

Estimation of Species Area Abundance from Point Abundance Data, Using Effective Detection Areas from Camera Traps

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Abstract

Estimations of species abundance are a common goal of wildlife monitoring surveys, but debate remains as to which methods are theoretically and practically most useful. Abundance-induced heterogeneity (AIH) models developed in the early 2000s allowed estimation of point abundance from repeated presence-absence data (e.g. occupancy models), and advanced estimation of point abundances of unmarked species. AIH models, however, do not provide an estimate of the effective detection area sampled. Therefore the absolute number of individuals in a survey area cannot be estimated directly. Recently, methods have become available to determine the effective detection area sampled by camera traps. Our objective was to present a novel method to estimate the absolute number of individuals of a species in an area from point abundance data using effective detection areas from camera traps. This would make AIH models available for population estimates. We applied this newly developed Species Area Abundance (SAA) model to a 3-month camera trapping data set of Bawean warty pigs (*Sus blouchi*) from Indonesia, and compared the result to an independent Random Encounter Model (REM) estimate from the same data. Population sizes and uncertainties estimated by the SAA and the REM model were comparable. Differences in density estimations between the REM and SAA model were not significant when mean group size was included in the REM. The less restrictive assumptions regarding camera trap placement of the SAA model compared to the REM might make it more practical to study cryptic and unmarked animal populations. Further studies are needed to determine the accuracy and practicality of the SAA model using a range of different sampling designs and focus species.

Keywords: Abundance-induced heterogeneity model; Bawean warty pig; Occupancy; Activity; Random encounter model; REM

Introduction

Estimation of population sizes has been one of the main goals in wildlife monitoring surveys [1]. Well into the second half of the previous century, survey methods were limited to capture-recapture and distance sampling studies using live traps, direct observations or indirect signs (i.e. feces), to estimate densities and population sizes [2-5]. The introduction of modern camera traps in the 1990's provided new ways to estimate abundance and initiated a surge in new research [6]. Most camera trap studies between 2008 and 2013, however, still used capture-recapture methods to estimate densities [7,8], a method limited to species that are individually marked [9,10].

For unmarked animal populations, camera trap studies increasingly make use of relative abundance-indices to make inferences [8]. Unfortunately, relative abundance-indices are not comparable between sites, habitats, different points in time and species, as detection probability is not constant [11,12]. Additionally, relative abundance-indices do not produce estimates of the absolute number of individuals that are required for management of endangered populations.

Presently, two camera trapping methods estimate absolute numbers of individuals: the abundance-induced heterogeneity model [13] and the Random Encounter Model [14]. However, both models still have their drawbacks when estimating absolute numbers of individuals in an area (from here on referred to as 'species area abundance').

Abundance-induced heterogeneity (AIH) models are based on an occupancy framework, in which binary survey data are gathered over repeated visits. The AIH model assumes that detection probability (r) is species specific and is related to its abundance N_i . Therefore variation in species detection probability at a sampled site, or point, can be used

to estimate its abundance. In the AIH model, the mean abundance of a species across all sampled sites is expressed as Mean point abundance or Poisson parameter Lambda (λ).

Lambda is estimated by the maximum likelihood of the binomial probability of observing a certain detection history over a set of T repeat visits, multiplied by the Poisson probability of the local presence of K animals on the site [15]. The key assumption of the AIH model is that the spatial distribution of the animals across survey sites follows a prior distribution (Poisson) [13]. Initially, the AIH model was developed for point count surveys of migratory birds, but researchers have more recently applied it to camera trap surveys (e.g. Argus pheasants *Argus argusianus* [16], Siamese Firebacks *Lophura diardi* [17]).

The limitation of the AIH model lies in its inability to estimate the effective detection area sampled. Estimations of species area abundance have been limited to a summation of Lambda over sampled sites and effective detection area is substituted for species characteristics such as average home range size [17,18]. Substitution, however, does not

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account for potential overlapping home-ranges, nor does it guarantee that camera traps effectively sample the home-range of a species.

The Random Encounter Model (REM) [14] was the first method to estimate the density and abundance of unmarked populations by taking detection probability of camera traps into account. This potentially provides a robust way to estimate species area abundance [19]. Further adjustments to the REM in 2011 allowed researchers to estimate the effective detection area of a camera trap for different species [20]. However, as the method is based on an ideal gas model, cameras must be placed randomly in relation to the movement of the target species. This restricts the sampling designs suitable for REM [21], and limits its use for cryptic species with low detection probability, that often require non-random sampling designs in order to generate sufficient captures.

Our objective is to present a novel method to estimate species area abundance of unmarked species that combines the advantages of the AIH- and REM models and that is suitable for a variety of sampling

designs. Specifically, our model combines the AIH model with estimating the effective detection area from camera traps.

Materials and Methods

A model for species area abundance estimation from point abundance data

Conceptually, our newly proposed species area abundance (SAA) model consists of 5 basic steps (Figure 1). (1) The effective detection area of the camera traps for the target species is determined, providing the area sampled by each trap. (2) Using presence-absence data from repeat surveys in an AIH model, the mean point abundance, i.e. the mean abundance of a species across all sampled sites, is estimated. (3) This estimate is extrapolated to species area abundance by multiplying the mean point abundance with the total number of sampling sites if the entire survey area was monitored by camera traps without overlap

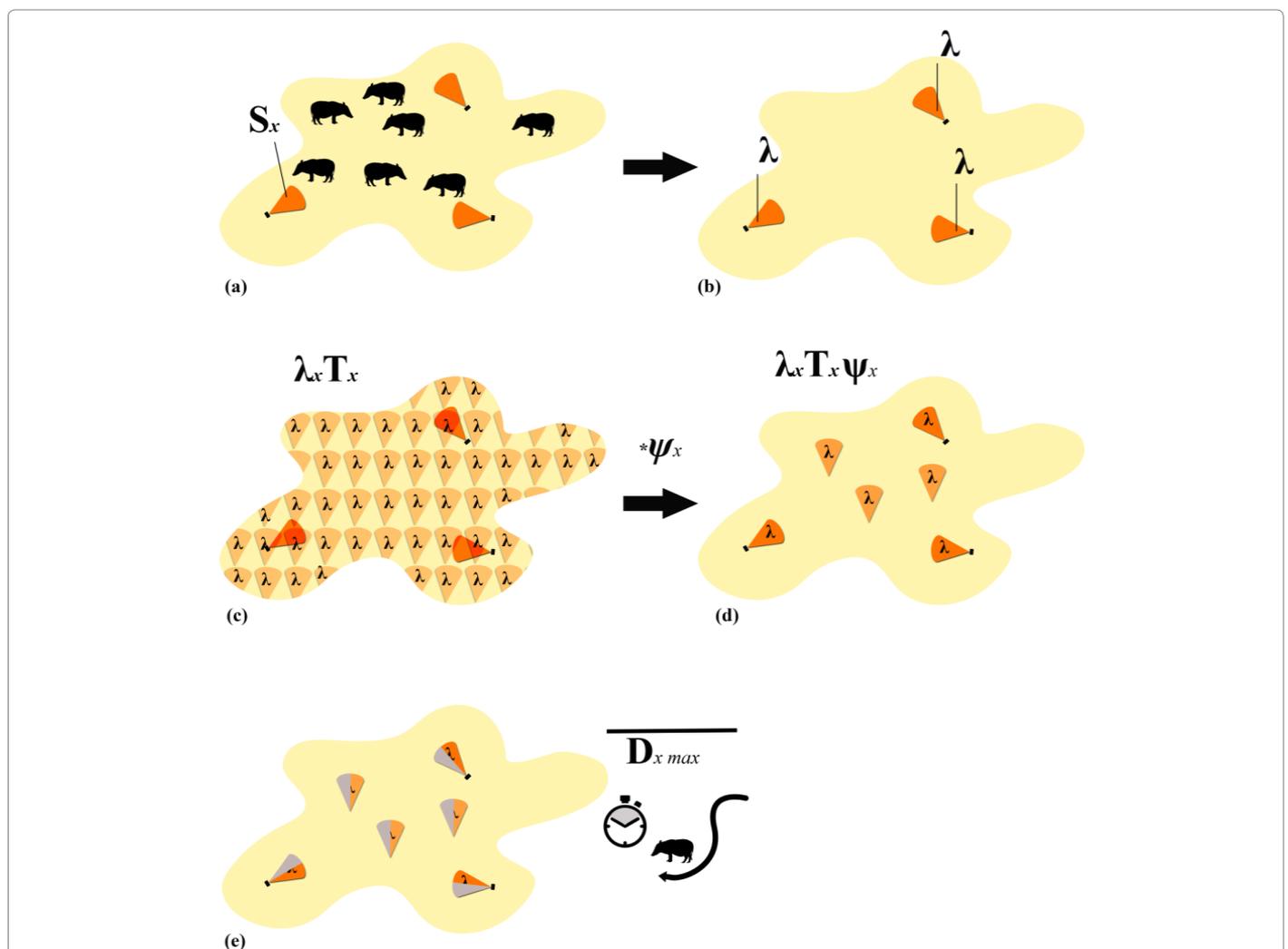


Figure 1: Schematic representation of the SAA model (a) a population is sampled using camera traps, with the effective area sampled by the camera traps indicated by the orange cones (S_x) (b) based on detection histories, mean point abundance across sampling sites is estimated (λ) (c) the estimate is extrapolated to area abundance by multiplying λ with the total number of sampling sites as if the entire survey area was monitored by camera traps (T_x) (d) the estimate is corrected for the total number of sites occupied, i.e. occupancy (ψ_x) (e) finally, the estimate is corrected for animal activity and movement by multiplying the camera operating time by the proportion of time spent active by the target species and dividing this by the average time the species spends at each occupied locality, equal to the average length of each detection event. The result is the maximum number of detection events ($D_{x \max}$). The estimate in (d) is divided by $D_{x \max}$ to provide the number of animals in the area at any given time, i.e. species area abundance.

between traps. (4) The extrapolated value is then corrected for the total number of sites occupied and (5) The resulting value is divided by the the maximum number of detections. The final estimate represents the number of individuals in the area at any given time, i.e. species area abundance. We will now explain the model in more detail.

Effective detection area

The effective detection area of a camera trap is related to both species body size and behaviour [20]. For species x , the effective detection area (S_x) of a camera trap is equal to the segment of a circle that is the product of the species-specific effective detection radius (r_x) and the species-specific effective detection angle (θ_x) [20].

$$S_x = \frac{\theta_x}{2} r_x^2 \quad (\theta \text{ in radians}) \quad (1)$$

At the effective detection radius and angle, the expected number of detections for a species is equal to the expected number of detections missed [22]. Effective detection radius and angle are estimated from the detection radius and angle of an animal at first capture, using functions for fitting standard linear covariate detection models [20]. The threshold values at which the number of detections equals the number of detections missed can be computed using a line transect model for angle and a point transect model for radius in distance [20,23].

Within a single species, large differences between body size (e.g., between sex or life-stages) should be taken into account by estimating the radius and angle of detection for each sex or life-stage.

Furthermore, when using a combination of different camera trap models in the same survey or project, the effective detection area has to be (i.e. effective detection radius and angle) estimated for each camera trap model. The effective detection area should then be weighted based on the contribution of each camera trap model to the total number of traps used.

The maximum number of sampling sites without overlap (T_x) for a species equals the size of the survey area (A) divided by the effective detection area.

$$T_x = \left(\frac{A}{S_x} \right) \quad (2)$$

Mean point abundance: Mean point abundance (ψ_x) can be estimated from the Royle-Nichols abundance-induced heterogeneity model [13].

Species area abundance: Species area abundance (N_x) can be calculated by multiplying the mean point abundance by the proportion of sites occupied (ψ_x) and the maximum number of local sampling sites.

$$N_x = \lambda_x \psi_x T_x \quad (3)$$

Equation 3 overestimates species abundance in an area, as it assumes a species to be present 24 h a day in each local sampling site. The result of equation 3, therefore, needs to be corrected for the maximum number of times a camera could detect an individual of a species.

Proportion of sites occupied: The proportion of sites occupied (ψ_x) can be estimated using single season occupancy models. Site covariates deemed important on the basis of the ecology of the target species should be included and several models compared. The total number of sites occupied is estimated as the sum of the mean of the

posterior distribution of occupancy at each site and then divided by the total number of sites sampled [24].

Maximum number of detections

The maximum number of times a camera can detect an individual of a species depends on the average time the camera traps are operated (t), the time a species spends at a local sampling site, and its level of activity throughout the day. If activity is defined as an animal being in movement [25], then the total amount of time in which detections could occur is equal to the total time the camera traps are operated, multiplied by the proportion of time spent active by the animal (v_x). A flexible circular distribution to time-of-detection from camera trap data can be used to estimate the proportion of time spent active [25]. This method has two assumptions: the level of activity is the only determinant of the rate at which the camera detects animals i.e., the camera operating times and animal activity times are independent of one another, and all individuals in the sampled population are active at the peak of the daily activity cycle. If these assumptions are met, trap rate is proportional to the level of activity and the total amount of time spent active proportional to the area under the trap rate curve.

The proportion of time spent active multiplied by the average time the cameras are operated gives the maximum operating time ($v_x \bar{t}$) available to detect a species. This maximum operating time, however, does not provide information on how many detection events could have occurred.

To calculate the maximum number of detection events, we must first assume that the presence of the camera traps does not alter the natural behaviour of the species. Secondly, we must assume that the local sites sampled are a representative sample of the habitats available in the area. If these assumptions are met, then the maximum number of detection events ($D_{x,max}$) equals the maximum operating time divided by the average time a species spent at each local sampling site per detection event (\bar{R}_x)

$$D_{x,max} = \frac{v_x \bar{t}}{\bar{R}_x} \quad (4)$$

The use of equation 4 requires that the camera sensors are setup to allow continuous detection, either through the use of video recordings or the use of photo recordings without intervals. To identify gaps in time when camera traps do not function during the research period, camera traps should be set to take a picture every day at midnight.

Species area abundance can now be formulated as the product of the mean point abundance, the proportion of sites occupied and the maximum number of local sampling sites divided by the maximum number of detection events.

$$\text{Species area abundance (SAA) model: } N_x = \frac{\lambda_x \psi_x T_x}{D_{x,max}} \quad (5)$$

Dividing the extrapolated abundance estimates by the maximum number of detection events thus provides a 'snapshot' or 'frozen-in-time' view of the number of animals in the area, similar to Distance sampling methods [26].

The SAA model assumes that all sampled local sites are accessible, animals are distributed homogenously over the habitat that they use, and abundance is constant for the duration of the survey. We recognize that this assumption might not be met in all cases. Stratified sampling within an animal's habitat can be an option if animals are clearly using specific parts of their habitat. Additionally, more cameras at random

locations are required to estimate density of species that are more aggregated or systematically distributed over their habitat. Next to this, abundance is assumed constant during the survey period. Therefore, repeated surveys need to be conducted in a sufficiently short time-period to ensure population closure.

Case study bawean warty pigs

We applied the SAA model to a camera-trapping dataset of Bawean warty pigs (*Sus blouchi*) from Bawean Island, Indonesia. Details of the random sampling design, population size estimates using REM modelling and an estimate of occupancy from these data can be found in Rademaker et al. [27]. Point abundance (n=102) (λ_x) was computed in PRESENCE from the Royle-Nichols model [28]. We used a Chi-Square (χ^2) Goodness-Of-Fit test to assess whether the Poisson distribution fitted the dataset at the 0.05 significance level [29]. Each 24 hour period of a single operating camera represented a repeated survey. Each camera trap operated for 7 days, resulting in 7 repeated surveys. Data on detection radius and angles were collected in the field using a video viewer, compass and measuring tape. Camera trap videos were played on the video viewer and a field assistant positioned him/herself at the first detection point. A compass was then laid on the center of the camera trap to measure the angle of detection. This procedure was then repeated using a measuring tape to estimate detection radius. Effective detection radius and angle were estimated by DISTANCE 6.0 using a point-transect model for radius, and a line-transect model for angle data [23]. Propagation of error approach was used to estimate the uncertainty of species area abundance [30]. Uncertainty of the species area abundance estimate N_x is equal to the square root of the squared sums of the uncertainty of the parameters λ_x , T_x and $D_{x\max}$, times the partial derivatives of these parameters

$$\sigma N_x = \sqrt{\left(\frac{\partial N_x}{\partial \lambda_x}\right)^2 \sigma \lambda_x^2 + \left(\frac{\partial N_x}{\partial T_x}\right)^2 \sigma T_x^2 + \left(\frac{\partial N_x}{\partial D_{x\max}}\right)^2 \sigma D_{x\max}^2} \quad (6)$$

Uncertainty of the parameters T_x and $D_{x\max}$ were themselves functions of uncertainty of the parameters θ_x , r_x and t and R_x (eqn 8) respectively.

$$\sigma T_x = \sqrt{\left(\frac{\partial T_x}{\partial \theta_x}\right)^2 \sigma \theta_x^2 + \left(\frac{\partial T_x}{\partial r_x}\right)^2 \sigma r_x^2} \quad (7)$$

$$\sigma D_{x\max} = \sqrt{\left(\frac{\partial D_{x\max}}{\partial t}\right)^2 \sigma t^2 + \left(\frac{\partial D_{x\max}}{\partial R_x}\right)^2 \sigma R_x^2} \quad (8)$$

We used a two-sample t-test for equal means [29], to determine whether there was a significant difference between abundance estimates of the SAA-and REM model.

Results

Species area abundance (SAA) Model

Bawean warty pigs were detected at 45 out of 102 sites with an average of ($\bar{x} \pm SE$) 0.73 ± 1.04 detection events per site over the repeat surveys. Mean point abundance was estimated at 1.06 ± 0.32 pigs. Chi-square Goodness-Of-Fit test showed no significant difference between observed and expected values, indicating model fit (Table 1). Mean parameter estimates to calculate species area abundance can be found

Survey No.	Parameters			Chi-square'
	No. of Detections	No. of Observed	No. of Expected	
1	0	96	91.4178	0.2297
	1	6	10.0132	1.6085
	>1	0	0.5734	0.0000
2	0	89	91.4178	0.0639
	1	13	10.0132	0.8909
	>1	0	0.5734	0.0000
3	0	92	91.4178	0.0037
	1	10	10.0132	0.0000
	>1	0	0.5734	0.0000
4	0	88	91.4178	0.1278
	1	14	10.0132	1.5874
	>1	0	0.5734	0.0000
5	0	93	91.4178	0.0274
	1	9	10.0132	0.1025
	>1	0	0.5734	0.0000
6	0	91	91.4178	0.0019
	1	11	10.0132	0.0972
	>1	0	0.5734	0.0000
7	0	91	91.4178	0.0019
	1	11	10.0132	0.0972
	>1	0	0.5734	0.0000
Survey total		714	714.0308	4.84
pooled		0	0.569	0.569
'df=15, p=0.99, Critical $\chi^2=7.26$				

Table 1: Goodness-Of-Fit test results for mean point abundance in presence.

Parameter	Mean	N	S.E.	S.E.%
λ_x	1.06	102	0.32	30.28
ψ_x	0.58	92		
T_x	15631461		0.35	0.00
A	46.6			
r	0.0039	63	0.00029	7.44
θ	22.46	62	0.033	0.15
$D_{x\max}$	22093		2507.28	11.35
t	596908	92	6539	1.10
R	15.67	57	1.77	11.30
v	0.58			

Table 2: Mean parameter estimates and standard error of mean point abundance (λ_x), proportion of sites occupied (ψ_x), maximum number of local sampling sites (T_x), survey area in km² (A), effective detection radius (r), effective detection angle (θ) maximum number of detection events ($D_{x\max}$), average camera operating time in seconds (\bar{t}), average time per detection event in seconds (\bar{R}) and activity level (v). Mean parameter estimates and standard error of r, θ , ψ and v were obtained from Rademaker et al.

in Table 2. Species area abundance of Bawean warty pigs on Bawean Island was estimated to be 436 ± 141 individual pigs ($\bar{x} \pm SE$) or 9.4 ± 3.0 pigs per km². Uncertainty of the SAA model estimate was 32.34%.

Random encounter model (REM)

Rademaker et al. [27] estimated density and total abundance of Bawean warty pigs with the same dataset, although using a REM. Density and total abundance were estimated in two ways: one estimate with mean group size as an upper limit estimate, and one estimate without group size as a lower limit estimate. The lower limit estimate equalled 3.7 ± 0.9 pigs/km² or 172 ± 42 pigs on the whole island. The upper limit estimate was 8.1 ± 1.9 pigs/km² or 377 ± 92 pigs on the whole island. The uncertainty in the total abundance estimate by the REM was

comparable to that obtained by the SAA model, however, slightly lower with 24.32%. The density estimate per km² obtained through the SAA model is significantly ($t(116.48)=-1.82, p=0.036$) different to that of the lower limit estimate by the REM, but not significantly ($t(170.96)=-0.36, p=0.359$) different to that of the upper limit estimate by the REM.

Discussion

Model uncertainty

We estimated species area abundance of Bawean warty pigs on Bawean Island by using mean point abundance from an abundance-induced heterogeneity model and effective camera trap detection areas. The result is credible, although the uncertainty in the estimation by the SAA model is high, with mean point abundance (λ_x), as the highest contributing parameter. Neither Royle and Nichols [13] nor O'Brien and Kinnaird [16] explicitly mention the uncertainty of mean point abundance for species assessed, although, the latter graphically report 95% CI of the estimates. Suwanrat et al. [17], report point abundance estimates of 0.49 ± 0.13 individuals ($\bar{x} \pm SE$), equal to an uncertainty of 26.53%.

When looking at uncertainties in REM estimates there is large variation in the literature. A study on Baird's tapir (*Tapirus bairdii*) yielded an average uncertainty of 54% [31] and an average uncertainty of 39% was reported for Harvey's duiker (*Cephalophus harveyi*) based on six different locations [32]. On the contrary an uncertainty of only 8% was reported in a study on European wildcats (*Felis silvestris silvestris*) [33] and an average uncertainty of 15% in a study of female African lionesses (*Panthera leo spp.*) in four habitats [34]. This shows the difficulty in defining an acceptable level of uncertainty in estimating abundance of unmarked species from camera trap data.

Model comparison

The abundance-induced heterogeneity model uses a Poisson distribution, and thus assumes that the spatial distribution of animals is homogeneous over the habitats [15]. In order to meet this assumption the number of animals inhabiting one sampling point should not be spatially correlated to the number of animals at other sampling points. This can be achieved by placing traps at a distance greater than the home range diameter of the focal species when using non-random sampling designs. Additionally, the abundance-induced heterogeneity model assumes that in order to accurately estimate the maximum number of detection events, sampled points are a representative sample of the habitats available in the area. These assumptions allow for non-random and random sampling designs.

The REM is derived from an ideal gas model in which particles are assumed to move randomly in relation to one another and the number of collisions or density of particles in the gas can be calculated based on this assumption. The key requirement for calculating animal density using the REM model is thus that the placement of the camera traps must be random in relation to the movement of the animals. Within habitats sampled by the researcher (e.g., secondary forest), landscape features that are used or avoided by the target species more than proportionally (e.g., trails, places with scratchmarks or feces), must therefore only be sampled in proportion to their coverage in the landscape to prevent violation of model assumptions [21]. Random (stratified) or systematic-interval sampling designs can meet this assumption [35,36]. Use of random or systematic sampling design makes the use of the REM limited for cryptic species whose detection probability is low and who disproportionately use certain landscape features. In that case, locally preferential placement is the only option to obtain any detection event

or to get a sufficient amount of observations to accurately estimate abundance as well as effective detection parameters.

The abundance induced heterogeneity model and the SAA model described in this paper do not have this limitation as they do not rely on trapping rate, but presence-absence data. An additional capture within a repeat survey resulting from a non-random movement of the target species in relation to a camera trap's position does not directly influence the abundance estimate as the number of presence detections during the survey is still 1. Available habitats must be sampled representatively, but at these sampling sites locally optimal locations within a certain radius (e.g., 100 m), such as trails, places with tracks, feces or other signs of recent activity, can be sampled and representative estimates of abundance can still be obtained [16]. This makes these models more suitable to estimate species area abundance of more rare or cryptic species. Repeated surveys do need to be conducted in a sufficiently short time-period to meet the assumption of population closure. Further studies are needed to determine the level of accuracy and practicality of the SAA model for different species and sampling designs.

Conclusion

We used the newly developed Species Area Abundance (SAA) model to estimate the abundance of Bawean warty pigs on Bawean. The standard error of estimated abundance on Bawean was slightly greater than the standard error of abundance estimated by an REM model used for comparison, but lay within the range of uncertainties of a number of other REM studies. An advantage of the SAA model in studying abundances of rare or cryptic species in an area are the less restrictive assumptions in terms of sampling design. Further studies are needed to determine the accuracy and practicality of species area abundance estimations under different sampling designs.

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