values for power and false positive rate (FPR) for occupancy and Royle-Nichols (R-N) models. HRSR = home-range spacing ratio, or ratio of detector spacing to the 95% home-range diameter.

black bears. Concerted efforts to capitalize on these by-catch data would be especially useful because instead of being restricted to a small reserve, they can span large landscapes, thus yielding more power to detect population change. A promise for the future is adoption of community (citizen) science data collection efforts that are designed to collect presence-non-detection data (Sun et al., 2021). These efforts can greatly enhance data collected in systematic surveys.

Estimating density directly avoids many of the issues highlighted by our study. However, density estimation is more costly and logistically challenging. If employing cameras, individual bears must be recognizable, given that current "unmarked" methods do no better than occupancy in detecting population trends of Asian bears (Morin et al., 2022). Combining more intensive SCR sampling with occupancy sampling between surveys provides a potential way to combine the advantages of both approaches (Chandler and Clark, 2014).

We end with a warning that monitoring small populations in small areas, for species like bears that often have large home ranges in relation to the area being monitored, is a true conundrum. Employing a "use design" that has multiple detectors per home range presents the danger of observing changes in populations that are not real, and that itself is counter to the goals of any monitoring program. Investigators would be wise to not employ such designs when aiming to investigate trends in populations. The only exception would be in detecting extreme changes in the population, in which case there is high power despite the spatial dependence.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02075.

References

Augeri, D.M., 2005. On the Biogeographic Ecology of the Malayan Sun Bear (Ph.D.). University of Cambridge, Cambridge, UK, 331 pp.

Babu, S., Karthik, T., Srinivas, G., Kumara, H.N., 2015. Linking critical patches of sloth bear *Melursus ursinus* for their conservation in Meghamalai hills, Western Ghats, India. Curr. Sci. 109, 1492–1498.

Bailey, L.L., Hines, J.E., Nichols, J.D., MacKenzie, D.I., 2007. Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. Ecol. Appl. 17, 281–290.

Banner, K.M., Irvine, K.M., Rodhouse, T.J., Donner, D., Litt, A.R., 2019. Statistical power of dynamic occupancy models to identify temporal change: informing the North American Bat Monitoring Program. Ecol. Indic. 105, 166–176.

Barata, I.M., Griffiths, R.A., Ridout, M.S., 2017. The power of monitoring: optimizing survey designs to detection occupancy changes in a rare amphibian population. Sci. Rep. 7, 16491. https://doi.org/10.1038/s41598-017-16534-8.

Bashir, T., Bhattacharya, T., Poudyal, K., Quereshi, Q., Sathyakumar, S., 2018. Understanding patterns of distribution and space-use by *Ursus thibetanus* in Khangchendzonga, India: initiative towards conservation. In: Mamm. Biol., 92, pp. 11–20.

Bisi, F., Cremonesi, G., Gaffi, L., Zibordi, F., Gagliardi, A., Gueli, L., Martinoli, A., Preatoni, D.G., 2019. Watching a movie or going for a walk? Testing different Sun bear (*Helarctos malayanus*) occupancy monitoring schemes. Hystrik, the Italian. J. Mammal. https://doi.org/10.4404/hystrix–00246-2019.

Burton, A.C., Fisher, J.T., Adriaens, P., Treweek, J., Paetkau, D., Wikstrom, M., Callender, A., Vardanyan, R., Stepanyan, A., 2018. Density and distribution of a brown bear (*Ursus arctos*) population within the Caucasus biodiversity hotspot. J. Mammal. 99, 1249–1260. https://doi.org/10.1093/jmammal/gyy081.

Chandler, R.B., Clark, J.D., 2014. Spatially explicit integrated population models. Methods Ecol. Evol. 5, 1351–1360.

Chandler, R.B., Royle, J.A., 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. Ann. Appl. Stat. 936–954.

Das, S., Dutta, S., Sen, S., Jijumon, A.S., Babu, S., Kumara, H.N., Singh, M., 2014. Identifying regions for conservation of sloth bears through occupancy modelling in north-eastern Karnataka, India. Ursus 25, 111–120. https://doi.org/10.2192/URSUS-D-14-00008.1.

Devarajan, K., Morelli, T.L., Tenan, S., 2020. Multi-species occupancy models: review, roadmap, and recommendations. Ecography 43, 1612–1624.

Dharaiya, N., Bargali, H.S., Sharp, T., 2020. Melursus ursinus (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2020: e. T13143A166519315. https://dx.doi.org/10.2305/IUCN.UK.2020–1.RLTS.T13143A166519315.en. Downloaded on 21 August 2021.

DNPWC and DFSC, 2018. Status of Tigers and Prey in Nepal. Department of National Parks and Wildlife Conservation & Department of Forests and Soil Conservation. Ministry of Forests and Environment, Kathmandu, Nepal.

Dorazio, R.M., 2007. On the choice of statistical models for estimating occurrence and extinction from animal surveys. Ecology 88, 2773–2782.

Ellis, M.M., Ivan, J.S., Schwartz, M.K., 2014. Spatially explicit power analyses for occupancy-based monitoring of wolverine in the U.S. Rocky Mountains. Conserv. Biol. 28, 52–62.

Efford, M.G., Boulanger, J., 2019. Fast evaluation of study designs for spatially explicit capture–recapture. Methods Ecol. Evol. 10, 1529–1535.

Efford, M.G., Dawson, D.K., 2012. Occupancy in continuous habitat. Ecosphere 3, 1–15. https://doi.org/10.1890/ES11-00308.1.

Efford, M.G., Mowat, G., 2014. Compensatory heterogeneity in spatially explicit capture–recapture data. Ecology 95, 1341–1348.

Efford, M.G., Dawson, D.K., Jhala, Y.V., Qureshi, Q., 2016. Density-dependent home-range size revealed by spatially explicit capture–recapture. Ecography 39, 676–688.

Emmet, R.L., Long, R.A., Gardner, B., 2021. Modeling multi-scale occupancy for monitoring rare and highly mobile species. Ecosphere 12 (7), e03637. https://doi. org/10.1002/ecs2.3637.

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.

Fuller, A.K., Linden, D.W., Royle, J.A., 2016. Management decision making for fisher populations informed by occupancy modeling. J. Wildl. Manag. 80, 794–802.

Fuller, A.K., Decker, D.J., Schiavone, M., Forstchen, A., 2020. Ratcheting up rigor in wildlife management decision making. Wildl. Soc. Bull. https://doi.org/10.1002/ wsb.1064.

Garshelis, D.L., Joshi, A.R., Smith, J.L.D., 1999. Estimating density and relative abundance of sloth bears. Ursus 11, 87–98.

Garshelis, D., Steinmetz, R., 2020. Ursus thibetanus, Asiatic black bear (amended version of 2016 assessment). ⟨https://doi.org/10.2305/IUCN.UK.2020-3.RLTS. T22824A166528664.en⟩.

Gaston, K.J., Blackburn, T.M., 2003. Dispersal and the interspecific abundance-occupancy relationship in British birds. Glob. Ecol. Biogeogr. 12, 373–379.

Garshelis, D.L., Pigeon, K., Hwang, M.-H., Proctor, M., McShea, W.J., Fuller, A.K., Morin, D.J., 2022. The need to step-up monitoring of Asian bears. Glob. Ecol. Conserv. https://doi.org/10.1016/j.gecco.2022.e02087.

Gopalaswamy, A.M., 2006. Estimating sloth bear abundance from repeated presence-absence data in Nagarahole-Bandipur National Parks, India (M.Sc.). University of Florida, Gainesville, Florida, USA. 51pp.

Guillera-Arroita, G., 2017. Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. Ecography 40, 281–295.

Guillera-Arroita, G., Ridout, M.S., Morgan, B.J.T., 2010. Design of occupancy studies with imperfect detection. Methods Ecol. Evol. 1, 131–139.

Guharajan, R., Arnold, T.W., Bolongon, G., Dibden, G.H., Abram, N.K., Woan, T.S., Magguna, M.A., Goossens, B., Te, W.S., Nathan, S.K.S.S., Garshelis, D.L., 2018. Survival strategies of a frugivore, the sun bear, in a forest-oil palm landscape. Biodivers. Conserv. 27, 3657–3677.

Harris, R.B., Schwarts, C.C., Mace, R.D., Haroldson, M.A., 2011. Study design and sampling intensity for demographic analyses of bear populations. Urus 22, 24–36.

Harrison, R.D., Sreekar, R., Brodie, J.F., Brook, S., Luskin, M., O'Kelly, H., Rao, M., Scheffers, B., Velho, N., 2016. Impacts of hunting on tropical forests in Southeast Asia: hunting in tropical forests. Conserv. Biol. 30, 972–981. https://doi.org/10.1111/cobi.12785.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models, first ed. Chapman and Hall/CRC, 352 pp.

He, F., Gaston, K.J., 2000. Occupancy-abundance relationships and sampling scales. Ecography 23, 503–511.

Hull, V., Zhang, J., Zhou, S., Huang, J., Li, R., Liu, D., Xu, W., Huang, Y., Quyang, Z., Zhang, H., Liu, J., 2015. Space use by endangered giant pandas. J. Mammal. 96, 230–236.

Hwang, M., Garshelis, D.L., Wu, Y., Wang, Y., 2010. Home ranges of Asiatic black bears in the central mountains of Taiwan: gauging whether a reserve is big enough. Ursus 21, 81–96.

IUCN, 2019. IUCN Standards and Petitions Committee. Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. Downloadable from ⟨http://www.iucnredlist.org/documents/RedListGuidelines.pdf⟩.

Johnson, D.S., Conn, P.B., Hooten, M.B., Ray, J.C., Pond, B.A., 2013. Spatial occupancy models for large data sets. Ecology 94, 801–808.

Joshi, A.R., Garshelis, D.L., Smith, J.L.D., 1995. Home ranges of sloth bears in Nepal: Implications for conservation. J. Wildl. Manag. 59, 204–214.

Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D., MacKenzie, D.I., 2011. Monitoring carnivore populations at the landscape scale: occupancy. Modelling of tigers from sign surveys. J. Appl. Ecol. 48, 1048–1056.

Keeney, R.L., 1992. Value-focused Thinking. Harvard University Press, Cambridge, Massachusetts, USA.

Latif, Q.S., Ellis, M.M., Saab, V.A., Mellen-McLean, K., 2018. Simulations inform design of regional occupancy-based monitoring for a sparsely distributed, territorial species. Ecol. Evol. 8, 1171–1185.

Legg, C.J., Nagy, L., 2006. Why most conservation monitoring is, but need not be, a waste of time. J. Environ. Manag. 78, 194–199.

Letro, L., Wangchuk, S., Dhendup, T., 2020. Distribution of Asiatic black bear and its interaction with humans in Jigme Singye Wangchuck National Park, Bhutan. Nat. Conserv. Res. 5, 44–52.

Linden, D.W., Fuller, A.K., Royle, J.A., 2017. Examining the occupancy-density relationship for a low density carnivore. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.12883. ⟨https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12883⟩.

Lindenmayer, D.B., Piggott, M.P., Wintle, B.A., 2013. Counting thebooks while the library burns: why conservation monitoring programs need a plan for action. Front. Ecol. Environ. 11, 549–555.

Linkie, M., Dinata, Y., Nugroho, A., Haidir, I.A., 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra. Biol. Conserv. 137, 20–27.

Lyons, J.E., Runge, M.C., Laskowski, H.P., Kendall, W.L., 2008. Monitoring in the context of structured decision-making and adaptive management. J. Wildl. Manag. 72, 1683–1692. https://doi.org/10.2193/2008-141.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

MacKenzie, D.I., Royle, J.A., Brown, J.A., Nichols, J.D., 2004. Occupancy estimation and modeling for rare and elusive populations. In: Thompson, W.L. (Ed.), Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters. Island Press, Washington, D.C., USA, pp. 149–172.

MacKenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42, 1105–1114.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling. Academic Press, San Diego, California, USA.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2017. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier, Oxford, UK.

Magoun, A.J., Ray, J.C., Johnson, D.S., Valkenburg, P., Dawson, F.N., Bowman, J., 2007. Modeling wolverine occurrence using aerial surveys of tracks in snow. J. Wildl. Manag. 71, 2221–2229.

McLellan, B.N., Proctor, M.F., Huber, D., Michel, S., 2017. Ursus arctos (amended version of 2017 assessment). The IUCN Red List of Threatened Species 2017: e. T41688A121229971. https://dx.doi.org/10.2305/IUCN.UK.2017–3.RLTS.T41688A121229971.en. Downloaded on 21 August 2021.

Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. Trends Ecol. Evol. 21, 668–673.

Morin, D.J., Boulanger, J., Bischof, R., Lee, D.C., Ngoprasert, D., Fuller, A.K., McLellan, B., Steinmetz, R., Sharma, S., Gopalaswamy, A.M., Nawaz, M.A., Karanth, U., Garshelis, D.L., 2022. Comparison of methods for estimating density and population trends for low-density Asian bears. Glob. Ecol. Conserv. 35, e02058.

Ngoprasert, D., Reed, D.H., Steinmetz, R., Gale, G.A., 2012. Density estimation of Asian bears using photographic capture–recapture sampling based on chest marks. Ursus 23, 117–133. https://doi.org/10.2192/URSUS-D-11-00009.1.

O'Brien, T.G., Baillie, J.E.M., Krueger, L., Cuke, M., 2010. The Wildlife Picture Index: monitoring top trophic levels. Anim. Conserv. 13, 335–343.

O'Connell, A.F., Bailey, L.L., 2011. Inference for occupancy and occupancy dynamics. In: O.'Connell, A.F., Nichols, J.D., Karanth, K.U. (Eds.), Camera Traps in Animal Ecology. Springer, Tokyo, Japan, pp. 191–205.

Pacifici, K., Reich, B.J., Dorazio, R.M., Conroy, M.J., 2016. Occupancy estimation for rare species using a spatially-adaptive sampling design. Methods Ecol. Evol. 7, 285–293.

Pavlacky, D.C., Blakesley, J.A., White, G.C., Hanni, D.J., Lukacs, P.M., 2012. Hierarchical multiscale occupancy estimation for monitoring wildlife populations. J. Wildl. Manag. 76, 154–162.

Puri, M., Srivathsa, A., Karanth, K.K., Kumar, N.S., Karanth, K.U., 2015. Multiscale distribution models for conserving widespread species: the case of sloth bear *Melursus ursinus* in India. Divers. Distrib. 21, 1087–1100.

Ramesh, T., Kalle, R., Sankar, K., Qureshi, Q., 2012. Factors affecting habitat patch use by sloth bears in Mudumalai tiger reserve, Western Ghats, India. Ursus 23, 78–85.

Ratnayeke, S., van Manen, F.T., Padmalal, U.K.G.K., 2007. Home ranges and habitat use of sloth bears *Melursus ursinus Inornatus* in Wasgomuwa National Park, Sri Landa. Wildl. Biol. 13, 272–284.

Rodríguez, J.P., 2021. Reverse the Red: achieving global biodiversity targets at national level. Oryx 55, 1–2. https://doi.org/10.1017/S0030605320001337.

Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84, 777–790.

Royle, J.A., Chandler, R.B., Sollmann, R., Gardner, B., 2013. Spatial Capture-recapture. Academic Press.

Sanderlin, J.S., Block, W.M., Ganey, J.L., 2014. Optimizing study design for multi-species avian monitoring programs. J. Appl. Ecol. 51, 860–870.

Sewell, D., Guillera-Arroita, G., Griffiths, R.A., Beebee, T.J.C., 2012. When is a species declining? Optimizing survey effort to detect population changes in reptiles. PLoS One 7, e43387.

Scotson, L., Fredriksson, G., Augeri, D., Cheah, C., Ngoprasert, D., Wai-Ming, W., 2017. Helarctos malayanus (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e.T9760A123798233. https://dx.doi.org/10.2305/IUCN.UK.2017–3.RLTS.T9760A45033547.en. Downloaded on 21 August 2021.

Sharief, A., Joshi, B.D., Kumar, V., Kumar, M., Dutta, R., Sharma, C.M., Thapa, A., Rana, H.S., Mukherjee, T., Singh, A., Thakur, M., Sharma, L.K., Chandra, K., 2020. Identifying Himalayan brown bear (*Ursus arctos isabellinus*) conservation areas in Lahaul Valley, Himachal Pradesh. Glob. Ecol. Conserv. 21, e00900 https://doi.org/10.1016/j.gecco.2019.e00900.

Seidensticker, J., Yoganand, K., Johnsingh, A.J.T., 2011. Sloth bears living in seasonally dry tropical and moist broadleaf forests and their conservation. In: McShea, W., Davies, S., Bhumpakphan, N. (Eds.), Dry Forests of Asia: Conservation and Ecology. Smithsonian Institution Press, Washington, D.C, pp. 217–236.

Srivathsa, A., Puri, M., Kumar, N.S., Jathanna, D., Karanth, U., 2018. Substituting space for time: empirical evaluation of spatial replication as a surrogate for temporal replication in occupancy modelling. J. Appl. Ecol. 55, 754–765. https://doi.org/10.1111/1365-2664.13005.

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., McKelvey, K., 2018. Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. Ecology 99, 172–183.

Sun, C.C., Royle, J.A., Fuller, A.K., 2019. Incorporating citizen science data in spatially explicit integrated population models. Ecology 100 (9), e02777.

Sun, C.C., Fuller, A.K., Royle, J.A., 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. PLoS One 9 (2), e88025. https://doi.org/10.1371/journal.pone.0088025.

Sun, C.C., Hurst, J.E., Fuller, A.K., 2021. Citizen science data collection for integrated wildlife population analyses. Front. Ecol. Evol. https://doi.org/10.3389/fevo.2021.682124.

Swaisgood, R., Wang, D., Wei, F., 2016. Ailuropoda melanoleuca (errata version published in 2017). The IUCN Red List of Threatened Species 2016: e.T712A121745669. https://dx.doi.org/10.2305/IUCN.UK.2016–2.RLTS.T712A45033386.en. Downloaded on 21 August 2021.

Tucker, J.M., Moriarty, K.M., Ellis, M.M., Golding, J.D., 2021. Effective sampling area is a major driver of power to detect long-term trends in multispecies occupancy monitoring. Ecosphere 12 (5), e03519. https://doi.org/10.1002/ecs2.3519.

Weir, L., Fiske, I.J., Royle, J.A., 2009. Trends in anuran occupancy from northeastern states of the North American Amphibian Monitoring Program. Herpetol. Conserv. Biol. 4, 389–402.

Whittington, J., Hebblewhite, M., Chandler, R.B., 2018. Generalized spatial mark–resight models with an application to grizzly bears. J. Appl. Ecol. 55, 157–168.

Wong, S.T., Servheen, C., Ambu, L., 2014. Home range, movement and activity patterns, and bedding sites of Mallayan sun bears *Helarctos malayanus* in the rainforest of Borneo. Biol. Conserv. 119, 169–181.

Wong, W.-M., Leader-Williams, N., Linkie, M., 2013. Quantifying changes in sun bear distribution and their forest habitat in Sumatra. Anim. Conserv. 16, 216–223. https://doi.org/10.1111/j.1469-1795.2012.00587.x.

Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. Trends Ecol. Evol. 16, 446–453.