Comparison of methods for estimating density and population trends for low-density Asian bears

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ABSTRACT

Populations of bears in Asia are vulnerable to extinction and effective monitoring is critical to measure and direct conservation efforts. Population abundance (local density) or growth (λ) are the most sensitive metrics to change. We discuss the value in implementing spatially explicit capture-recapture (SCR), the current gold standard for density estimation, and open population SCR (OPSCR) to monitor changes in density over time. We provide guidance for designing studies to provide estimates with sufficient power to detect changes. Because of the wide availability of camera traps and interest in their use, we consider six density estimation methods and their extensions developed for use with camera traps, with specific consideration of assumptions and applications for monitoring Asian bears. We conducted a power analysis to calculate the precision in estimates needed to detect changes in populations with reference to IUCN Red List criteria. We performed a systematic review of empirical studies implementing camera trap abundance estimation methods and considered sample sizes, effort, and model assumptions required to achieve

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adequate precision for population monitoring. We found SCR and OPSCR, reliant on "marked" individuals, are currently the only methods with enough power to reliably detect even moderate to major (20–80%) declines. Camera trap methods with unmarked individuals rarely achieved precision sufficient to detect even large declines (80–90%), although with some exceptions (e.g., situations with moderate population densities, large number of sampling sites, or inclusion of ancillary local telemetry data. We describe additional estimation options including line transects, direct observations, monitoring age-specific survival and reproductive rates, and hybrid/integrated methodologies that may have potential to work for some Asian bear populations. We conclude monitoring changes in abundance or density is possible for most Asian bear populations but will require collaboration among researchers over broad spatial extents and extensive financial investment to overcome biological and logistical constraints. We strongly encourage practitioners to consider study design and sampling effort required to meet objectives by conducting simulations, power analyses, and assumption checks prior to implementing monitoring efforts, and reporting standardized dispersion measures such as coefficients of variation to allow for assessment of precision. Our guidance is relevant to other low-density and wide-ranging species.

1. Introduction

All four bear species endemic to Asia are considered vulnerable to extinction: sun (*Helarctos malayanus*), sloth (*Melursus ursinus*), and Asiatic black bears (*Ursus thibetanus*) due to suspected population declines, and giant pandas (*Ailuropoda melanoleuca*) because the estimated total population size is small (Garshelis et al., 2022 this series). Likewise, brown bear (*Ursus arctos*) populations in south Asia tend to be small and isolated, with most listed as Vulnerable, Endangered or Critically Endangered on the IUCN Red List (McLellan et al., 2017), even though this species is not globally threatened because it is faring well in North America, Europe, and northern Asia.

Conservationists frequently must prioritize actions and rely on monitoring data to indicate when and where action is necessary or to evaluate the outcome of actions. For example, managers or conservationists may need to know if a population is in decline or recovering, identify areas that contain sustainable populations, or evaluate if protection of a specific area resulted in increases in the bear population. That is, there is a need to monitor population change. However, logistics, constraints on species-specific data collection, and analytical challenges often limit applications for effective, reliable, and replicable monitoring of Asian bears (Garshelis et al. 2022 and Proctor et al., 2022). Here we evaluate the use of density estimation as a monitoring tool in the context of Asian bears, but also more broadly for low-density species that can be camera-trapped or genetically sampled.

1.1. Why is abundance or density the preferred parameter for monitoring population trends?

Estimating how many individuals are in a population or area at a certain point in time (abundance, *N*) is one of the most effective ways to assess population status (Caughley, 1977; Williams et al., 2002). Temporal changes or spatial differences in abundance can indicate impacts to a population earlier than occurrence or change in range. Similarly, changes in abundance (population growth rate, λ) is the most sensitive population metric to evaluate if an existing population responds positively to conservation actions (Kéry and Royle, 2020). More coarse metrics such as changes in distribution require that portions of a populations range become locally extirpated before a change in status will be registered, whereas estimating population growth can show an increase or decrease in the number of bears before local extirpation. While occupancy has been successfully implemented to monitor population change of territorial species such as northern spotted owls (*Strix occidentalis caurina*, Yackulic et al., 2014), and sparsely distributed solitary species such as tigers (*Panthera tigris*, Karanth et al., 2011) or fishers (*Pekania pennanti*, Fuller et al., 2016), home ranges of Asian bears commonly overlap (Izumiyama and Shiraishi, 2004; Wong et al., 2004; Bellemain et al., 2007; Ratnayeke et al., 2007; Hwang, . et al., 2010), particularly in situations with increased resource availability (Zhang et al., 2014). This means many bears may be lost before a spatial area becomes extirpated. Occupancy also requires a minimum number of sampling units at a spacing many times greater than the average size of a bear's home range. As a result, small areas will not fit enough sampling units at the correct spacing (MacKenzie and Royle, 2005; Efford and Dawson, 2012; but see Fuller et al., this series). Thus, directly assessing changes in abundance may be the most effective way of evaluating if a bear population is stable or in peril with enough time to respond.

Often, ecologists prefer to estimate density (*D* = *N*/area) rather than abundance to enable comparisons over time or in different places. If a population is geographically closed (the population is sufficiently isolated from other populations and there is no immigration and emigration occurring outside of the sampled area), it may be enough to estimate abundance at different points in time to assess population growth (e.g., brown bears in the Gobi Desert; Tumendemberel et al., 2021). But few populations are geographically isolated and abundance estimation and inference is limited to undefined effective sampling areas determined by movement of bears relative to the placement of sampling devices across the study area (the detector array or grid; Efford, 2004; Borchers and Efford, 2008; Royle and Young, 2008). In these circumstances, differences in movements within home range from one sampling period to the next, or in different areas, can change the abundance estimates even if there is no change in the actual population. By standardizing abundance estimates over units of space (such as bears per 100 km^2), we can better compare differences in populations without bias.

1.2. Overview of density estimation methods for Asian bear populations

While estimation of N or D is the preferred objective, it also requires intensive sampling and analytic methods. The main challenge in estimating density is that it is seldom possible to observe or census all individuals due to the cryptic nature of bears, as well as their low densities across large areas. Indices of abundance using counts of the number of photos of bears or tallies of their signs detected during standardized surveys can be biased by differences in activity, movements, and behavior (Sollmann et al., 2013b; Gopalaswamy et al., 2015). For example, differences in available food resources from one year to another may affect the number of trees climbed for food (and resulting bear claw marks observed) even if the population size is unchanged. Distribution of resources can also change home range size and habitat use, resulting in different encounter rates of bears at a camera trap grid, even if there is still the same number of bears. Thus, many methods for estimating density are based on capture-recapture and require the identification of individual bears to correct for biases resulting from differing detection probabilities (p).

The challenge in applying capture–recapture approaches to Asian bears is identifying individual bears, which is a prerequisite to accurately estimate abundance or density with precision (Amstrup et al., 2005). Sun bears, sloth bears, and Asiatic black bears can be distinguished by patterns in their chest blazes, and some populations of brown bears have prominent markings that can aid in individual recognition (Nawaz et al., 2008). However, typically these marks are not easily or fully visible in camera-trap photos. To obtain sufficiently clear photos of these markings to distinguish individuals may require up to three camera traps per station and suspending a bait to make the bear stand up (Ngoprasert et al., 2012). Identifying individuals from fecal DNA has previously been problematic for

Table 1
Select methods for monitoring density, abundance, and population growth.

Approach	Acronym used in present review	References	Software and packages available
Spatially explicit capture-recapture (also referred to as spatial capture-recapture)	SCR	We use a general term to refer to all approaches including integration over the full likelihood (Borchers and Efford, 2008), maximum likelihood estimation (MLE) with data augmentation (Royle et al., 2014), and Bayesian estimation with data augmentation (Royle and Young, 2008) Bischof et al. (2020) and Turek et al. (2020)	secr (R) oSCR (R) DENSITY SPACECAP (R) Implementations in JAGS and nimble nimbleSCR (R)
Open population spatially explicit capture-recapture	OPSCR	Gardner et al. (2010) Ergon and Gardener (2014) Bischof et al. (2016) Chandler et al. (2018) Gardner et al. (2018) Efford and Schofield (2019) Bischof et al. (2020) Turek et al. (2021)	secr (R) oSCR (R) Implementations in JAGS and nimble nimbleSCR (R)
Royle-Nichols model N-mixture models	R-N	Royle and Nichols (2003) Royle (2004)	unmarked (R) MARK (gui) unmarked (R) Implementations in JAGS
Unmarked spatially explicit capture-recapture (also referred to as spatial count or spatially correlated count models)	USCR	Chandler and Royle (2013) Royle et al. (2014) Ramsey et al. (2015)	Implementations in JAGS and nimble
Unmarked spatially explicit capture-recapture models with informed priors or some proportion of the population marked	USCR+	Burgar et al. (2018) Johnson (2019)	Implementations in JAGS and nimble
Spatial mark–resight	SMR (USCR+)	Sollmann et al. (2013a)Whittington et al. (2018); Efford and Hunter (2018)	Implementations in JAGS and nimblescr
Generalized spatial mark–resight	Gen-SMR (USCR+)	Whittington et al. (2019) Jimenez et al. (2019)	Implementations in JAGS and nimble
Random thinning spatial mark–resight	RT-SMR	Jiménez et al. (2021)	Implementation in nimble
Random encounter model	REM	Rowcliffe et al. (2008) Caravaggi (2017)	remBoot (R)
Random encounter and staying time model	REST	Nakashima et al. (2018)	
Time-to-event model	TTE	Moeller et al. (2018)	spaceNtime (R)
Space-to-event model	STE	Moeller et al. (2018)	spaceNtime (R)
Instantaneous sampling	IS	Moeller et al. (2018)	spaceNtime (R)
Camera trap DISTANCE sampling	CTDS	Howe et al. (2017)	DISTANCE (gui) distance (R) Dsim (R)
Line transect DISTANCE sampling	LTDS	Buckland et al. (2001) Thomas et al. (2010) Buckland et al. (2015)	DISTANCE (gui) distance (R) Dsim (R)
Estimating trend based on age-specific survival and reproductive rates		Eberhard, 1994	

Asian bears due to generally low individual identification success rates (Dutta et al., 2015) and the difficulty of finding bear feces in tropical environments where decomposition rates are high (Wong et al., 2002; Steinmetz et al., 2013; but see Fredriksson et al., 2006 and Zhan et al., 2006 for exceptions). Genetic capture-recapture methods have been applied to brown bears throughout Europe, and brown bears and American black bears (*Ursus americanus*) in North America using DNA gathered from hair-snare traps (initially developed for bears) and rub trees (Woods et al., 1999; Kendall et al., 2019). Researchers have been able to obtain hair samples from Asiatic black bears (Vaeokhaw et al., 2020), sun bears (Tee et al., 2020), and sloth bears (Sharma et al., 2013; Dutta et al., 2015) for pilot studies and population genetics analyses. But detection rates and required effort for hair trapping have rarely been explored for Asian bear populations (but see Tumendemberel et al., 2015 and Burton et al., 2018).

A recent proliferation of "unmarked" methods attempt to mitigate the logistical and financial challenges of identifying individuals when estimating density. These models do not require individuals to have unique marks but instead make more restrictive assumptions or require ancillary data about individual movement to parse activity and detection biases from abundance (Gilbert et al., 2021). Several of these methods may have applications to Asian bears but scrutiny of the assumptions relative to each species and environmental context is necessary and further validation including potential for biases and assessment of power to detect population change is needed before attempting to apply for monitoring objectives (Amburgey et al., 2021).

The objectives of this article are to assess approaches and identify limitations and future directions to improve density estimation for Asian bears (Table 1). Four of the five criteria the IUCN uses to assess Red List status are contingent on estimates of population size or realized, inferred, or projected population decline (IUCN, 2012). Therefore, it is imperative to consider how study design and analytical method may affect precision and ability to detect a decline over time. In view of this, we used power calculations to establish standards for precision of population estimates to detect population changes or differences among study areas (Efford and Boulanger, 2019). We conducted a literature review of existing empirical studies (of any species) using camera traps to estimate abundance or density to assess how well different methods achieve required levels of precision. We discuss design considerations of approaches to improve precision and identify possible applications and limitations of each method for scenarios specific to monitoring Asian bears.

2. Potential analytical methods for estimating abundance and density for Asian bears

2.1. Mark–recapture and spatially explicit capture-recapture with individual identification (marks)

Failure to account for heterogeneity (differences) in the probability of detection, *p,* across space and time can bias estimates. Estimating *p* commonly involves an initial marking of a sample (*M*). Historically marking of bears was accomplished using physical tags, but now is often done using existing "marks" distinguishable on photographs or genotypes obtained from hair or scat. The population is later resampled (with n_2 bears detected of which m_2 were identified as being previously detected) and *p* estimated from the proportion of previously detected bears in the second session (m_2/n_2). Dividing the number of marked bears known to be in the population by their proportion in the population yields an estimate of population size. The challenge with applying this type of estimator is that it assumes detection probabilities are similar for all bears within a sampling occasion. Data collected to track changes in populations typically begin as counts of detections, but rarely are all individuals detected. In reality, *p* can also vary by individual and through time in response to capture, seasonal effects, and susceptibility to being sampled. One approach is to confront variation in *p* with stringent assumptions (e.g., no changes in population size; no births, deaths, immigration, and emigration) between sampling occasions (the most notable being closed models; Otis et al., 1978; White et al., 1982). Another problem is that bears tend to be wide-ranging, and in continuous habitats the animals along the edges of the sampled area live partly in and partly out of the geographic
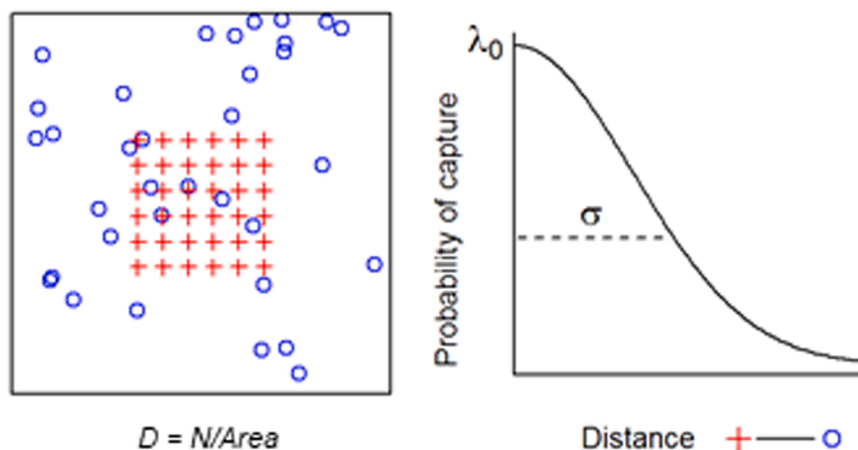
Fig. 1. Spatially explicit capture–recapture. The animal population is viewed as a scatter of individual activity centers in 2 dimensions (left, blue circle; parameter D density). The probability of detection at a fixed detector (red cross) is related to the distance between the activity center and detector (right; parameters λ_0 intercept and σ spatial scale). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

area of interest. This creates an ill-defined estimate of population size and can inflate the estimate of density derived by dividing abundance by area, since the real area that the animals use is larger than the sampled area (Wilson and Anderson, 1985; Boulanger and McLellan, 2001).

SCR models address many of the above issues by utilizing spatial information obtained by recaptures (repeated detections) of bears at different traps on sampling grids to estimate the probability of detection at various distances from the individual's estimated activity center. This can be conceptualized as 1) an overall estimate of detection probability (g_0), or encounter rate (λ_0), at the location of the activity center and 2) an estimate of the rate of decline in detection probability with increasing distance (σ) between the detector and the activity center. A statistical model is fitted to the observations to remove potential bias when some individuals escape detection, and the population lacks a natural boundary. The statistical model includes submodels for the spatial distribution of animals (strictly, a spatial point process for their activity centers) and for the probability of detecting an animal at a point, given the distance from that point to its activity center (Fig. 1).

SCR models estimate the home range center of each bear detected on the sampling grid based on the configuration of detectors (e.g., physical traps, hair traps, camera traps) relative to where the bear was detected and its estimated movements. The location of estimated home range centers, and thus density, can then be related to habitat and anthropogenic covariates (Royle et al., 2013; Efford, 2014a). There are several modeling approaches to SCR (Table 1) using both MLE with full integration over the sampling area, MLE with conditional likelihood (*n*|*N*; Borchers and Efford, 2008; Sutherland et al., 2019) and Bayesian estimation with data augmentation (Royle et al., 2013). The availability of software and R packages have allowed for the rapid adoption of SCR methods to bear population size estimation.

A challenge in the application of SCR methods is how to efficiently sample areas to allow the most individuals to be detected while also ensuring enough spatial recaptures to estimate the detection kernel (this requires multiple detectors within an individual home range). SCR methods have the advantage that trap layout is modeled and therefore the conventional CR assumption that all bears in the area have a non-zero detection probability can be relaxed. However, it is still important that the traps sample the target area of interest in a representative fashion. For example, if sampling occurs only in areas where detection is expected to be high, then derived density estimates would pertain to these areas and should not be extrapolated to entire area with different habitats that might support different bear densities. Systematic sampling using grid cells (where a detector is placed in one grid cell) or sub-grids/cluster sampling (Humm and Clark 2017; Clark, 2019) can increase spatial extent and number of individuals available for detection and provide representative sampling of the landscape. Several recent papers provide guidelines for sampling designs using SCR (Sun et al., 2014; Clark, 2019; Efford and Boulanger, 2019; P. Dupont et al., 2021; G. Dupont et al., 2021; Durbach et al., 2021).

An underlying question in study design is the optimal trap spacing and number of traps required to obtain accurate and precise estimates. If we assume that methods applied in empirical studies produce unbiased estimates of density, the coefficient of variation
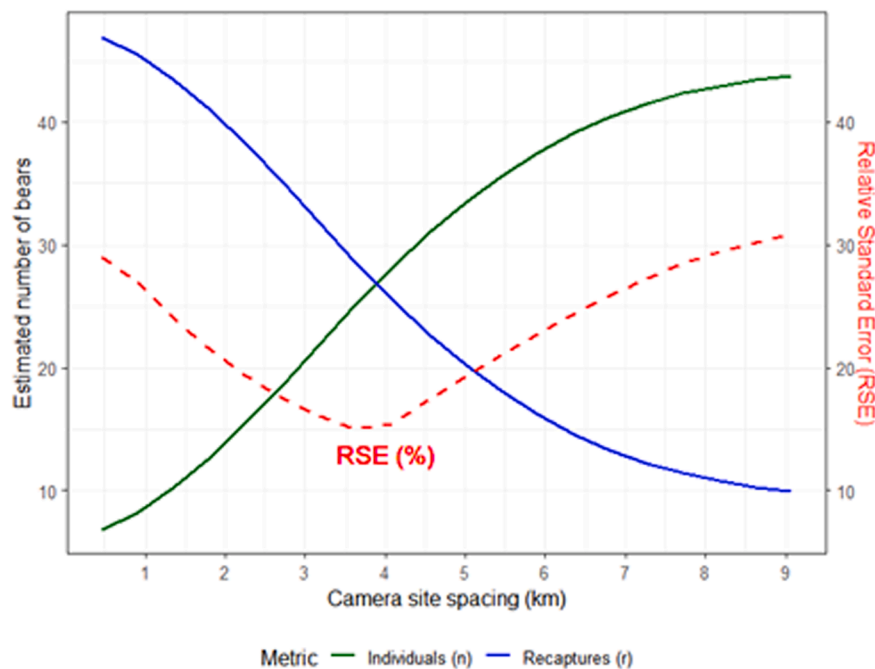

Fig. 2. Illustration of the use of empirical data and simulations for assessing the relationship between camera trap spacing, the estimated number of individuals detected, total recaptures, for a fixed 6 × 6 grid where trap spacing (and overall grid size) is varied. Also shown on the 2nd axis is the associated precision (RSE; here equivalent to % CV). The data for this graph are for sun bear camera trap data with detection at home range center (g_0) = 0.19 and spatial scale (σ) = 2.27 km (Ngoprasert et al., 2012) sampled for five sessions in a 6 × 6 rectangular grid with an assumed density of 5 bears per 100 km^2.
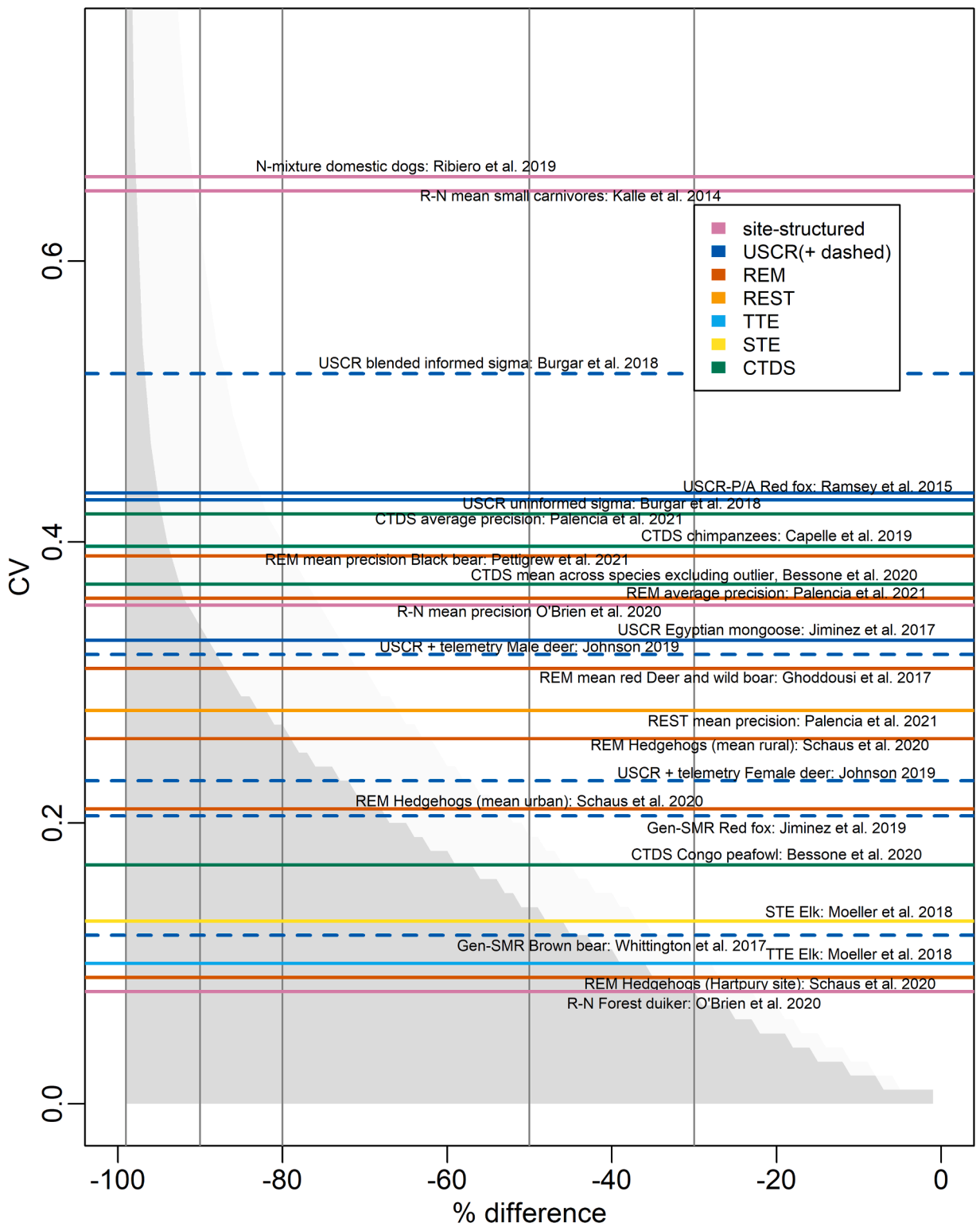
(CV; a measure of precision where lower values indicate greater precision) serves as a useful metric to assess the efficacy of density estimation methods. A recent review of empirical studies using camera traps for SCR found the CV of density estimates averaged 0.31, with only 21% of studies reporting a CV < 0.20 (Green et al., 2020), a commonly accepted benchmark for precision to be considered useful for wildlife management (Pollock et al., 1990; Williams et al., 2002). However, several SCR studies on North American bears (using hair traps instead of cameras) have shown greater precision, in part because resources allowed for extensive sampling of large spatial extents (including cluster designs) over which studies were conducted, exposing a greater sample of bears to capture (Morehouse and Boyce, 2016; Humm and Clark 2017; Boulanger et al., 2018; Kendall et al., 2019; Stetz et al., 2019) compared to the studies reviewed by Green et al. (2020). Precision of SCR estimates is also affected by local density of the bears and sampling effort. For example, a cluster design study employed to estimate bear densities across Florida, USA, showed variable precision for study areas with two levels of density and different numbers of hair traps (Humm and Clark 2017). Precision was similar for an area with higher bear density (0.13 bears/100 km^2) with 190 traps (CV = 0.13) compared to an area with lower bear density (0.08 bears/100 km^2) with 324 traps (CV = 0.13), but precision was lower (CV = 0.24) for an area of approximately the same high density (0.13 bears/100 km^2) when only 83 traps were sampled (Humm and Clark 2017). Apart from sampling effort, these variations in precision are also influenced by detection probabilities, which are often difficult to pre-determine. However, it appears that study areas with higher densities will require less intensive sampling, although there is nonetheless a threshold of minimum effort below which precision will suffer, even at higher densities.

Optimal placement of traps can be approximated by a design where the number of individuals (n) sampled equals the number of total recaptures (r) with precision of estimates, as indicated by relative standard error (RSE=$SE(\widehat{D})/\widehat{D}$), being approximated by $1/\sqrt{\min[\widehat{f_0}](E(n), E(r))}$. Basically, this means that the overall precision of estimates will be determined by either the number of bears detected, or the total number of recapture events, whichever is smallest. Mark–recapture studies strive to obtain estimates with an RSE (similar here to CV) of 0.20 or less (Pollock et al., 1990; Williams et al., 2002). Using estimates of g_0 and σ it is possible to approximate the number of detections and redetections as a function of different trap layouts and from this, assess optimal trap spacing for sampling detectors (Efford and Boulanger, 2019). For example, using sun bear camera trapping data from Ngoprasert et al. (2012), we estimated the number of bears detected, and the number of recaptures, with a uniform sampling grid of 36 camera traps and an assumed density of 5 bears/100 km^2 sampled for five occasions. For these simulations it was assumed that the number of camera traps was fixed and therefore changing trap spacing changed the overall size of the sampling grid and the resulting number of bears subject to detection. In this case the optimal trap spacing is 3.7 km (Fig. 2); closer than this, too few bears are detected with 36 camera traps because only a small area is covered, and with wider spacing the recapture rate of individual bears becomes too small because successive cameras are out of range of individual bears, given bears' average movements around their home ranges. Bear density in this case does not influence optimal spacing but does influence the estimated level of precision. These results are similar to the findings of Ngoprasert et al. (2012), who used a 1.5–2 km trap spacing, but learned subsequently from simulations that a 4-km spacing (and hence larger study area) would have improved the precision of their density estimates. They concluded, after conducting a significant field effort in two study areas, that due to the low precision of their estimates, their estimates "have limited value for monitoring purposes," and they recommended using simulations to improve future study designs (Ngoprasert et al., 2012). The best design in this case increased spacing to 3.7 km so that the number of bears detected roughly equaled the number of recapture events.

The approximation method is available in the *secrdesign* package (Efford, 2015) and its associated web-based Shiny app (https://www.stats.otago.ac.nz/secrdesignapp/). This method allows efficient testing of various sampling configurations under a variety of assumed detection and density scenarios which can be cross-validated using simulations. Simulation studies are critical in assessing designs and easily implemented using *secrdesign* or writing functions to employ in oSCR R package (an alternative SCR package employing MLE; Sutherland et al., 2019). Simulations are more difficult for Bayesian implementation of SCR as there is often extensive computation time required for each iteration of each design scenario. However, this does not mean that simulation should not be attempted if planning to use a Bayesian SCR model. When likelihoods are compatible, or if only the basic SCR parameters are being assessed (N/D, g_0 and σ), survey designs can be evaluated using MLE approaches (e.g., oSCR) but real data may still be analyzed using Bayesian SCR models. Hence, MLE approximations and simulations could still be used to calculate other metrics associated with different study designs that indicate desired precision (i.e., number of individuals detected, number of spatial recaptures, distance moved between recaptures) without requiring running each model with simulated data to convergence.

2.1.1. Open population spatially explicit capture-recapture

Conservationists are often more interested in determining the direction and rate of population change (hereafter trend) than simply population size. Population trends can be derived by comparing SCR density estimates over time (Kendall et al., 2019), although this requires high precision for each estimate to detect differences and extensive computational resources. Open, non-spatial capture-recapture (CR) population models (which allow births, deaths, immigration, and emigration) have been used to estimate trends in bear demography and relate these changes to environmental factors (Boulanger et al., 2004; Housty et al., 2014; Stetz et al., 2019). Like non-spatial CR models, SCR models can be expanded to populations that are demographically open (Ergon and Gardner, 2014; Bischof et al., 2016; Chandler et al., 2018). In addition to submodels for the observation process and the point process for activity center distribution, open population spatial capture-recapture (OPSCR) models include, at a minimum, submodels for recruitment, mortality, and between season movement. OPSCR can thus produce estimates of vital rates, movement/dispersal distances, as well as time series of density and abundance. Thus, instead of stringing together static snapshots of populations with non-spatial SCR models, OPSCR models allow the combined estimation of spatial population dynamics and can therefore be used to make population forecasts and project outcomes of different scenarios (Bischof et al., 2020). By modeling dynamics explicitly, OPSCR models also make better use of

N-mixture domestic dogs: Ribiero et al. 2019
R-N mean small carnivores: Kalle et al. 2014
USCR blended informed sigma: Burgar et al. 2018
USCR-P/A Red fox: Ramsey et al. 2015
USCR uninformed sigma: Burgar et al. 2018
CTDS average precision: Palencia et al. 2021
CTDS chimpanzees: Capelle et al. 2019
REM mean precision Black bear: Pettigrew et al. 2021
CTDS mean across species excluding outlier, Bessone et al. 2020
REM average precision: Palencia et al. 2021
R-N mean precision O'Brien et al. 2020
USCR Egyptian mongoose: Jiminez et al. 2017
USCR + telemetry Male deer: Johnson 2019
REM mean red Deer and wild boar: Ghoddousi et al. 2017
REST mean precision: Palencia et al. 2021
REM Hedgehogs (mean rural): Schaus et al. 2020
USCR + telemetry Female deer: Johnson 2019
REM Hedgehogs (mean urban): Schaus et al. 2020
Gen-SMR Red fox: Jiminez et al. 2019
CTDS Congo peafowl: Bessone et al. 2020
STE Elk: Moeller et al. 2018
Gen-SMR Brown bear: Whittington et al. 2017
TTE Elk: Moeller et al. 2018
REM Hedgehogs (Hartpury site): Schaus et al. 2020
R-N Forest duiker: O'Brien et al. 2020

Legend:
- site-structured
- USCR(+ dashed)
- REM
- REST
- TTE
- STE
- CTDS

(caption on next page)

Fig. 3. Precision of estimates as measured by coefficient of variation (CV; y-axis) from a selection of empirical studies found during systematic review of unmarked methods (colored horizontal lines; site-structured = Royle-Nichols [R-N] or N-mixture, USCR = unmarked spatial capture-recapture, USCR+ = USCR with ancillary data such as telemetry included or with a proportion of the population marked including random thinning spatial mark–resight [RT-SMR] and generalized spatial mark–resight [Gen-SMR], REM = random encounter model, REST = random encounter and staying time, TTE = time-to-event, STE = space-to-event, CTDS = camera trap distance sampling) that reported CV or mean and dispersion to calculate CV (SD or SE; horizontal lines). Only studies that achieved CV ≤ 0.69 (power to detect 99% decline) are included. The dark gray polygon represents the precision needed to detect a difference in populations (x-axis) with 80% power and α < 0.05, according to IUCN Red List Criteria A (vertical lines; see Table 2). The light gray polygon represents the precision needed to detect a difference in populations (x-axis) with 80% power and more liberal α < 0.20 expected to balance Type I and Type II error rates. Increased precision resulted from specific study designs (greater numbers of camera stations often resulted in greater precision) and population densities (higher densities tended to result in greater precision). Thus, while the REM model using 120 camera trap stations over 6 nights (and movement data from nearly 1000 camera trap stations) to estimate hedgehog density had sufficient precision (CV = 0.09) to detect a 40% population decline in one study, the same approach may not achieve the same precision depending on sampling design, effort, assumptions violated or met, or amount of data In comparison the average CV = 0.31 for REM estimates of abundant red deer and wild boar with 67 camera trap stations surveyed for 11 months, and 5 of 8 sites in the hedgehog study did not produce CV< 0.20. Further illustrating the interplay of study design and site context including population density and behavior, the R-N method achieved greatest precision reported for one species of forest duikers at a particular study site (CV = 0.08), but averaged CV = 0.36 across all study sites using the same standardized methodology (camera trap stations and duration; O'Brien et al., 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the available information than single-season SCR models, as detections of individuals across multiple years inform individual states in the absence of observations (Bischof et al., 2020). Furthermore, OPSCR models also allow integration of dead recovery data (individuals known to have died), potentially improving precision of parameter estimates further (G. Dupont et al., 2021; P. Dupont et al., 2021).

OPSCR models require multiple seasons of data (usually multiple years for large carnivores such as bears) and the longer-term perspective on monitoring brings higher resource demands. This can, to some extent, be mitigated by aforementioned propagation of information between years: as population dynamics are modeled explicitly, study design may accommodate gaps in monitoring, especially for long-lived species, like bears, that may be recaptured over multiple years and whose dynamics are less volatile (Milleret et al., 2020). Drawbacks of OPSCR models are their current lack of utilities for performing goodness-of-fit testing and greater complexity compared with traditional SCR models. Established methods and software (both maximum likelihood and Bayesian) are available for SCR models and have grown in use and functionality since these models were first described (Efford, 2004), whereas OPSCR is still less accessible to investigators. However, here too, tools are emerging, including software for fitting of models using maximum likelihood (Efford and Schofield, 2019; Glennie et al., 2019) and utilities for building and fitting Bayesian OPSCR models (Augustine, 2018; Augustine et al., 2020). Since conventional open capture-recapture models have been developed extensively, it is also useful to combine closed SCR estimates with conventional open CR models which are already well established in the conservation community (see Duangchantrasiri et al., 2016 for an application with tigers). Finally, application of OPSCR models to large scale analyses – including those that may involve transboundary bear populations in Asia – face a substantial computation challenge due to the potentially huge number of calculations involved at large scales. High-performance computing and parallelization can mitigate this challenge, as can recent developments in SCR and ecological computation in general, such as features that significantly reduce the number and increase the speed of calculations (Turek et al., 2020). With the help of such functionality, a large-scale (>500 000 km^2) Bayesian OPSCR analysis was recently performed on a trans-boundary brown bear population in Scandinavia, using 7 years of non-invasive genetic sampling data and involving ~13 000 samples from ~3000 individuals (Bischof et al., 2020).

2.2. Evaluation of methods to estimate density using camera traps when individual bears cannot be identified (no marks)

A large number of conservation studies in Asia now rely on camera trapping, and for some taxa, especially felids, individuals are identifiable by their natural markings, enabling monitoring with the methods described above. However, the natural markings of most Asian bears are on their chest, so unless a lure is used to prompt them to stand up in front of a camera (Ngoprasert et al., 2012), they would not be individually distinguishable on camera trap photos. Overcoming this obstacle with analytical methods for estimating abundance of unmarked animals could allow for a leap forward in bear monitoring. A recent review (Gilbert et al., 2021) identified and described six analytical frameworks for estimating abundance or density of unmarked animals with camera traps: 1) site-structured models including Royle-Nichols (R-N; Royle and Nichols, 2003) and N-mixture (Royle, 2004) models, 2) unmarked SCR [USCR, also referred to as spatial counts (SC); Chandler and Royle (2013)], 3) random encounter models (REM; Rowcliffe et al., 2008), 4) time-to-event models (TTE; Moeller et al., 2018), 5) space-to-event (STE) and the instantaneous sampling model (IS; Moeller et al., 2018) extension, and 6) camera trap distance sampling (CTDS; Howe et al., 2017).

The most evident issue with applying several of these methods to Asian bear populations is the large amount of spatio-temporal heterogeneity in home range overlap that commonly occurs among individuals within bear populations (Izumiyama and Shiraishi, 2004; Wong et al., 2004; Ratnayeke et al., 2007, 2014). Unmarked methods attempt to disentangle repeated detections of the same individual from detections of different individuals at the same location using assumptions about independence among camera traps, home range size and degree of movement, or relying heavily on assumptions about camera placement, detection windows, and animal active periods and speed of movement (Gilbert et al., 2021). Small violations of these assumptions (detailed extensively in Gilbert et al., 2021) can result in strong biases and reduced precision, rendering the resulting estimates useless at best, and misleading at worst

(Cusack et al., 2015; Gilbert et al., 2021; Loonam et al., 2021). Further, like SCR, USCR methods estimate density for a defined area explicitly. The remaining methods estimate abundance for the camera locations without reference to space (R-N and N-mixture) or for the collective viewsheds of the cameras and assume the camera trap locations sampled adequately represent the entirety of the area which may result in different study design considerations. Thus, unmarked density estimation methods should not be selected based on the structure of data already collected, but instead should be chosen before initiation of a study with consideration of how well a target population may adhere to assumptions and the potential to achieve a specific objective. A drawback of unmarked methods for monitoring is that open population models are not possible if individuals cannot be tracked through time because survival and recruitment are not separately identifiable. Population growth can only be estimated with unmarked methods by comparing multiple estimates over time, and detection of trend relies on the precision of estimates at each sampling period.

We do not repeat the extensive overview and comparison of methods from Gilbert et al. (2021) here, but instead consider each approach for the conservation and monitoring of Asian bears. We extended the previous review of unmarked camera trapping methods, adding new studies published from 2019 to July 22, 2021, found by searching Google Scholar [search terms: (method type) camera trap density, or (method type) camera trap abundance]. We extracted density and abundance estimates, dispersion measures, number of camera trap stations, and length of surveys, to draw out possible circumstances and study design considerations that may provide guidance on the use of camera traps for estimating density of unmarked Asian bears.

We employed two-tailed power analysis (Appendix S3 of Efford and Boulanger, 2019) to calculate the CV of estimates required to detect differences in populations from − 1% to − 99% with standard thresholds of 80% power and α < 0.05 to adhere to standards for inferring statistical significance, and a less conservative α < 0.20 to balance Type I and II error rates (Fig. 3). Based on the power analysis with α < 0.05, required CVs ranged from 0.07 to detect a − 30% difference, 0.26 to detect a − 80% difference, and 0.33 to detect a − 90% difference. Estimates with CVs ≥ 0.40 and ≥ 0.69 could not detect a difference of − 95% or − 99%, respectively. We compared reported CVs and derived CVs when means and standard error or standard deviation was reported for each study (SE/μ or SD/μ) and included in Fig. 3.

We assessed precision of empirical density and abundance estimates as useful or practicable if they could be expected to detect ≤ 30–90% population decline, based on the power to detect population declines that would result in a different IUCN Red List status (Table 2; IUCN, 2012), and we considered methods that produced CV ≤ 0.20, the threshold previously established for wildlife management (Pollock et al., 1990; Williams et al., 2002) as advantageous. Many studies only reported 95% Confidence or Credible Intervals (95%CI). Due to the asymmetrical nature of abundance estimates we did not attempt to derive CVs from these estimates, but instead calculated the ratio of the 95%CI range to the mean estimate to quantify precision (CI width). By comparing the CI width with the CV when both were reported, we found CI width ≤ 1 frequently corresponded with CVs with 80% power to detect − 80% difference when α < 0.05, and ≤ 1.5 with CVs with 80% power to detect a − 99% difference. The review and assessments below are not comprehensive but highlight potential uses and issues. Practitioners interested in applying any of these methods should consult the studies referenced for more information on assumptions and limitations of methods, particularly as it pertains to accuracy and bias (not addressed here, but see Gilbert et al., 2021 for an extensive review).

The greatest hindrance to the use of camera traps to estimate density using unmarked estimation methods is the reduced precision typical of estimates from most empirical studies (Cappelle et al., 2021; Palencia et al., 2021) compared to accepted standards for wildlife management (CV ≤0.20; Williams et al., 2002) and those achieved by empirical SCR studies (Morehouse and Boyce, 2016; Humm and Clark 2017; Table 3). Uncertainty around estimates may propagate through inadequate power due to limitations on number of camera traps that can be afforded (logistically and financially), or model misspecification. Number of detections is also influenced by movement patterns, population density, size of study area (influencing number of possible camera trap stations), type of habitat (affecting detection range of camera), type of camera, camera setup, and duration of surveys (Table 3). In each case, it will be important to consider the degree to which the observation process is expected to adhere to model assumptions, thereby affecting bias. The variability of success (in achieving the precision threshold) across sample sizes, densities and duration shown in Fig. 3 and Table 3 demonstrate there are no hard and fast rules or minimum metrics that will ensure sufficient precision, likely due to circumstances that cannot currently be accounted for. However, in general CV improved with higher density, more camera traps, and longer surveys. Below, we discuss the assumptions and limitations of existing unmarked methods applied to camera trap data, to demonstrate how these methods can be evaluated by practitioners prior to selection and implementation.

Table 2
Coefficient of variation (CV) needed to detect population changes corresponding to IUCN Red List Criteria A (IUCN, 2012), calculated using a two-tailed power analysis (Efford and Boulanger, 2019) with standard thresholds of 80% power and α < 0.05%, and 80% power and a more liberal α < 0.20 expected to balance Type I and Type II error rates. Presently three Asian bears are classified as VU based on criteria A.

Red List Criteria	Red List Category	% decline	CV required (α < 0.05)	CV required (α < 0.20)
A2, A3, A4	VU	≥ 30%	0.07	0.10
A1	VU	≥ 50%	0.14	0.19
A2, A3, A4	EN	≥ 50%	0.14	0.19
A1	EN	≥ 70%	0.21	0.30
A2, A3, A4	CR	≥ 80%	0.26	0.39
A1	CR	≥ 90%	0.33	0.58

VU = Vulnerable; EN = Endangered; CR = Critically endangered.

Table 3

Effort and duration required for a selection of studies that resulted in density or abundance estimates with a coefficient of variation (CV) ≤ 0.20. All studies highlighted also produced at least one estimate that did not meet the precision threshold, with the exception of Whittington et al. (2018) (unmarked spatial capture-recapture generalized spatial marked-resight model) and Moeller et al. (2018) (only one estimate reported for each model). Lack of precision in empirical estimates from these studies and others are detailed in the text.

Study	Species (country)	Model	Duration	Number of trap locations	Density or abundance (CV)	Note
Humm and Clark (2017)	American black bears (USA)	SCR[a] cluster design	6 1-week occasions	190 324 134	12.7/100 km^2 (0.13) 8.2/100 km^2 (0.13) 13.2/100 km^2 (0.17)	Ocala-St John's Apalachicola Big Cypress
Morehouse and Boyce (2016)	Brown bears (Canada)	SCR multistrata (2013 estimates)	7 3-week occasions	902	1.5/100 km^2 (0.17) 1.4/100 km^2 (0.20) 0.9/100 km^2 (0.15) 0.8/100 km^2 (0.20)	Females Recovery zone Females Support zone Males Recovery zone Males Support zone
O'Brien et al. (2020)	Ogilby's duiker Blue duiker (Cameroon) Bay duiker Yellow-backed duiker (Republic of Congo) Harvey's duiker (Tanzania) Black-fronted duiker (Rwanda)	R-N[b]	6 5-day occasions	60	$\overline{N}$= 1.13 (0.08) $\overline{N}$= 2.12 (2.12) $\overline{N}$= 1.97 (0.16) $\overline{N}$= 3.01 (0.15) $\overline{N}$= 2.18 (0.15) $\overline{N}$= 0.94 (0.14)	Korup National Park (NP) Nouabale-Ndoki NP Udzungwa NP Virunga NP
Schaus et al. (2020)	Hedgehogs (England)	REM[c]	6 nights	120 112 119	680/100 km^2 2590/100 km^2 1750/100 km^2	Hartpury Southwell Ipswich East
Moeller et al. (2018)	Elk (USA)	TTE[d]	29 nights	80	$\hat{N}$ = 2217 (0.10)	
Moeller et al. (2018)	Elk (USA)	STE[e]	29 nights	80	$\hat{N}$ = 1718 (0.13)	
Whittington et al. (2018)	Brown bears (Canada)	USCR+[f] (Gen-SMR[g])	16 2-week occasions	214	1.2/100 km^2 (0.12)	averaged over annual sessions years
Bessone et al. (2020)	Congo peafowl	CTDS[h]	mean = 38.5 nights	750	91/100 km^2 (0.17)	

[a] spatial capture-recapture.
[b] Royle-Nichols.
[c] random encounter model.
[d] time-to-event model.
[e] space-to-event model.
[f] unmarked SCR with additional data.
[g] generalized spatial mark–resight.
[h] camera trap distance sampling.

2.2.1. Site-structured models

Site-structured models including Royle-Nichols (R-N) model, based on binary detection/non-detection data (Royle and Nichols, 2003), and N-mixture models, which use count data (Royle, 2004), extrapolate density or abundance over large areas based on counts corrected to account for imperfect detection at independent camera sites. These models require independent detections among camera trap sites (i.e., the same bear is not detected at multiple camera traps) so spacing of camera traps must be large for bears (>2x home range size radius) to avoid multiple spatial detections and ensure there is no overlap in effective sampling areas (the total area being sampled by a camera). This contrasts with SCR methods, where recaptures of the same individual at multiple traps is required. Estimates from N-mixture models will also be biased if multiple individuals are detected multiple times at the same camera trap, but cannot be differentiated, and so should only be used for solitary and territorial species.

Abundance estimates from empirical studies using site-structured models were generally imprecise and derived CVs were 0.65 (Kalle et al., 2014; R-N averaged across species, CV range = 0.30–1.00), 0.66 (Ribeiro et al., 2019; N-mixture) and 0.70 (Brodie et al., 2015a; R-N, averaged across species, CV range = 0.11–1.26). Several studies using site-structured models did not emphasize or report abundance or density estimates explicitly, instead using the models to better understand spatial covariates that influence density or

abundance (Brodie et al., 2015b; Duquette et al., 2014; Xiao et al., 2018). Even those studies that did report specific density or abundance estimates focused more on relationships among spatial covariates as drivers of abundance. These studies typically relied on model selection using information–criteria, highlighting the usefulness of site-structured models in identifying covariates that affect detection (e.g., vegetation heterogeneity; Duquette et al., 2014) and abundance (e.g., human activity; Xiao et al., 2018).

Precision of estimates is dependent on the number of camera trap sites; low-density populations require a greater number of trap sites to compensate for low detection rates (Duarte et al., 2018). For example, Schlichting et al. (2020) evaluated the use of N-mixture models to monitor changes in wild pig (*Sus scrofa*) populations following animal removal and produced more precise estimates of abundance with 42 cameras in a high-density population (CI width = 0.27–0.28) than with 55 cameras in a lower density population (CI width = 0.36–0.38). A study using R-N to estimate point abundance for nine forest duiker species (Bovidae, Cephalophinae) in six national parks in central and east Africa showed some exceptions to the trend of imprecision (O'Brien et al., 2020; CV averaged across species = 0.36, CV range = 0.08 – 1.33). Five of six sites in this study collected data following a standardized protocol including 60 cameras (TEAM Network, 2011). The least precise estimate (CV = 1.33) was for the least abundant population (estimated 0.09 duikers at each site) and six of 15 estimates derived CVs < 0.20, with the 60 traps, but there was no direct relationship between abundance and precision, suggesting other sources of variation in the amount of information obtained per site (e.g., variation in detection probability due to differences in space use behavior) also affect precision.

Knowing that spatial variability in the detection of bears can be high, multiple camera traps within a general area, together comprising a single sampling location should likely improve detection and the robustness of abundance estimates (Kolowski et al., 2021). Equally, an expansive spatial extent will likely be needed for low density Asian bear populations to achieve adequate sample sizes to fit models that produce abundance estimates with acceptable precision for most conservation objectives. While restrictive for use in single small areas, like a particular reserve, the R-N model might work well for monitoring on the scale of states, countries or regions if the study design adheres to model assumptions (Gilbert et al., 2021). For example, Linden et al. (2017) sampled fishers, a low density, solitary mesocarnivore, across a large extent of New York State (USA) with CI width = 0.43. Site-structured models could also be used in 2-stage adaptive monitoring framework (Conroy et al., 2008), indicating where more intensive monitoring may yield the greatest information.

For populations and species with expansive ranges (e.g., brown bear, Asiatic black bear), only site-structured models may be logistically feasible to implement considering the number of camera traps required at a spatial scale necessary to detect 30–90% range-wide declines in abundance necessary to trigger changes in IUCN Red List status (IUCN, 2012). However, both R-N and N-mixture models are sensitive to assumption violations and estimates should be critically assessed (Gilbert et al., 2021). R-N model estimates only retain a relationship to abundance when the species is relatively rare and should not be used in moderate or high-density populations or populations with high amounts of individual home range overlap (Gopalaswamy et al., 2012). In addition, effective sampling area for both site-structured models is assumed ad hoc, and not estimated explicitly, so if the objective was to compare population estimates for units within a larger contiguous population, inference will be confounded if the true effective sampling area changes over time between estimates (a possible outcome when individual home range movements change among sampling periods). Extrapolation to an effective sampling area will be further exacerbated when undescribed sources of heterogeneity in density that cannot often be described by available spatial covariates (such as poaching) are present (Duarte et al., 2018; but see Moore et al., 2021 for an example where this is included).

Estimates from N-mixture models can be biased when assumptions are violated and, under these circumstances, have been suggested to be relative abundance indices (Barker et al., 2018; Link et al., 2018). If the bias is consistent, then estimates from one time period to the next may still adequately reflect magnitudes of decline accurate enough for Red Listing (Table 2). Repeated counts over time could be combined with other data sources in integrated population models allowing for estimation of population trend with other sources of data (Schaub et al., 2007). However, estimates from N-mixture models should not be used for objectives that require absolute estimates of abundance unless adherence to closure assumptions can be verified (Royle, 2004).

2.2.2. Unmarked Spatial Capture–Recapture (USCR)

Unmarked SCR (USCR) has appeal as an ecological model representing the distribution of individuals over an estimated effective sampling area (area is estimated, not defined ad hoc, so density estimates across study sites and over time are comparable). The model accounts for imperfect detection of individuals (based on where a camera trap is located in relation to an animal's activity center; Chandler and Royle, 2013; Royle et al., 2013) by estimating baseline detection probability (λ_0) and the scaling parameter (σ) akin to SCR, but based on spatially correlated counts of detections at detectors. Unfortunately, there is only a narrow range of circumstances when USCR would be expected to produce adequately precise and unbiased estimates under sampling designs typically deployed (without additional information estimated from ancillary data, see below). Augustine et al. (2019) framed the problem using the Identity Diversity Index (IDI), quantifying how uncertainty surrounding USCR estimates increases in magnitude as the number of individuals that can possibly be detected at a camera trap increases (the more overlap among individual home ranges, the greater the uncertainty and the poorer the precision in the estimates). The IDI shows how uncertainty renders comparisons between estimates impractical even at low densities as home range size and overlap increases (Augustine et al., 2019).

Poor precision in USCR estimates limits the usefulness of this method for nearly all identified conservation needs without strong a priori knowledge on home range movements or ancillary data such as telemetry or a proportion of the population with identifiable marks (Augustine et al., 2019). One empirical study implementing USCR with American black bears appears an outlier to this trend of imprecision (Evans and Rittenhouse, 2018) and raises some skepticism (Gilbert et al., 2021). The study used Markov chain Monte Carlo (MCMC) code customized in R and we were unable to replicate the high degree of precision using the data provided in the repository and widely available MCMC samplers (JAGS, and the sampler function in the SCR book package). As a result, we did not include the

estimates from the study in our review.

Ultimately, USCR estimates are unlikely to detect differences in Asian bear population densities over time or among areas without ancillary data (e.g., telemetry data; Johnson, 2019) or a proportion of the population being individually identifiable (Augustine et al., 2019). We refer to USCR with ancillary data as USCR+ to distinguish it from uninformed USCR. Additional data are most effective when they inform both λ_0 and the scaling parameter σ, and when variability in individual movements is low, which may not be realistic for many Asian bear populations. Additionally, differences in landscape influencing animal movements and camera sets (e.g., whether on trails or baited) can change the relationship between σ estimated from telemetry and camera traps and will limit the application of telemetry data sets from other locations and seasons. The lowest CV for USCR+ was found for female white-tailed deer (*Odocoileus virginianus*) when telemetry data were used to estimate a home range kernel (Johnson, 2019; Fig. 3). Average CV was 0.23 for females compared to 0.32 for males that show greater individual variability in home range movements (Karns et al., 2011). When only an informed σ was used to estimate fisher density (Burgar et al., 2018), CV ranged from 0.31 to 0.52, depending on the informed prior selected. In this comparison, using estimated home range kernels for estimation of white-tailed deer density (Johnson, 2019) not only resulted in greater precision compared to the fisher example, but reduced subjectivity in selection of a single informed prior for the scaling parameter.

Spatial mark–resight (SMR) approaches build on USCR models but include information on a fraction of the population that have unique marks. More precisely, a portion of a bear population may have known marks (such as naturally occurring scars or researcher placed tags) while the remaining individuals are not uniquely identifiable. Mark–resight methods have been adapted within a SCR framework (SMR and generalized SMR, Gen-SMR; Efford and Hunter, 2018; Whittington et al., 2018) to allow for uncertainty in the proportion of marked animals sampled, missed or with unidentifiable marks (an extension of Gen-SMR; Jimenez et al., 2019), and when marked status is unknown (random thinning SMR; Jiménez et al., 2021). This approach has been further generalized to situations where partial identification extends to most individuals in the sampled population (Spatial Partial Identity Models, SPIMs; Augustine et al., 2019) where individuals do not need to be identifiable in all photographs. In most cases, estimate precision will be highly dependent on design, but also the proportion of individuals marked, and the identification rate of individuals with marks. A camera trap study in Canada was able to estimate brown bear density with high precision (CV = 0.12) using a generalized SMR model without telemetry data (Gen-SMR), 214 camera traps, and 22 easily identified, collared individuals (Whittington et al., 2018). Conversely, a study of Andean bears (*Tremarctos ornatus*) in Ecuador using 71 camera traps produced poor precision (CV = 0.40) when there was a large proportion of photos of individuals with facial markings that could not be identified (45 detections of marked individuals, 53 unmarked detections, and 41 unknown status; Augustine et al. unpublished data).

If sufficient ancillary data are available (e.g., kernels estimated from telemetry data or a sample of identifiable bears), USCR+ could be an effective method to address several monitoring needs (but see Ruprecht et al., 2021). While there will likely not be sufficient detections to fit models over single small reserves, more moderate sized reserves (many times the size of a bear home range) or a network of reserves within a region may be able to fit USCR+ models and estimate realized density for each parcel over the effective sampling area (also allowing for prioritization of areas for conservation actions). The USCR+ model may also be able to estimate population size for a geographically isolated population of sufficient size to generate detections of enough individuals, but the spatial extent of the population is not so large to require an overly extensive camera trapping grid (with spacing appropriate to animal ranging behavior). Under the right circumstances, USCR+ may also be able to provide a range of possible starting values for projection models in Red List Criterion E and validate surrogates or less intensive methods. Adequate sample size and spacing will be critical to achieving unbiased, precise estimates, and studies should not be implemented without a priori simulations to ensure costly monitoring activities can be expected to produce usable results.

2.2.3. Random Encounter Model (REM), and Random Encounter and Staying Time model (REST)

The remaining unmarked methods developed for camera traps (REM, REST, TTE, STE, IS, and CTDS) estimate density for the collective viewshed (area within view of the camera) of all cameras in the study area and assume what is estimated for the viewshed is representative of the population (Gilbert et al., 2021). The REM (Rowcliffe et al., 2008) and REST (Nakashima et al., 2018, 2020) extension use measurements or assumptions about animal movement (average speed) and detections at camera traps positioned randomly across a study area to estimate density based on the total area of all camera viewsheds (Rowcliffe et al., 2008). Cameras are stratified across heterogeneous habitats, and placed randomly with respect to animal movement, thus not positioned to maximize detections (i.e., not focused on trails or in relation to areas where animal activity would be higher such as feeding or resting areas), which may seem counterintuitive to most experienced camera trap researchers.

Similar to the methods above, REM assumption violations result in biased estimates and precision can often be too large to detect meaningful differences (Fig. 3). For example, placing cameras in preferred areas would overestimate density to an unknown degree (Rowcliffe et al., 2008). The random placement requirement is especially problematic for low-density populations where detections would be especially low, reducing statistical power. Attaining enough detections of a sparse population over a time interval adhering to temporal closure will be difficult without a spatially extensive camera trap network.

Total number of cameras also impacts precision. For example, Cusack et al. (2015) estimated density of lions (*Panthera leo*) with high to moderate precision (CI width = 0.50–1.10) from 167 to 168 camera trap locations over multiple months, whereas a study estimating American black bear density in Quebec, Canada, generated poor precision (0.39 CV) with 99 locations but only 3 weeks of operation (Pettigrew et al., 2021). The second greatest precision achieved for any study reviewed (CV = 0.09 for one site with 120 cameras deployed over 6 nights) used the REM in a citizen science camera trap survey for hedgehogs over 7 survey areas (one surveyed in two consecutive years; Schaus et al., 2020). However, density of hedgehogs is exceptionally high (3.9–88.6/km^2) relative to Asian bears, and the total survey effort resulted in 802 video detections (21% of footage) from 967 cameras and 6016 camera-trap nights, and

five of eight surveys still did not produce CV< 0.20 (including the lowest density estimate with CV = 0.38; Schaus et al., 2020).

Ultimately, while achieving high precision is possible with this approach, it will require extensive sampling effort for low density populations, followed by extensive data processing (Palencia et al., 2021). Underestimation of average movement speed also over-estimates density (Carbajal-Borges et al., 2014; Loonam et al., 2020), as does not accounting for periods of inactivity (Cusack et al., 2015). These biases can be compounded when movement and activity are different for different sampling areas or times (Pettigrew et al., 2021). Consequently, reliance on movement data from other study locations can be problematic.

The REST model also assumes random placement of cameras relative to animal movement but uses the "staying time" within a viewshed (estimated either from video clips or in consecutive pictures from the camera trap data set) instead of independent estimates of movement speeds required for REM model, and may reduce the associated bias with biased estimates of speed (Nakashima et al., 2018, 2020). However, these models have not yet been thoroughly scrutinized to understand power and biases that may result from estimates of staying time and an assumption of perfect detection within a viewshed (animals are never missed by cameras within the viewshed). A recent pilot study compared detection differences between two camera types and found that different detection probabilities for the camera types could bias estimates from the REST model by nearly 10% (Yajima and Nakashima, 2021). The initial application estimated duiker density with CV = 0.23–0.29 (Nakashima et al., 2018).

Average CVs from a recently published comparison of methods with empirical data showed REST estimates had greater precision (mean CV = 0.28; Palencia et al., 2021) compared to REM and CTDS (described below), but the sample sizes required demonstrated the method may only be useful in high density populations. Another study estimated density of four sympatric ungulates occurring at different densities (Nakashima et al., 2020) and found precision was positively related to density estimates (3.6 and 0.39 CI width for lowest and highest density estimates, respectively). Noted of particular concern is when camera trap operation is compromised (e.g., trigger speeds are not fast enough, detection bursts are not complete, etc.), as this will result in, for example, estimates of staying time truncated by an unknown amount of time (Palencia et al., 2021).

2.2.4. Time-to-Event (TTE), Space-to-Event (STE), and Instantaneous Sampling (IS)

Like the REM, the TTE model (Moeller et al., 2018) also uses independently obtained estimates of movement rates, although for the TTE model these are only used to set an appropriate sampling period for estimation of the time to first detection (based on the average speed of individuals in a population, including periods of rest). The TTE model estimates abundance using repeated measures of the time it takes for the first motion-triggered photo to be collected on a camera, and the estimated time an individual could be expected to be found in a viewshed. The TTE model can be extended to estimate spatial variation in density and also be extended to allow for estimation of detection (otherwise assumed to be perfect; Moeller et al., 2018). However, as cameras are still placed randomly, detection rates may be too low for low-density species and it was initially only recommended for relatively moderate to high-density populations (Moeller et al., 2018). Nonetheless, it was found to provide estimates with acceptable precision for a population of sparsely distributed, solitary felids (Loonam et al., 2020). However, this study violated the assumption of random placement of camera traps and could therefore have resulted in biased, and potentially overly precise, estimates of density.

The STE model and IS extension collapse the TTE detections to substitute space for time in the equation, eliminating the need for the inclusion of movement rates, but sacrifices precision as a result (Moeller et al., 2018). The STE and IS estimators require time-lapse photos instead of photos produced by a motion sensor. Instead of using the time required for an animal to pass in front of a camera, the method repeatedly samples the set of camera sites in a random fashion to find the number of camera sites required before a detection is recorded. This removes issues with variability in motion sensor and detector fields for cameras but can result in an enormous amount of data to process and be prohibitive for low-density species that will be rarely be detected using time-lapse photos. In the two available comparisons (Moeller, and Loonam et al., 2018, 2020), STE and IS models produced less precise estimates compared to TTE model.

Increasing the duration of surveys can increase detection but will also violate the assumption that the individuals detected are those in the immediate proximity of a detector as more individuals may move through an area and be detected over time (akin to a temporal closure violation). Thus, keeping sampling sessions short will be particularly important for modeling spatial covariates on density (distribution of individuals is heterogeneous) in the TTE application, when camera traps are densely spaced, and when there are seasonal or migratory movement patterns that may occur with changes in available resources over time. When sample sizes are adequate, empirical evaluations of TTE have shown greater precision than other unmarked camera methods (CI width ranged from 0.45 to 0.62 for cougars (*Puma concolor*) with 67 – 74 camera traps per site deployed over 5 months; Loonam et al., 2020), assuming estimates are unbiased. An evaluation of the TTE model using simulated walk models found estimates generally robust to territoriality and aggregation (both violate the assumptions of a Poisson distribution), but like REM models, misspecification of movement speeds can easily bias density estimates (Loonam et al., 2021), as will non-random placement of cameras. Since movement speeds are not currently available for Asian bears, methods requiring such data will not be useful until these data are obtained (using GPS-collared bears).

2.2.5. Camera trap distance sampling (CTDS)

Camera trap DS (Howe et al., 2017) uses data on the distances individuals are detected from the camera to correct for imperfect detection and estimate density within the collective viewshed, assuming this is representative of the total area of interest. Cameras are assumed to be placed randomly with respect to animal movement, and distance reference points within each camera viewshed must be measured during camera set-up, and for each detection during data processing, which requires additional time. Greater precision is achieved with greater numbers of detections within a viewshed to estimate distance detection functions well, and this can be accomplished using many cameras or longer duration surveys (as increased time of deployment also allows for more detections within

a single viewshed), but a threshold for a minimum number of camera trap stations is still evident (Cappelle et al., 2019; 2021). For example, Palencia et al. (2021) used CTDS to estimate red deer, wild boar, and red fox densities with CV = 0.42 using 20–25 camera traps deployed for 2–5 months. Although 20–25 camera locations are too few (Cappelle et al., 2021) and precision was not sufficient to detect a difference with 80% power, another study with cameras deployed at 743 locations for an average of 36 days only improved precision to an average CV = 0.37 (mean of 13 species, with one extremely poor outlier removed; Bessone et al., 2020).

Based on a range of simulated designs, CTDS could be expected to produce density estimates with CV = 0.10–0.20 with 50 cameras deployed over 100 days (Cappelle et al., 2021). An empirical application in the same study with four times as many cameras (200 camera traps) deployed for 8–10 months only achieved this level of precision using empirical designed-based variance for the most abundant species, Maxwell's duiker (*Philantomba maxwellii*; $\widehat{D} = 19.7$ individual/km^2 and CV = 0.11) and bootstrapped variances produced CV < 0.20 for all but the least detected species (forest elephant; *Loxodonta africana cyclotis*), including for leopards (*Panthera pardus*; $\widehat{D} = 0.05$ individual/km^2 and CV = 0.18).

Special consideration should be given to individual and population traits found to affect precision of CTDS estimates. First, heterogeneity in spatial distribution of a population reduces overall precision. Precision may be increased by increasing sample sizes within different strata of expected density (Bessone et al., 2020). Second, distance sampling assumes the presence of the detector does not change the behavior of the detected animals, such as curious bears investigating cameras. To address substantial bias that can result from attraction or avoidance of cameras or human odors from camera trap deployment, Cappelle et al. (2018) left-truncated detections to eliminate photos of individuals inspecting cameras, while Bessone et al. (2020) removed all photos indicating reactivity and recommended waiting until the end of the survey to conduct measurements of reference objects.

Other considerations include estimating an animal's availability for detection (a component of detection; Rowcliffe et al., 2014; Cappelle et al., 2019), which assumes an entire population is available for detection during the defined peak activity period (Cappelle et al., 2021). Cappelle et al. (2019) attempted to account for detection unavailability in chimpanzees due to their semi-arboreal nature, estimating activity time on the ground from the temporal distribution of camera trap records, which could have applicability to some Asian bears. Differences in availability estimates (described in Rowcliffe et al., 2014 and Cappelle et al., 2019) were negligible when sample sizes were large enough, but not accounting for detection unavailability could bias density estimates (Bessone et al., 2020). Additionally, one problem in such design-based approaches with potentially small camera viewsheds (typical in tropical forest environments) is that the data gathered may be highly overdispersed and the sample selection of camera trap sites may not be representative of the larger area of inference. As a result, the conversion of density to abundance may not be straightforward.

2.3. Hybrid approaches

Recently developed integrated models incorporate multiple types of data including count and presence-non-detection data (Blanc et al., 2014; Zipkin et al., 2017), which can be collected at large spatial extents at relatively low cost. These data can be combined with more intensively collected capture-recapture data, which is usually restricted to smaller spatial extents due to the high cost and logistical considerations.

Extending beyond integrating multiple data types, integrated population models combine abundance estimates with demographic rates like survival or reproduction (Schaub et al., 2007; Chandler and Clark, 2014). Chandler and Clark (2014) collected American black bear hair over a 6-year time period, but only genotyped hairs in alternate years in an effort to save money and to increase the temporal extent of sampling. In the 3 years with no genotyping, the hair data were modeled as detection data since there is no individual identification. Simulations suggested that incorporation of the binary detection data resulted in increased precision and lower bias when compared with SCR data alone (Chandler and Clark, 2014).

Recent efforts have combined systematic capture-recapture data collection on small study areas with opportunistically collected citizen science data conducted at a much larger spatial extent (Sun et al., 2019, 2021). Camera trap photos of American black bears collected by citizen scientists provided presence-non-detection data, which was combined with systematically collected SCR data, resulting in increased precision and accuracy of abundance estimates (Sun et al., 2019). Combining these two different data types required separate and independent detection processes for the SCR and presence-non-detection data. A useful model extension for Asian bears might be to allow for presence-only data such as that found in sign surveys or observations provided by local residents, which can be much quicker to process than camera trapping data. There are many methodological considerations when interpreting and processing sign data (Proctor et al., 2022) in addition to requiring a different detection process than presence-non-detection data. Further, when integrating presence-non-detection data with presence-only data, investigators should examine the data for spatial biases that often occur when using opportunistic data collection approaches (Simmonds et al., 2020).

Another recent integrated SCR model incorporated one survey method with individual detections and another survey type with unidentified (unmarked) detections (Tourani et al., 2020). The model was applied to brown bears in Pakistan and the authors suggested that integrated multiple observation process models are most useful when detection probability is low, there are large number of unidentified detections (e.g., camera trap observations, or hair or fecal samples that fail to produce individual identities), and home range overlap among individuals is low. All examples of integrated population models suggest that data integration yields more reliable population estimates with increased precision and reduced bias, and therefore hold great promise for Asian bear population monitoring.

2.4. Other approaches with potential

2.4.1. Line-transect distance sampling (LTDS)

In some circumstances it may also be possible to estimate density using direct sightings of bears while conducting line transects for distance sampling (Thomas et al., 2010; Buckland et al., 2015). Distance models estimate density from detection probabilities based on the distance that individuals are observed from a transect line. One drawback of this method is it requires many visual observations to fit a detection function. Hence, this method will not be applicable in habitats with dense understory and reduced detection likelihood, as is the case for many Asian bear populations. However, this method has already been used extensively for polar bears (*U. maritimus*; Aars et al., 2009; Stapleton et al., 2014, 2016). There may be opportunities in more open habitats for sloth and brown bears and in areas where greater population densities allow for enough individuals to be detected. Distance models are design-based so do not require precise information about space use or movement rates. However, an important assumption is that animals do not move before being observed (e.g., away from the observer) or after being observed and then observed again. Study design tools exist within available software to aid in study design and sampling effort (Thomas et al., 2010; Buckland et al., 2015; Marshall, 2019; Miller et al., 2019). Perhaps the most promising application of this method is using sloth bear detections recorded during large-scale ungulate survey transects conducted regularly within the Malenad landscape of India (Karanth et al., 2020). In this case, it may be possible to combine detection distances over years of sampling to fit detection functions, even though encounters of sloth bears in any single year are likely be too low for a sparsely distributed population.

2.4.2. Estimating trend from age specific survival and reproduction

The trend of a population can be estimated by combining age-specific survival and reproduction in a projection model, assuming a stable age distribution (Caswell, 2000). For bears, this method typically relies on monitoring females with radio-collars. This method has been used in North America on brown bears but requires extensive amounts of data on individual collared bears (Garshelis et al., 2005; Mace et al., 2012; McLellan, 1989; 2015; McLellan et al., 2021; Schwartz et al., 2006). Although there have been some studies employing collared bears in Asia, sample sizes have generally not been adequate to produce sufficiently precise estimates of reproduction and survival.

An advantage of trend estimates generated from measures of age-specific reproduction and survival is that they indicate how well the population is coping under the current conditions (Caughley, 1977; McLellan, 1989; Schwartz et al., 2006). Also, unlike estimating trend from two or more estimates or even using open capture-recapture methods, monitoring radio-collared animals can provide detailed information on the reasons why the population is changing, specifically the identification of factors impacting reproduction or survival. The main challenge with radio collar studies is obtaining adequate sample sizes to allow precise estimates of trend. A solution is to incorporate multiple data sources from collars, surveys, and other demographic indicators through the use of integrated population models.

2.5. When limitations prohibit the estimation of abundance, density, or population trends with precision

We have focused on methods with potential to estimate abundance, density, and population trends with precision. However, these approaches may not always be possible for a variety of reasons (financial limitations, expertise, small spatial extent limiting sample sizes, etc.) which could be verified using simulations of possible study designs. For example, it will be difficult to estimate abundance or density with high precision within small areas that contain few individuals. When this is the case, we still urge researchers to consider methods that can result in individual identification, because it will allow for inclusion in larger collaborative efforts and can provide baseline data for future studies. Thus, effort should still be made to identify individuals, either by chest blazes for Asiatic black bears, sun bears, and sloth bears, or by collecting hair and scat for genetic identification (see Proctor et al., 2022).

The minimum number of individuals detected can provide a rough but useful population estimate in a very small population, which should be much better for monitoring than indices such as sign/ha or photos/100 trap-nights, which can be a biased surrogate of abundance (Sollmann et al., 2013b). When sampling is evenly stratified and individual detection rates are high, number of individuals detected can trend well with changes in abundance (Slade and Blair, 2000), but this should only be used when an area is small enough that sampling can achieve adequate coverage of all possible individuals. For example, this method has been successfully applied with small populations of rhinos in Asia where individuals are identifiable on camera trap photos (Haryono et al., 2015). An important assumption of this method is that detection rates are sufficiently high such that a large portion of the population is identified, and each subsequent sample has similarly high detection so that results are not simply a random draw of a sliver of the population (White, 2005; Bischof et al., 2020). Lures may be particularly useful for this method so as to significantly increase detection. Even when using minimum numbers of individuals detected, detection probabilities can be estimated using the same repeated sampling as capture-recapture methods, with the number of times individuals are detected divided by the number of possible detections, to ensure that detection rates are high enough to assume correlation with local abundance. Spatial locations should also be recorded as the individual detections could be used later as part of a larger data set over time or as part of a more extensive collaboration.

2.6. Targeted monitoring

Ultimately, monitoring efforts should be structured to detect changes in populations and investigate potential causes of the decline ("targeted monitoring", sensu Nichols and Williams, 2006). In some cases, tracking relationships between demographic parameters and these covariates can provide more inference and power than just tracking trends in abundance. Several methods described above

(SCR, OPSCR, CTDS, and TTE models) incorporate spatial covariates that could allow for extrapolation across a larger spatial extent to assess spatial and temporal trends. The effect size of change may be more pronounced in parts of a study area, identifiable using covariates or density surface models. For example, Kendall et al. (2019) used SCR to analyze trend in grizzly bears. While their overall estimate of λ had wide confidence limits, their study documented hot spots of notable trends within the focal study area. Other studies have linked bear population trends to salmon abundance in a coastal area (Boulanger et al., 2004) as well as static values of risk and resource selection function values (Boulanger et al., 2018). In all these cases, the precision of density or trend estimates was not high; however, density could be inferred through the use of covariate relationships. Thus, there is often more information in mark–recapture data sets than just point estimates of density or abundance and we suggest researchers use various tools available to assess components of variation that produce the observed trend.

However, extrapolation may be limited if poaching is the greatest driver of change, since this attribute is difficult to measure (but see Moore et al., 2021). Density estimation methods could be used to search for more specific attributes correlated with population declines, such as changes in human activity, or encroachment of human land use, but these will need to be included a priori in study designs to ensure adequate variation in covariates sampled. Working within an adaptive monitoring framework (Lyons et al., 2008; Lindenmayer and Likens, 2009) with clearly defined objectives will allow for continued evaluation of causes of change, and updating and refining our understanding of threats and boons to Asian bear populations.

3. Current needs and future directions

Estimating Asian bear population densities or trends will require extensive effort and coordination to be effective. Currently, only methods that include individual identification (SCR, OPSCR, SMR) have been shown to yield the precision needed to detect even declines of 50% in bear populations. Sample sizes requirements will generally prohibit the use of unmarked methods for low density populations (Duarte et al., 2018; Moeller et al., 2018; Bessone et al., 2020). Further, while unmarked methods require less information and model parameters, there is far greater risk of bias in estimates resulting from model assumptions that are difficult to validate. The inconsistencies in precision of unmarked empirical estimates, even within the same study designs, sites, and species (Table 3), likely demonstrate unaccounted assumption violations pertaining to animal movement and we would expect these issues to extend to most Asian bear populations.

More studies evaluating the success of different hair snare devices (Tee et al., 2020), genetic amplification rates (Phoebus et al., 2020; Tee et al., 2020) and camera trap setups (Ngoprasert et al., 2012; Higashide et al., 2020) that yield high success in individual identification will be particularly useful for future monitoring studies. Whereas detection can be significantly improved with lures, these would create a bias in current unmarked methods; however, behavioral responses to lures or bait can be incorporated into SCR models and are likely essential in obtaining an adequate sample size of captures and recaptures. Hence, research into effective lures or baits is well worth the effort, especially since attractiveness is known to vary by species and even study site (Ngoprasert, unpublished data). Given the effort needed to identify individuals by chest marks and the low identification rate in camera trap photos, SMR using individuals identified with confidence as the marked proportion of the population (Whittington et al., 2018) or an extension to Gen-SMR models that allows for marks to not always be identified (Jimenez et al., 2019) is a promising approach for camera trap monitoring of sun, sloth bears, and Asiatic black bears.

Unmarked camera trap methods such as REST, STE, and CTDS may be able to detect very large population increases or decreases (>80%) in Asian bear populations, as may REM, TTE and USCR+ approaches if local telemetry data are available or a large enough proportion of the target population is marked. However, practitioners should be aware of the low power of these methods to detect smaller changes (Fig. 3) even when assumptions are met, especially with low numbers of individuals and/or a low number of camera trap locations. Thus, it may be prudent to evaluate the cost and effort associated with an extensive camera trap effort aimed at estimating abundance, but only able to detect catastrophic declines, compared to occupancy surveys that could be conducted with fewer cameras or even sign, and would likely be able to detect similar magnitudes of population change across a landscape (Sunarto et al., 2012; Karanth et al., 2020) or evaluate conservation success (Linkie et al., 2015).

The potential of unmarked methods to estimate abundance requires more critical assessment. There has been a plethora of recent publications comparing SCR estimates to unmarked methods, but rarely is the information provided to allow practitioners to truly assess the usefulness of these methods. Methods that account for individual identity will likely always outperform unmarked methods in estimation, but still may lack adequate precision if not properly designed and implemented (Efford and Boulanger, 2019; Green et al., 2020). This is easily demonstrated by comparing CVs (as we have done here), which is more useful than examining overlap of confidence intervals. For example, in one study Bayesian Credible Intervals overlapped for all comparisons of fisher density estimates (Burgar et al., 2018), but unmarked estimates had much larger CVs (CVs were 70–148% times larger using USCR approaches). By providing the CV the authors allowed for the approach to be considered in terms of specific objectives, correctly identified limitations to the approach, and were able to discuss future directions for improvement. Our review highlights the importance of empirical studies in validating methods for field applications, but we need to be honest in our assessments and focus on the success of the application in terms of ability to meet objectives. We encourage researchers to report and discuss dispersion for estimates and CV, not just the convergence of estimates. The power calculations provided in Table 2 here and Appendix S3 in Efford and Boulanger (2019) allow for explicitly assessing trade-offs between Type I and Type II error rates (as do the simulations in Schaus et al. (2020)).

While telemetry studies are expensive, invasive, and difficult to implement, many methods of monitoring may benefit from home range estimates, movement rates, vital rates, and other information that can be gathered from collared bears. Home range estimates from specific areas for different species can improve SCR study designs and inform USCR(+) model parameters. Resource selection functions can be incorporated into SCR models and increase precision and enhance inference using informative covariates (Royle et al.,

2013; Sollmann et al., 2016; McClintock et al., 2021). Movement rates could be estimated from telemetry data for TTE and REM models and assumptions about independence of individual bear movements could be tested. Finally, collaring individuals could allow for known fate survival, although we recognize this may be especially difficult in many places in Asia, where poaching may be the main cause of mortality (and most poached bears would not be found). While it would take years of data and large sample sizes to estimate trends with matrix models (Garshelis et al., 2005), detecting changes in survival or recruitment may be the only way to monitor new threats or improvements for small populations or areas over time (Laufenberg et al., 2018; Harihar et al., 2020). Cormack-Jolly-Seber models (Lebreton et al., 1992) and other open population models that use detections of marked individuals over time (genetic, natural, or placed marks) may also allow for monitoring of changes in population without estimating density or growth and lead to future collaborations including larger OPSCR efforts (Bischof et al., 2020) or inclusions in integrated population models (Schaub and Abadi, 2011), other open population models (Hostetter et al., 2021), or long-term integrated assessments (Laufenberg et al., 2018, McLellan et al., 2019).

4. Conclusions

Effective monitoring requires a critical evaluation of methods and their assumptions in relation to the ecology and behavior of the species, likely population size and geographical extent, logistical and financial constraints, and specific aims in terms of an observable magnitude of population change. We strongly encourage study-specific simulations and power analyses to help to ensure that study designs are effective. Crucially important is that significant population declines are detected with sufficient time to act. This will require high precision and accordingly large sample sizes. For low density populations, this will require extensive spatial scales and thus collaborations and coordination of study designs and sampling protocols. Our guidance follows the example set by tiger conservation efforts in India (Karanth et al., 2020) and apex predator conservation in Scandinavia (Bischof et al., 2020).

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.

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References

Aars, J., Marques, T.A., Buckland, S.T., Andersen, M., Belikov, S., Boltunov, A., Wiig, Ø., 2009. Estimating the Barents Sea polar bear subpopulation size. Mar. Mammal. Sci. 25 (1), 35–52.

Amburgey, S.M., Yackel Adams, A.A., Gardner, B., Hostetter, N.J., Siers, S.R., McClintock, B.T., Converse, S.J., 2021. Evaluation of camera trap-based abundance estimators for unmarked populations. Ecol. Appl. 31 (7), e02410 https://doi.org/10.1002/eap.2410.

Amstrup, S.C., McDonald, T.L., Manly, B.F.J., 2005. Handbook of Capture-recapture Analysis. Princeton University Press, Princeton, New Jersey, USA.

Augustine, B.C., 2018. OpenPopSCR, GitHub repository. ⟨https://github.com/benaug/OpenPopSCR⟩.

Augustine, B.C., Royle, J.A., Murphy, S.M., Chandler, R.B., Cox, J.J., Kelly, M.J., 2019. Spatial capture–recapture for categorically marked populations with an application to genetic capture–recapture. Ecosphere 10 (4), e02627.

Augustine, B.C., Kéry, M., Olano Marin, J., Mollet, P., Pasinelli, G., Sutherland, C., 2020. Sex-specific population dynamics and demography of capercaillie (Tetrao urogallus L.) in a patchy environment. 2020. Popul. Ecol. 62, 80–90.

Barker, R.J., Schofield, M.R., Link, W.A., Sauer, J.R., 2018. On the reliability of N-mixture models for count data. Biometrics 74 (1), 369–377.

Bellemain, E., Nawaz, M.A., Valentini, A., Swenson, J.E., Taberlet, P., 2007. Genetic tracking of the brown bear in northern Pakistan and implications for conservation. Biol. Conserv 134, 537–547. https://doi.org/10.1016/j.biocon.2006.09.004.

Bessone, M., Kühl, H.S., Hohmann, G., Herbinger, I., N'Goran, K.P., Asanzi, P., Da Costa, P.B., Dérozier, V., Fotsing, E.D., Beka, B.I., Iyomi, M.D., 2020. Drawn out of the shadows: Surveying secretive forest species with camera trap distance sampling. J. Appl. Ecol. 57 (5), 963–974.

Bischof, R., Brøseth, H., Gimenez, O., 2016. Wildlife in a politically divided world: insularism inflates estimates of brown bear abundance. Conserv. Lett. 9 (2), 122–130. https://doi.org/10.1111/conl.12183.

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Tourani, M., Ordiz, A., de Valpine, P., Turek, D., Royle, J.A., Gimenez, O., Flagstad, Ø., Åkesson, M., Svensson, L., Brøseth, H., Kindberg, J., 2020. Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. Proc. Natl. Acad. Sci. USA 117 (48), 30531–30538. https://doi.org/10.1073/pnas.2011383117.

Bischof, R., Turek, D., Milleret, C., Ergon, T., Dupont, P., de Valpine, P., 2020. nimbleSCR: Spatial Capture-Recapture (SCR) Methods Using "nimble". R package version 0.1.0.

Blanc, L., Marboutin, E., Gatti, S., Zimmermann, F., Gimenez, O., 2014. Improving abundance estimation by combining capture–recapture and occupancy data: example with a large carnivore. J. Appl. Ecol. 51, 1733–1739.

Borchers, D.L., Efford, M.G., 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics 64 (2), 377–385.

Boulanger, J., Himmer, S., Swan, C., 2004. Monitoring of grizzly bear population trend and demography using DNA mark–recapture methods in the Owikeno Lake area of British Columbia. C. J. Zool. 82, 1267–1277.

Boulanger, J., McLellan, B., 2001. Closure violation in DNA-based mark–recapture estimation of grizzly bear populations. C. J. Zool. 79, 642–651.

Boulanger, J., Nielsen, S.E., Stenhouse, G.B., 2018. Using spatial mark–recapture for conservation monitoring of grizzly bear populations in Alberta. Sci. Rep. 8, 5204.

Brodie, J.F., Giordano, A.J., Ambu, L., 2015. Differential responses of large mammals to logging and edge effects. Mamm. Biol. 80 (1), 7–13.

Brodie, J.F., Giordano, A.J., Dickson, B., Hebblewhite, M., Bernard, H., Mohd-Azlan, J., Anderson, J., Ambu, L., 2015. Evaluating multispecies landscape connectivity in a threatened tropical mammal community. Conserv. Biol. 29 (1), 122–132.

Buckland, S.T., Rexstad, E., Marques, T.A., Oedekoven, C.S., 2015. Distance Sampling: Methods and Applications. Methods in Statistical Ecology. Springer, Cham. https://doi.org/10.1007/978-3-319-19219-2.

Burgar, J.M., Stewart, F.E., Volpe, J.P., Fisher, J.T., Burton, A.C., 2018. Estimating density for species conservation: comparing camera trap spatial count models to genetic spatial capture-recapture models. Glob. Ecol. Conserv. 15, e00411.

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 (5), 1249–1260.

Cappelle, N., Després-Einspenner, M.L., Howe, E.J., Boesch, C., Kühl, H.S., 2019. Validating camera trap distance sampling for chimpanzees. Am. J. Primatol. 81 (3), e22962.

Cappelle, N., Howe, E.J., Boesch, C., Kühl, H.S., 2021. Estimating animal abundance and effort–precision relationship with camera trap distance sampling. Ecosphere 12 (1), e03299.

Carbajal-Borges, J.P., Godínez-Gómez, O., Mendoza, E., 2014. Density, abundance and activity patterns of the endangered Tapirus bairdii in one of its last strongholds in southern Mexico. Trop. Conserv. Sci. 7 (1), 100–114.

Caravaggi, A., 2017. remBoot: an R package for random encounter modelling. J. Open Source Softw. 2 (10), 176.

Caswell, H., 2000. Matrix Population Models, 1. Sinauer, Sunderland, MA, USA.

Caughley, G., 1977. Analysis of Vertebrate Populations. John Wiley and Sons, London.

Chandler, R.B., Hepinstall-Cymerman, J., Merker, S., Abernathy-Conners, H., Cooper, R.J., 2018. Characterizing spatio-temporal variation in survival and recruitment with integrated population models. Auk 135 (3), 409–426. https://doi.org/10.1642/AUK-17-181.1.

Chandler, R., Clark, J., 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. 7 (2), 936–954.

Clark, J.D., 2019. Comparing clustered sampling designs for spatially explicit estimation of population density. Popul. Ecol. 61, 93–101.

Conroy, M.J., Runge, J.P., Barker, R.J., Schofield, M.R., Fonnesbeck, C.J., 2008. Efficient estimation of abundance for patchily distributed populations via two-phase, adaptive sampling. Ecology 89 (12), 3362–3370.

Cusack, J.J., Swanson, A., Coulson, T., Packer, C., Carbone, C., Dickman, A.J., Kosmala, M., Lintott, C., Rowcliffe, J.M., 2015. Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. J. Wildl. Manag. 79 (6), 1014–1021.

Duangchantrasiri, S., Umponjan, M., Simcharoen, S., Pattanavibool, A., Chaiwattana, S., Maneerat, S., Kumar, N.S., Jathanna, D., Srivathsa, A., Karanth, K.U., 2016. Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv. Biol. 30 (3), 639–648.

Duarte, A., Adams, M.J., Peterson, J.T., 2018. Fitting N-mixture models to count data with unmodeled heterogeneity: bias, diagnostics, and alternative approaches. Ecol. Modell. 374, 51–59.

Dupont, P., Milleret, C., Tourani, M., Brøseth, H., Bischof, R., 2021. Integrating dead recoveries in open-population spatial capture–recapture models. Ecosphere 12 (7), e03571.

Dupont, G., Royle, J.A., Nawaz, M.A., Sutherland, C., 2021. Optimal sampling design for spatial capture-recapture. Ecology 102, e03262.

Duquette, J.F., Belant, J.L., Svoboda, N.J., Beyer, D.E., Albright, C.A., 2014. Comparison of occupancy modeling and radiotelemetry to estimate ungulate population dynamics. Popul. Ecol. 56 (3), 481–492.

Durbach, I., Borchers, D., Sutherland, C., Sharma, K., 2021. Fast, flexible alternatives to regular grid designs for spatial capture–recapture. Methods Ecol. Evol. 12, 298–310.

Dutta, T., Sharma, S., Maldonado, J.E., Panwar, H.S., Seidensticker, J., 2015. Genetic variation, structure, and gene flow in a sloth bear (Melursus ursinus) meta-population in the Satpura-Maikal landscape of Central India. PLoS One 10 (5), e0123384.

Efford, M., 2004. Density estimation in live-trapping studies. Oikos 106, 598–610.

Efford, M.G., Dawson, D.K., 2012. Occupancy in continuous habitat. Ecosphere 3, 1–14.

Efford, M.G., Hunter, C.M., 2018. Spatial capture–mark–resight estimation of animal population density. Biometrics 74, 411–420.

Efford, M., Schofield, M., 2019. A spatial open-population capture--recapture model. Biometrics 76 (2), 392–402. https://doi.org/10.1111/biom.13150.

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

Ergon, T., Gardner, B., 2014. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data. Methods Ecol. Evol. 5 (12), 1327–1336. https://doi.org/10.1111/2041-210X.12133.

Evans, M.J., Rittenhouse, T.A.G., 2018. Evaluating spatially explicit density estimates of unmarked wildlife detected by remote cameras. J. Appl. Ecol. 55 (6), 2565–2574.

Fredriksson, G.M., Wich, S.A., Trisno, 2006. Frugivory in sun bears (Helarctos malayanus) is linked to El Nino-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. Biol. J. Linn. Soc. 89, 489–508.

Fuller, A.K., Linden, D.W., Royle, J.A., 2016. Management decision making for fisher populations informed by occupancy modeling. J. Wildl. Manag. 80 (5), 794–802.

Gardner, B., Reppucci, J., Royle, J.A., 2010. Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. Ecology 91, 3376–3383.

Gardner, B., Sollmann, R., Kumar, N.S., Jathanna, D., Karanth, K.U., 2018. State space and movement specification in open population spatial capture-recapture models. Ecol. Evol. 8 (20), 10336–10344. https://doi.org/10.1002/ece3.4509.

Garshelis, D.L., Gibeau, M.L., Herrero, S., 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis country. Alta. J. Wildl. Manag. 69 (1), 277–297.

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. (this issue).

Gilbert, N.A., Clare, J.D., Stenglein, J.L., Zuckerberg, B., 2021. Abundance estimation of unmarked animals based on camera-trap data. Conserv. Biol. 35 (1), 88–100.

Glennie, R., Borchers, D.L., Murchie, M., Harmsen, B.J., Foster, R.J., 2019. Open population maximum likelihood spatial capture-recapture. Biometrics 75, 1345–1355.

Gopalaswamy, A.M., Karanth, K.U., Kumar, N.S., Macdonald, D.W., 2012. Estimating tropical forest ungulate densities from sign surveys using abundance models of occupancy. Anim. Conserv. 15 (6), 669–679.

Gopalaswamy, A.M., Delampady, M., Karanth, K.U., Kumar, N.S., Macdonald, D.W., 2015. An examination of index-calibration experiments: counting tigers at macroecological scales. Methods Ecol. Evol. 6 (9), 1055–1066.

Green, A.M., Chynoweth, M.W., Şekercioğlu, Ç.H., 2020. Spatially explicit capture-recapture through camera trapping: a review of benchmark analyses for wildlife density estimation. Front. Ecol. Evol. 8, 473.

Harihar, A., Pandav, B., Ghosh-Harihar, M., Goodrich, J., 2020. Demographic and ecological correlates of a recovering tiger (Panthera tigris) population: lessons learnt from 13-years of monitoring. Biol. Conserv. 252, 108848.

Haryono, M., Rahmat, U., Daryan, M., Raharja, A., Muhtarom, A., Firdaus, A., Rohaeti, A., Subchiyatin, I., Nugraheni, A., Khairani, K., 2015. Monitoring of the Javan rhino population in Ujung Kulon National Park. Java. Pachyderm 56, 82–86.

Hostetter, N.J., Lunn, N.J., Richardson, E.S., Regehr, E.V., Converse, S.J., 2021. Age-structured Jolly-Seber model expands inference and improves parameter estimation from capture-recapture data. PLoS One 16 (6), e0252748.

Housty, W.G., Noson, A., Scoville, G.W., Boulanger, J., Jeo, R.M., Darimont, C.T., Filardi, C.E., 2014. Grizzly bear monitoring by the Heiltsuk people as a crucible for First Nation conservation practice. Ecol. Soc. 19 (2), 70.

Howe, E.J., Buckland, S.T., Després-Einspenner, M.L., Kühl, H.S., 2017. Distance sampling with camera traps. Methods Ecol. Evol. 8 (11), 1558–1565.

Humm, J., Clark, J.D., 2017. Estimates of abundance and harvest rates of female black bears across a large spatial extent. J. Wildl. Manag. 85, 1321–1331.

Hwang, M.-H., Garshelis, D.L., Wu, Y.-H., 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, 2012. IUCN Red List Categories and Criteria: Version 3.1, Second ed. IUCN, Gland, Switzerland and Cambridge, UK, pp. iv–32.

Izumiyama, S., Shiraishi, T., 2004. Seasonal changes in elevation and habitat use of the Asiatic black bear (Ursus thibetanus) in the Northern Japan Alps. Mamm. Study 29, 1–8.

Jimenez, J., Chandler, R., Tobajas, J., Descalzo, E., Mateo, R., Ferreras, P., 2019. Generalized spatial mark–resight models with incomplete identification: an application to red fox density estimates. Ecol. Evol. 9 (8), 4739–4748.

Jiménez, J., Augustine, B.C., Linden, D.W., Chandler, B., Royle, R., J.A, 2021. Spatial capture–recapture with random thinning for unidentified encounters. Ecol. Evol. 11 (3), 1187–1198.

Johnson, J.T., 2019. White-tailed Deer Camera Surveys: Density estimation and spatio-temporal dynamics. Doctoral dissertation, University of Georgia.

Kalle, R., Ramesh, T., Qureshi, Q., Sankar, K., 2014. Estimating seasonal abundance and habitat use of small carnivores in the Western Ghats using an occupancy approach. J. Trop. Ecol. 30 (5), 469–480.

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 (4), 1048–1056.

Karanth, K.U., Kumar, N.S., Karanth, K.K., 2020. Tigers against the odds: Applying macro-ecology to species recovery in India. Biol. Conserv. 252, 108846.

Karns, G.R., Lancia, R.A., DePerno, C.S., Conner, M.C., 2011. Investigation of adult male white-tailed deer excursions outside their home range. Southeast. Nat. 10 (1), 39–52.

Kendall, K.C., Graves, T.A., Royle, J.A., Macleod, A.C., McKelvey, K.S., Boulanger, J., Waller, J.S., 2019. Using bear rub data and spatial capture-recapture models to estimate trend in a brown bear population. Sci. Rep. 9, 16804.

Kéry, M., Royle, J.A., 2020. Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 2: Dynamic and Advanced Models. Academic Press.

Kolowski, J.M., Oley, J., McShea, W.J., 2021. High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time. Ecosphere 12 (2), e03350.

Laufenberg, J.S., Clark, J.D., Chandler, R.B., 2018. Estimating population extinction thresholds with categorical classification trees for Louisiana black bears. PLoS One 13 (1), e0191435.

Lebreton, J.D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62 (1), 67–118.

Linden, D.W., Fuller, A.K., Royle, J.A., Hare, M.P., 2017. Examining the occupancy–density relationship for a low-density carnivore. J. Appl. Ecol. 54 (6), 2043–2052.

Lindenmayer, D.B., Likens, G.E., 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends Ecol. Evol. 24 (9), 482–486.

Link, W.A., Schofield, M.R., Barker, R.J., Sauer, J.R., 2018. On the robustness of N-mixture models. Ecology 99 (7), 1547–1551.

Linkie, M., Martyr, D.J., Harihar, A., Risdianto, D., Nugraha, R.T., Leader-Williams, N., Wong, W.M., 2015. Safeguarding Sumatran tigers: evaluating effectiveness of law enforcement patrols and local informant networks. J. Appl. Ecol. 52 (4), 851–860.

Loonam, K.E., Ausband, D.E., Lukacs, P.M., Mitchell, M.S., Robinson, H.S., 2021. Estimating abundance of an unmarked, low-density species using cameras. J. Wildl. Manag. 85 (1), 87–96.

Loonam, K.E., Lukacs, P.M., Ausband, D.E., Mitchell, M.S., Robinson, H.S., 2020. Assessing the robustness of time-to-event models for estimating unmarked wildlife abundance using remote cameras. Ecol. Appl. 31 (6), e2388.

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 (8), 1683–1692.

McClintock, B.T., Abrahms, B., Chandler, R.B., Conn, P.B., Converse, S.J., Emmet, R.L., Gardner, B., Hostetter, N.J., Johnson, D.S., 2021. An integrated path for spatial capture–recapture and animal movement modeling. Ecology, e03473.

MacKenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42 (6), 1105–1114.

McLellan, B.N., 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age–sex composition. C. J. Zool. 67 (8), 1856–1860.

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 20 November 2021.

McLellan, M.L., McLellan, B.N., Sollmann, R., Wittmer, H.U., 2021. Vital rates of two small populations of brown bears in Canada and range-wide relationship between population size and trend. Ecol. Evol. 11 (7), 3422–3434.

Mace, R.D., Carney, D.W., Chilton-Radandt, T., Courville, S.A., Haroldson, M.A., Harris, R.B., Jonkel, J., McLellan, B., Madel, M., Manley, T.L., Schwartz, C.C., 2012. Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. J. Wildl. Manag. 76 (1), 119–128.

Marshall, L., 2019. Dssd: Distance Sampling Survey Design. ⟨https://CRAN.R-project.org/package=dssd⟩.

Miller, D.L., Rexstad, E., Thomas, L., Marshall, L., Laake, J.L., 2019. Distance sampling in R. J. Stat. Softw. 89 (1), 1–28. https://doi.org/10.18637/jss.v089.i01.

Milleret, C., Dupont, P., Chipperfield, J., Turek, D., Brøseth, H., Gimenez, O., de Valpine, P., Bischof, R., 2020. Estimating abundance with interruptions in data collection using open population spatial capture–recapture models. Ecosphere 11 (7), e03172.

Moeller, A.K., Lukacs, P.M., Horne, J.S., 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. Ecosphere 9 (8), e02331.

Moore, J.F., Uzabaho, E., Musana, A., Uwingeli, P., Hines, J.E., Nichols, J.D., 2021. What is the effect of poaching activity on wildlife species? Ecol. Appl. 31 (7), e02397.

Morehouse, A.T., Boyce, M.S., 2016. Grizzly bears without borders: Spatially explicit capture–recapture in southwestern Alberta. J. Wildl. Manag. 80 (7), 1152–1166.

Nakashima, Y., Fukasawa, K., Samejima, H., 2018. Estimating animal density without individual recognition using information derivable exclusively from camera traps. J. Appl. Ecol. 55 (2), 735–744.

Nakashima, Y., Hongo, S., Akomo-Okoue, E.F., 2020. Landscape-scale estimation of forest ungulate density and biomass using camera traps: applying the REST model. Biol. Conserv. 241, 108381.

Nawaz, M.A., Swenson, J.E., Zakaria, V., 2008. Pragmatic management increases a flagship species, the Himalayan brown bears, in Pakistan's Deosai National Park. Biol. Conserv. 141, 2230–2241. https://doi.org/10.1016/j.biocon.2008.06.012.

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.

Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. Trends Ecol. Evol. 21 (12), 668–673.

O'Brien, T.G., Ahumada, J., Akampurila, E., Beaudrot, L., Boekee, K., Brncic, T., Hickey, J., Jansen, P.A., Kayijamahe, C., Moore, J., Mugerwa, B., 2020. Camera trapping reveals trends in forest duiker populations in African National Parks. Remote. Sens. Ecol. Conserv. 6 (2), 168–180.

Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62, 3–135.

Palencia, P., Rowcliffe, J.M., Vicente, J., Acevedo, P., 2021. Assessing the camera trap methodologies used to estimate density of unmarked populations. J. Appl. Ecol. 58 (8), 1583–1592.

Pollock, K.H., Nichols, J.D., Brownie, C., Hines, J.E., 1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107, 3–97.

Pettigrew, P., Sigouin, D., St-Laurent, M.H., 2021. Testing the precision and sensitivity of density estimates obtained with a camera-trap method revealed limitations and opportunities. Ecol. Evol. 11 (12), 7879–7889.

Phoebus, I., Boulanger, J., Eiken, H.G., Fløystad, I., Graham, K., Hagen, S.B., Sorensen, A., Stenhouse, G., 2020. Comparison of grizzly bear hair-snag and scat sampling along roads to inform wildlife population monitoring. Wildl. Biol. 2020, 3.

Proctor, M.F., Garshelis, D.F., Thatte, P., Steinmetz, R., Crudge, B., McLellan, B.N., McShea, W.J., Ngoprasert, D., Nawaz, M.A., Wong, S.T., Sharma, S., Fuller, A., Dharaiya, N., Pigeon, K., Hwang, M.-h., Fredriksson, G., Wang, D., Li, S., 2022. A critical review of field methods for monitoring Asian bears. Glob. Ecol. Conserv. (this issue).

Ramsey, D.S., Caley, P.A., Robley, A., 2015. Estimating population density from presence–absence data using a spatially explicit model. J. Wildl. Manag. 79 (3), 491–499.

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 Lanka. Wildlife Biol. 13 (3), 272–284.

Ribeiro, F.S., Nichols, E., Morato, R.G., Metzger, J.P., Pardini, R., 2019. Disturbance or propagule pressure? Unravelling the drivers and mapping the intensity of invasion of free-ranging dogs across the Atlantic Forest hotspot. Divers. Distrib. 25 (2), 191–204.

Rowcliffe, J.M., Field, J., Turvey, S.T., Carbone, C., 2008. Estimating animal density using camera traps without the need for individual recognition. J. Appl. Ecol. 45 (4), 1228–1236.

Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60 (1), 108–115.

Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84 (3), 777–790.

Royle, J.A., Young, K.V., 2008. A hierarchical model for spatial capture–recapture data. Ecology 89 (8), 2281–2289.

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

Ruprecht, J.S., Eriksson, C.E., Forrester, T.D., Clark, D.A., Wisdom, M.J., Rowland, M.M., Johnson, B.K., Levi, T., 2021. Evaluating and integrating spatial capture-recapture models with data of variable individual identifiability. Ecol. Appl. 31 (7) https://doi.org/10.1002/eap.2405.

Sharma, S., Dutta, T., Maldonado, J.E., Wood, T.C., Panwar, H.S., Seidensticker, J., 2013. Selection of microsatellite loci for genetic monitoring of sloth bears. Ursus 24 (2), 164–169.

Schaub, M., Abadi, F., 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. J. Ornithol. 152 (1), 227–237.

Schaus, J., Uzal, A., Gentle, L.K., Baker, P.J., Bearman-Brown, L., Bullion, S., Gazzard, A., Lockwood, H., North, A., Reader, T., Scott, D.M., 2020. Application of the Random Encounter Model in citizen science projects to monitor animal densities. Remote. Sens. Ecol. Conserv. 6 (4), 514–528.

Schlichting, P.E., Beasley, J.C., Boughton, R.K., Davis, A.J., Pepin, K.M., Glow, M.P., Snow, N.P., Miller, R.S., VerCauteren, K.C., Lewis, J.S., 2020. A rapid population assessment method for wild pigs using baited cameras at 3 study sites. Wildl. Soc. Bull. 44 (2), 372–382.

Schwartz, C.C., Haroldson, M.A., White, G.C., Harris, R.B., Cherry, S., Keating, K.A., Moody, D., Servheen, C., 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildl. Monogr. 161 (1), 1–8.

Simmonds, E.G., Jarvis, S.G., Henrys, P.A., Isaac, N.J.B., O'Hara, R.B., 2020. Is more data always better? A simulation study of benefits and limitations of integrated distribution models. Ecography 43, 1413–1422.

Slade, N.A., Blair, S.M., 2000. An empirical test of using counts of individuals captured as indices of population size. J. Mammal. 81 (4), 1035–1045.

Sollmann, R., Gardner, B., Parsons, A.W., Stocking, J.J., McClintock, B.T., Simons, T.R., Pollock, K.H., O'Connell, A.F., 2013. A spatial mark–resight model augmented with telemetry data. Ecology 94 (3), 553–559.

Sollmann, R., Mohamed, A., Samejima, H., Wilting, A., 2013. Risky business or simple solution–Relative abundance indices from camera-trapping. Biol. Conserv. 159, 405–412.

Sollmann, R., Gardner, B., Belant, J.L., Wilton, C.M., Beringer, J., 2016. Habitat associations in a recolonizing, low-density black bear population. Ecosphere 7 (8), e01406.

Schaub, M., Gimenez, O., Sierro, A., Arlettaz, R., 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. Conserv. Biol. 21 (4), 945–955.

Stapleton, S., Atkinson, S., Hedman, D., Garshelis, D., 2014. Revisiting Western Hudson Bay: using aerial surveys to update polar bear abundance in a sentinel population. Biol. Conserv. 170, 38–47.

Stapleton, S., Peacock, E., Garshelis, D., 2016. Aerial surveys suggest long-term stability in the seasonally ice-free Foxe Basin (Nunavut) polar bear population. Mar. Mamm. Sci. 32 (1), 181–201.

Steinmetz, R., Garshelis, D.L., Chutipong, W., Seuaturien, N., 2013. Foraging ecology and coexistence of Asiatic black bears and sun bears in a seasonal tropical forest in Southeast Asia. J. Mammal. 94 (1), 1–18.

Stetz, J.B., Mitchell, M.S., Kendall, K.C., 2019. Using spatially-explicit capture-recapture models to explain variation in seasonal density patterns of sympatric ursids. Ecography 42 (2), 237–248.

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

Sun, C., Hurst, J.E., Fuller, A.K., 2021. Citizen science data collection for integrated wildlife population analyses. Front. Ecol. Evol. 9, 682124 https://doi.org/10.3389/fevo.2021.682124.

Sunarto, S., Kelly, M.J., Parakkasi, K., Klenzendorf, S., Septayuda, E., Kurniawan, H., 2012. Tigers need cover: multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7 (1), e30859.

Sutherland, C., Royle, J.A., Linden, D.W., 2019. oSCR: a spatial capture–recapture R package for inference about spatial ecological processes. Ecography 42 (9), 1459–1469.

Tee, T.L., Lai, W.L., Wei, T.K.J., Shern, O.Z., van Manen, F.T., Sharp, S.P., Te Wong, S., Chew, J., Ratnayeke, S., 2020. An evaluation of noninvasive sampling techniques for Malayan sun bears. Ursus 2020 (31e16), 1–12.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A., Burnham, K.P., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. J. Appl. Ecol. 47 (1), 5–14.

Tourani, M., Dupont, P., Nawaz, M.A., Bischof, R., 2020. Multiple observation processes in spatial capture–recapture models: how much do we gain? Ecology 101 (7), e03030.

Tumendemberel, O., Proctor, M., Reynolds, H., Boulanger, J., Luvsamjamba, A., Tserenbataa, T., Batmunkh, M., Craighead, D., Yanjin, N., Paetkau, D., 2015. Gobi bear abundance and inter-oases movements, Gobi Desert, Mongolia. Ursus 26 (2), 129–142.

Tumendemberel, O., Tebbenkamp, J.M., Zedrosser, A., Proctor, M.F., Blomberg, E.J., Morin, D.J., Rosell, F., Reynolds, H.V., Adams, J.R., Waits, L.P., 2021. Long-term monitoring using DNA sampling reveals the dire demographic status of the critically endangered Gobi bear. Ecosphere 12 (8), e03696.

Turek, D., Milleret, C., Ergon, T., Brøseth, H., Dupont, P., Bischof, R., De Valpine, P., 2021. Efficient estimation of large-scale spatial capture–recapture models. Ecosphere 12 (2), e03385.

Vaeokhaw, S., Ngoprasert, D., Swatdipong, A., Gale, G.A., Klinsawat, W., Vichitsoonthonkul, T., 2020. Effects of a highway on the genetic diversity of Asiatic black bears. Ursus 2020 (31e3), 1–15.

White, G.C., Anderson, D.R., Burnham, K.P., Otis, D.L., 1982. Capture-recapture and Removal Methods for Sampling Closed Populations. Los Alamos National Laboratory, NM, USA.

White, G.C., 2005. Correcting wildlife counts using detection probabilities. Wildl. Res. 32 (3), 211–216.

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.

Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and Management of Animal Populations. Academic Press.

Wilson, K.R., Anderson, D.R., 1985. Evaluation of two density estimators of small mammal population size. J. Mammal. 66 (1), 13–21.

Woods, J.G., Paetkau, D., Lewis, D., McLellan, B.N., Proctor, M., Strobeck, C., 1999. Genetic tagging of free-ranging black and brown bears. Wildl. Soc. Bull. 27 (3), 616–627.

Wong, S.T., Servheen, C.W., Ambu, L., 2002. Food habits of Malayan sun bears in lowland tropical forests of Borneo. Ursus 13, 127–136.

Wong, S.T., Servheen, C.W., Ambu, L., 2004. Home range, movement and activity patterns, and bedding sites of Malayan sun bears Helarctos malayanus in the rainforest of Borneo. Biol. Conserv. 119 (2), 169–181.

Xiao, W., Hebblewhite, M., Robinson, H., Feng, L., Zhou, B., Mou, P., Wang, T., Ge, J., 2018. Relationships between humans and ungulate prey shape Amur tiger occurrence in a core protected area along the Sino-Russian border. Ecol. Evol. 8 (23), 11677–11693.

Yackulic, C.B., Reid, J., Nichols, J.D., Hines, J.E., Davis, R., Forsman, E., 2014. The roles of competition and habitat in the dynamics of populations and species distributions. Ecology 95 (2), 265–279.

Yajima, G., Nakashima, Y., 2021. Can video traps reliably detect animals? Implications for the density estimation of animals without individual recognition. Mammal. Study 46 (3), 1–7.

Zhan, X., Li, M., Zhang, Z., Goossens, B., Chen, Y., Wang, H., Bruford, M.W., Wei, F., 2006. Molecular censusing doubles giant panda population estimate in a key nature reserve. Curr. Biol. 16 (12), R451–R452.

Zhang, Z., Sheppard, J.K., Swaisgood, R.R., Wang, G., Nie, Y., Wei, W., Zhao, W., Wei, F., 2014. Ecological scale and seasonal heterogeneity in the spatial behaviors of giant pandas. Integr. Zool. 9 (1), 46–60.

Zipkin, E.F., Rossman, S., Yackulic, C.B., Wiens, J.D., Thorson, J.T., Davis, R.J., Grant, E.H.C., 2017. Integrating count and detection–nondetection data to model population dynamics. Ecology 98 (6), 1640–1650.