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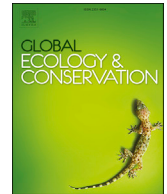
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Original Research Article

Abundance estimation from multiple data types for group-living animals: An example using dhole (*Cuon alpinus*)

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A R T I C L E   I N F O

A B S T R A C T

Large carnivores are declining globally and require baseline population estimates for management, however large-scale population estimation is problematic for species without unique natural marks. We used camera trap records of dhole *Cuon alpinus*, a group-living species, from three national parks in Thailand as a case study in which we develop integrated likelihood models to estimate abundance incorporating two different data sets, count data and detection/non-detection data. We further investigated relative biases of the models using different proportions of data with lower versus higher quality and assessed parameter identifiability. The simulations indicated that the relative bias on average across 24 tested scenarios was 2% with a 95% chance that the simulated data sets obtained the true animal abundances. We found that bias was high (>10%) when sampling 60 sites with only 5 sampling occasions. We tested four additional scenarios with varying proportions of count data. Our model tolerated the use of relatively low proportions of the higher quality count data, but below 10% the results began to show bias (>6%). Data cloning indicated that the parameters were identifiable with all posterior variances shrinking to near zero. Our model demonstrates the benefits of combining data from multiple studies even with different data types. Furthermore, the approach is not limited to camera trap data. Detection/non-detection data from track surveys or counts from transects could also be combined. Particularly, our model is potentially useful for assessing populations of rare species where large amounts of by-catch datasets are available.

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1. Introduction

Animal conservation often starts with basic information regarding the size of threatened populations (Sutherland, 2000). Population estimation surveys are possible for globally threatened carnivores with unique marks such as tigers *Panthera tigris* (Karanth, 1995), Asiatic leopard *Panthera pardus* and clouded leopard *Neofelis nebulosa* (Borah et al., 2014; Ngoprasert et al., 2017), Asian bears *Ursus thibetanus* and *Helarctos malayanus* (Ngoprasert et al., 2012). Population estimation is much more

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problematic for species without such marks (e.g., dhole *Cuon alpinus*, Golden cat *Catopuma temminckii*, etc.). Although DNA mark-recapture can be used for unmarked animals, the cost of specialist researchers and laboratories puts significant constraints on this type of survey (Chandler and Clark, 2014). There are several alternatives to estimating populations of unmarked animals (Royle and Nichols, 2003; Royle, 2004; Kery and Royle, 2016). In particular, Royle and Nichols (2003) introduced the use of detection/non-detection data from direct or indirect surveys to estimate abundance based on repeated surveys similar to an occupancy framework. The model has been applied to several taxa (Reynolds et al., 2010; Miller et al., 2011; Gopalaswamy et al., 2012). Royle (2004) then extended the model to data based on observed counts of animals (Brodie and Giordano, 2013; Belant et al., 2016; Kutal et al., 2016; Smith et al., 2017). Subsequently, Chandler and Royle (2013) developed a model to account for spatial correlations in count data by incorporating coordinates of detectors in conjunction with count data at each detector. This model uses correlations among the count data to determine the locations of animal activity centers and the abundance is then estimated based on the number of individual activity centers.

Despite these advances, many threatened species in numerous tropical forest landscapes still lack even rough population estimates (Ripple et al., 2014), except for a few charismatic species such as tigers. Population estimates of most other tropical carnivores for example have been restricted to relatively small survey areas (e.g., Gray and Prum, 2012; Athreya et al., 2013; Steinmetz et al., 2013; Borah et al., 2014; Carter et al., 2015; Jacobson et al., 2016). Major limitations are often logistical in tropical countries which harbor many secretive/rare species. Fortunately, recent increases in the use of camera traps for wildlife monitoring in tropical Asia (such as for tiger) now provides a valuable source of by-catch data for the study of rarer species at broader scales (Jenks et al., 2012; Linkie et al., 2013), although the limitation of such data is that each camera-trap study is typically designed differently depending on the specific objectives and the landscape context. Previously, such differences among available studies meant that the by-catch data was valuable for species occurrence but not usable for population estimation (Jenks et al., 2012; Ngoprasert et al., 2012; Linkie et al., 2013).

Fortunately, another family of recent techniques, integrated likelihood models (or integrated population models, IPM), can utilize multiple data types in a single model, thereby creating larger datasets and more precise estimates (McCrea et al., 2010; Abadi et al., 2012; Freeman and Besbeas, 2012). Likewise, using multiple data types in one model potentially reduces the need for large individual survey efforts (or large sample size requirements per survey), while maintaining the ability to obtain relatively precise and unbiased parameter estimates (Abadi et al., 2010; Lahoz-Monfort et al., 2014). Such models can utilize independent datasets from the same population based on different methods e.g., dead recoveries and capture-recapture (Fieberg et al., 2010), capture-recapture, reproductive success and annual population counts (Abadi et al., 2012; McCaffery and Lukacs, 2016; Weegman et al., 2016). Alternatively, these models can also use data from the same site but from different survey years (Zipkin et al., 2017), and as well as datasets of different quality (Pacifici et al., 2017). We therefore believe that IPM could particularly benefit species that lack unique marks by providing an opportunity to collect and utilize data that will generate more precise, unbiased parameter estimates across broader landscapes.

The dhole is a relatively well-described species with a large geographic range scattered across Asia (Kamler et al., 2015). However, its population status is poorly known, even though it is categorized as globally endangered (Kamler et al., 2015), with only one local abundance (study area <250 km^2) estimate available for the entire species (Selvan et al., 2014). The main reason for this lack of a population estimate is the absence of unique (individual) coat patterns. Dholes are territorial and are often detected during camera trap surveys throughout Asia although they are rarely a target species (Kawanishi and Sunquist, 2004; Johnson et al., 2006; Gray, 2012, Jenks et al., 2012; Selvan et al., 2014; Riordan et al., 2015; Moo et al., 2017; Thapa and Kelly, 2017). Camera trap surveys typically provide detection/non-detection data for species occurrence models. However, photographs can also provide information on minimum group sizes from counts of individuals within a photo frame (Suwanrat et al., 2015); thus, count data can be used to estimate species abundance. We present an approach that combines two types of data (count and detection/non-detection) to estimate the abundance of dhole, a group-living unmarked animal. We demonstrate the application of the model by analyzing by-catch camera trap data obtained from a bear monitoring program and by-catch from a study that focused on leopards. We believe our model provides a useful approach for estimating the abundance of dhole and other unmarked wildlife populations over larger landscapes.

2. Methods

2.1. Model description: count data

First, we estimated group size using counts of individuals in individual photographs from camera traps. We assumed that the number of group members in a photo is correlated with the total number of individuals in a group. We used beta-binomial mixture models that accounted for non-independent detections of individuals in our repeated count data (Martin et al., 2011). The parameter of interest was the number of individuals (*N*) per sampling site (e.g. camera trap station). The total number of individuals at a site was assumed to follow a Poisson distribution with rate parameter λ, the mean number of individuals per site. These parameters were unobserved in the data (biological process) but estimated from observation processes later. Field observations (observation process) were based on the number of individuals detected at multiple sites during repeated surveys. The individuals observed (*C*) were assumed to follow a binomial distribution of size *N* and individual detection probability *p*. However, detection of an individual was assumed to be correlated with the detection of each of the other members of the group, so detection probability *p* was assumed to follow a beta distribution with two shape parameters, alpha

(α) and beta (β). The correlation within group members produced heterogeneity in detection probabilities among members. We can measure the correlation coefficient (*rho*) by the derived parameter $rho = 1/(\alpha + \beta + 1)$ following Martin et al. (2011).

$N_i \sim$ Poisson (λ)
$C_{ij} \sim$ Beta-Binomial (N_i, p_{ij}, *rho*)
$p_{ij} \sim$ Beta (α_1, β_1)

Where *i* is indicates site and *j* indicates the temporal replicate (occasion).

2.2. Model description: detection/non-detection data

For the second process, data Y_{ij} was derived from detection and non-detection at sites. In this case, the detection process was assumed to be similar to the one above but without information regarding the number of group members present in the detection history. However, the probability of detecting one or more individuals *r*, is a function of the number of individuals at a site, *N*, and individual heterogeneity in the detection process. We modeled this process following Royle and Nichols (2003), but the probability of detection *p* of individual animals in the sample unit was assumed to follow a beta distribution instead of a binomial. We assumed that the detection probability differs between our two survey protocols thus the parameter values of the beta distribution are estimated separately.

$N_i \sim$ Poisson (λ)
$Y_{ij} \sim$ Bernoulli (r_{ij})
$r_{ij} = 1 - (1 - p_{ij})^{N_i}$
$p_{ij} \sim$ Beta (α_2, β_2)

The joint parameter between the two processes is animal abundance (*N*) and expected mean (λ). We combined the likelihood of the two processes to calculate the total abundance of animals. The model can also incorporate covariates to explain the variation in abundance for each site. A generalized linear model with a Poisson distribution can be incorporated via a log link function. Sampling covariates can also be added to the model in the same way as site covariates.

$$\log(\lambda_i) = \beta_0 + \beta_1 * \text{covariate}_i$$

2.3. Simulation study

We evaluated model performance using simulations. The model scenarios were set up to mimic dhole biology. We assumed the true value of site abundance followed a Poisson distribution with a mean of one individual (simulated data ranged from 0 to 8 individuals) (Grassman et al., 2005; Jenks et al., 2015). The plausible detection probability was assumed to be low for this endangered species (Selvan et al., 2014; Srivathsa et al., 2014); we set possible average detection probabilities to (0.30, 0.20, 0.15, 0.10). Correlation coefficients among individuals (*rho*) were unknown, however we assumed that it was much lower than the detection probability at a given site. Abundance at the sampled units (True *N*) was generated under a beta-binomial mixture model for a total of 60 or 120 sites, then the data was divided into two parts (1) count data and (2) detection/non-detection data. We changed the count data to detection/non-detection data for analysis of the second process. We assumed the count data was much less available than detection/non-detection data, the typical data derived from occupancy studies using camera traps. Thus, we generated abundances using a ratio of count relative to detection/non-detection data of 20:40 (60 sites) for our small data set and 50:70 (120 sites) for our larger dataset. We set the individual detection probability at a given site for the count data to be higher than the individual detection probability for the detection/non-detection data for each run, because sites with relatively high detection probabilities might reasonably have enough detections to provide count data. The simulation was designed for temporal replicates of 5, 10 and 30 occasions of camera trap operations (total 24 scenarios, Appendix 1). This spans the range of survey occasions found in other large mammal surveys in the region (Zaw et al., 2008; Johnson et al., 2009; Chutipong et al., 2014).

In addition, we simulated data sets with one additional covariate. We assumed that the abundance differs between parks because the variation of prey availability or levels of protection were different among parks. The park covariate was a factor (0 or 1). We used a sample size equal to 120 sites and 10 capture occasions as an "intermediate" scenario with a relatively large number of camera trap locations tested with both high and low detection probabilities (scenario 25 and 26). Prey and park covariates affected λ with a log link function.

$$\log(\lambda_i) = \beta_0 + \beta_1 * \text{prey}_i + \beta_2 * \text{park}_i$$

For comparison, we also ran scenarios to assess biases where the researcher excluded the use of lower quality data (detection/non-detection) and instead used only higher quality count data. We referred to these two simulations as scenarios 27 and 28 in Appendix 1.

We investigated the effect of the ratio of count data to detection/non-detection data by varying the relative proportion of count data (scenarios 29 to 32), ranging from 10%, 30%, 50% or 70% respectively. We were focusing on cases where researchers may try to apply this method with a high proportion of low-quality data such as detections/non-detections from sign surveys. Sign surveys are also a practical technique for cryptic species in large landscapes. Also, even camera traps sometimes yield few detections of rare species, especially with by-catch data. The 10% proportion of good quality data is more of a warning message to researchers to consider the type/quality of data in such analysis. We set up these simulations based on scenarios of 120 sample sites, 30 sampling occasions, a probability of detection at 0.3 for count data and 0.2 for detection/non-detection, and correlation coefficients among individuals at 0.2 and 0.1 respectively.

We simulated 100 replicates for each scenario to evaluate bias and precision of the estimator. Total abundance over all sites in each simulation was used to compare with the 'true' values. We also evaluated the frequency of how often the true values were inside the 95% credible intervals of the parameter estimates. In addition, we reported the relative bias of the total abundance estimated compared to the true abundance for each run (N-hat − True N/True N), where relative bias > 0 indicated over-estimation and <0 indicated underestimation of the true abundance. We also evaluated the relationship between N-hat and True$N$ with a standard linear regression. A well-calibrated model will have an estimated intercept not different from zero and an estimated slope not different from one. The simulations were analyzed using a Bayesian analysis with JAGS (Plummer, 2003) through package "jagsUI" (Kellner, 2018) in R program (R Core Team, 2018). We used vague priors for all parameters (flat uniform distribution for covariates affected λ and a gamma distribution for α and β). Model convergence was assessed by using the R-hat value < 1.05, where a value close to 1 indicated successful convergence (Gelman and Hill, 2007) and by examining the trace plots of the chains (Gelman et al., 2014). See Appendix 2 for the simulation code and script for the analysis of the dhole data.

2.4. Dhole surveys

We demonstrated our model by analyzing dhole data from camera trap surveys in two forest complexes. First, a survey conducted in the World Heritage Dong Phayayen-Khao Yai Forest Complex, DPKY (http://whc.unesco.org/en/list/590). This complex consisted of five study areas, Khlong E-Tow (KET, December 2009−February 2010), Khlong Samor-Pun (KSP, March−May 2010) and Khao Kampang (KKP, December 2010−May 2011) in Khao Yai National Park, and Baan Thai Samukee (BTS, December 2012 to May 2013) and Lam Plai Mat (LPM, November 2013 to August 2014) in the Dong Phayayen forest complex (Fig. 1). The camera-trap setup protocol was designed for monitoring Asiatic Black Bear (*Ursus thibetanus*) and Sun Bear (*Helarctos malayanus*) (Ngoprasert et al., 2015). We used passive infrared-based digital camera-traps to photograph animals visiting bait stations. Three camera-traps were mounted on trees approximately 3−4 m apart and facing each other in a triangular arrangement. Camera trap stations were set 1.5−4 km apart. However, based on dhole movements in a site in Thailand (Grassman et al., 2005), the trap spacing was shorter than the mean daily distance moved (2214 m) increasing the chances of double counting. Therefore, spatial correlation of dhole detections was evaluated using the *variogram* function in the gstat package (Pebesma, 2004; Gräler et al., 2016). One trap from each pair of trap stations less than 2 km apart were randomly removed to reduce this correlation. After removing spatial correlated traps, we used 117 camera-trap stations surveyed from December 2009−May 2011 in Khao Yai National Park (72 camera-trap stations) and December 2012−August 2014 in Dong Phayayen forest complex (45 camera-trap stations). Camera-traps were operational 38 to 182 trap days. Dhole were rarely present at a given camera-trap station more than once per day. Multiple detections of dhole at a single station were typically within relatively short time interval (<1 h), and in this case we included only the highest number of individuals counted. The station was non-reward baited which allowed us to estimate group size. We used each day (24-h period) as a sample occasion. Consecutive photographs of dhole within a sample occasion were used to estimate the maximum number of individuals, i.e., daily detection counts. We refer to this DPKY dataset using subscript 1 for the detection parameters in the model description below.

A second dataset, a survey conducted in the Kaeng Krachan National Park (hereafter Kaeng Krachan), (http://whc.unesco.org/en/tentativelists/5593), where the data was recorded as detection/non-detection per one-day trapping occasions. In Kaeng Krachan, passive infrared-based film camera-traps were used to survey leopard from November 2003−January 2004 (Ngoprasert et al., 2007) and tiger in January to March 2001 (Ngoprasert and Lynam, 2002), in which all camera locations were focused along the animal trails. Camera-traps were set at 32 stations (9 stations with two-sided camera-traps in 2001 and 23 stations with a single-sided camera-trap in 2003−2004) within two different areas. Camera-trap stations were operational for 9 to 38 trap days. The camera-traps were set for 24-h operation for all data sets. We used the last day a camera was working to calculate the number of trap days per camera. We referred to the Kaeng Krachan dataset by using subscript 2 for the detection parameters in the model description below.

To compare dhole density between the two forest complexes, we converted estimates of total abundance to density by dividing the estimated population size (N) by the effective sample area of the camera traps. We used the average home range radius to calculate the effective sample area. A circular buffer was applied for each camera trap station with a radius equal to the average home range. We used an average home range radius 3.7 km based on Grassman et al., (2005), Jenks et al., (2015), and R. Sukmasuang personal communication 2019.

2.5. Site covariates

Dhole prey (Gaur *Bos gaurus*, Sambar *Rusa unicolor*, Wild pig *Sus scrofa* and Muntjac *Muntiacus muntjak* and *Muntiacus feae*) were detected by the same cameras. We estimated the availability of prey in each trap station using counts of independent
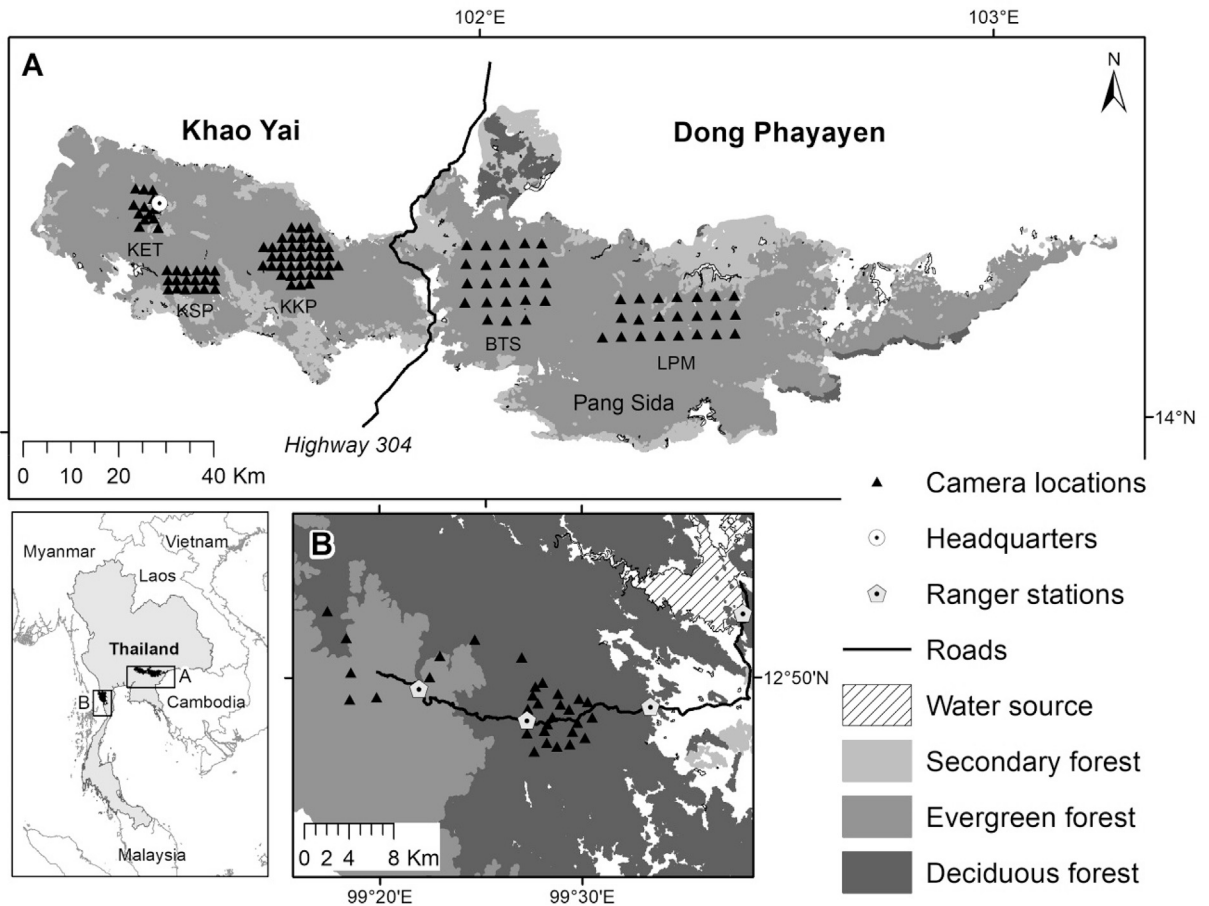
Fig. 1. Map of study area and camera-trap stations in Dong Phayayen-Khao Yai Forest Compex (A) and Kaeng Krachan Forest Complex (B).

photographs. Independent photographs were defined as those separated by $\geq$ 30 min (O'Brien et al., 2003). The sum of prey photographs at each camera-trap station was used to calculate a relative prey abundance index (RAI) per trap day. We calculated the total number of trap days at a given camera-trap station by summing trap days of all active cameras. We used the prey abundance index as a site covariate in the model. However, the use of RAI with different trap setups would provide a biased RAI (Sollmann et al., 2013), thus we used RAI here for demonstration purposes only.

2.6. Assessment of parameter identifiability

Parameter identifiability is problematic where the model structure is complex (Lele et al., 2010) or the data inadequate (Dennis et al., 2015; Kéry, 2018), we therefore assessed identifiability of parameters by using data cloning (Lele et al., 2007). A parameter is identifiable where the posterior variance tends to be smaller (shrinking to zero) with increasing numbers of clones (Lele et al., 2007). We determined the adequate number of clones by evaluating the posterior variance against the number of copies. The data were cloned from 1, 5, 10 and 20 copies. We ran the model with a prey covariate as this model was the best supported using actual field data (see results) where the parameter for monitoring included p_{count}, $p_{\text{detection}}$, rho_{count}, $rho_{\text{detection}}$, β_0 and β_1.

3. Results

3.1. Simulation study

All simulations successfully converged with 100% of R-hats lower than 1.05 and posterior distributions drawn from >2400 effective samples for all parameters in all models. The posterior distributions of detection probability for count data for each of the scenarios were generally close to the true value (Appendix 3 a). However, when correlation was high and detection probability was low, $\hat{p}_1$ was negatively biased and the bias increased with increasing sampling occasions. The precision of

estimates increased with increasing sampling occasions more than increasing the number of sites. $\hat{\rho}_1$ was positively biased, especially when low (Appendix 3 c). The precision of $\hat{\rho}_1$ generally decreased with more sampling occasions or sites. The estimated detection probability and correlation for detection/non-detection data ($p2$) followed a similar pattern, except the positive bias in the correlation was worse (Appendix 3 b and d).

The estimates of the beta coefficient of the intercept (β_0) were negatively biased and imprecise when the number of occasions was low and with fewer sites (Fig. 2 a). Both bias and precision of $\widehat{\beta_0}$ improved most with adding more sampling occasions rather than more sites. $\widehat{\beta_1}$ appears less biased than $\widehat{\beta_0}$ overall, and there was greater improvement with adding more sites than sampling occasions (Fig. 2 b).

The simulations indicated that the estimated mean relative bias for the total population size ranged from -15% to 16% among the 24 scenarios, but the relative bias on average across all scenarios was 2% (Appendix 1). The 95% CrI of the estimated total N included the True N 85−98% of the time across all scenarios. We found that the bias was high (>10%) when sampling 60 sites with only 5 sampling occasions. Increasing the number of sampling occasions always reduced bias, and in some cases could reduce it as much as doubling the number of sites. The benefit of more sampling occasions diminishes when the correlation between individuals is higher. The estimated slopes of the calibration regressions were close to 1 when the simulated data had a low correlation coefficient among individuals (0.1 and 0.05) using 30 occasions regardless of the total number of sites (Fig. 3). Precision of the estimates was not affected by changing the detection probabilities and correlation coefficients.

Adding an additional parameter slightly increased the bias compared to the same scenario with only a single covariate. There was a mean relative bias of 6%, when p and *rho* were high (compare scenario 25 to scenario 23 in Appendix 1). In contrast, there was a negative bias of -6% (compare scenario 26 to scenario 5) where p and *rho* were low. As expected, the biases of scenarios 27 and 28 were large when analyzed with count data only even though we used 30 occasions.

The simulation indicated our model was not very sensitive to the ratio of count to detection/non-detection data (Appendix 1). The relative biases were low (<3%) when the proportion of count data was 30%, 50% or 70% in the simulated data (scenarios 30−32). However, the result using a proportion of only 10% for the count data (scenario 29) was biased high, although relatively modest (6%).

3.2. Estimated dhole abundance

We photographed dhole at 26 camera-trap stations out of a total of 149 (17/117 stations in DPKY with count data and 9/32 in Kaeng Krachan with detection/non-detection data). The largest recorded group size was 6 individuals in Khao Yai National Park and 5 individuals in the Dong Phayayen forest complex. The constant model had the lowest DIC value, and the model with the prey covariate had the second-highest level of support (delta DIC 1.39, Table 1). The prey coefficient was negative, but the credible interval overlapped with zero. The prey covariate model estimated a total dhole abundance of the two forest complexes that was similar to the constant model and the model with park as a covariate. The convergence was successful with a R-hat < 1.001 and a posterior distribution draw of >5300 MCMC effective samples for all parameters. The individual detection probability was 15 times higher in Kaeng Krachan compared to DPKY, and the correlation coefficient 2.6 times higher in Kaeng Krachan than DPKY as well. However, the total abundance was lower in Kaeng Krachan because the trap stations were fewer. The park model ranked third with a delta DIC of 2.45. The detection probability and the correlation coefficient were identical to the prey model. The model with two covariates had a delta DIC of 3.56. Data cloning indicated that the parameters were identifiable with all posterior variances shrinking to near zero with 20 clones (Appendix 4).

The density estimate was higher in Kaeng Krachan compared to DPKY (3.0 versus 2.2 individuals per 100 km^2 respectively) based on abundance estimates from the constant model. The effective sample area was 1651 km^2 for DPKY and 335 km^2 for Kaeng Krachan.

4. Discussion

Our integrated population model was motivated by our search for a better method for estimating wildlife populations with by-catch data, especially for group-living species with unidentifiable individuals, which face a number of significant constraints regarding population estimation. Specifically, our approach combined the Martin et al. (2011) and Royle and Nichols, 2003 type models into an integrated population estimate. Our model demonstrates the benefits of combining camera-trap data from multiple studies even with different data types. Furthermore, the approach is not limited to camera trap data. Detection/non-detection data from track surveys or counts from transects could also be combined. We also demonstrated how data can be used to estimate abundances of group-living species at larger scales by combining different data types.

As expected, our results indicated having more sites provides better results than having fewer sites, and from our simulations sample sizes >60 across both survey types are needed to obtain well-calibrated, unbiased and precise estimates. Estimation would be improved further if some sites shared both types of surveys, although this is unlikely to occur given the nature of combining by-catch data from multiple surveys. Once a survey is in place, the primary option for improving estimation is extending the duration of monitoring at each site (Fig. 3). The number of occasions can also be adjusted after the fact by changing the temporal resolution over which photographs are aggregated. Photos should be aggregated at the finest temporal resolution consistent with the assumption of independence of observations. The proportion of different data types was less important as long as the amount of high-quality data was not too low (>30% in our simulations). 30 sampling
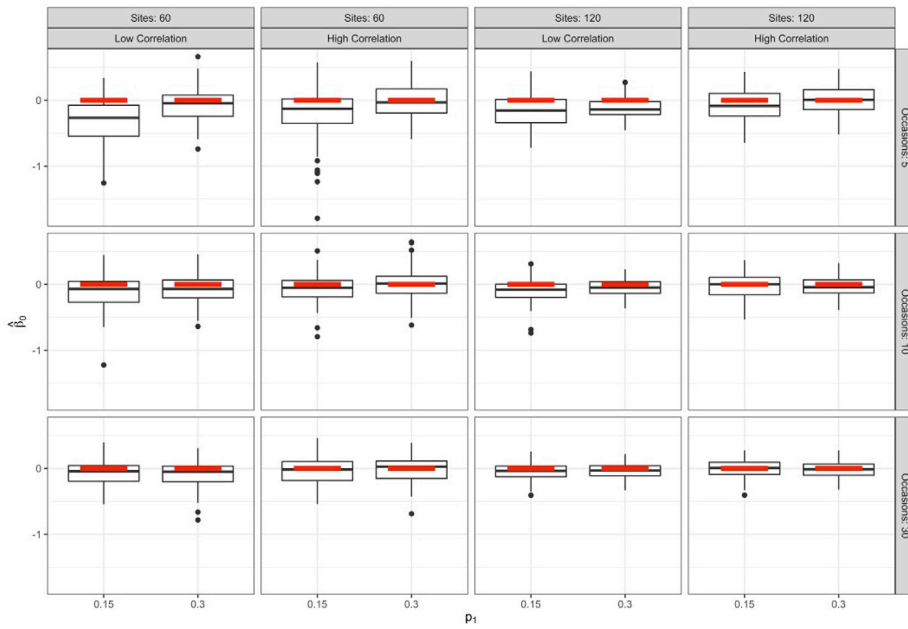
(a)
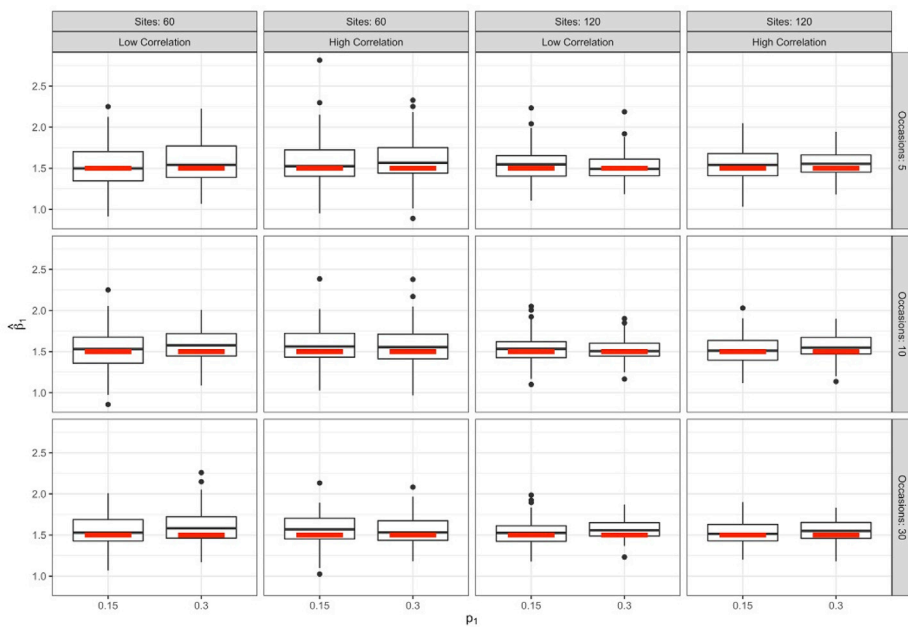
(b)

Fig. 2. Regression coefficient estimates from 24 scenarios where the red line indicates the true value. (a): intercept (β_0), (b): beta coefficient (β_1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

occasions is recommended if the number of sites is low (<60). Our model was able to tolerate the use of a relatively low proportion of higher quality (count) data, but at 10% the results began to show bias. Our real data had sample sizes larger than we simulated and with a higher proportion of count data relative to detection sites—these produced a narrow credible interval.
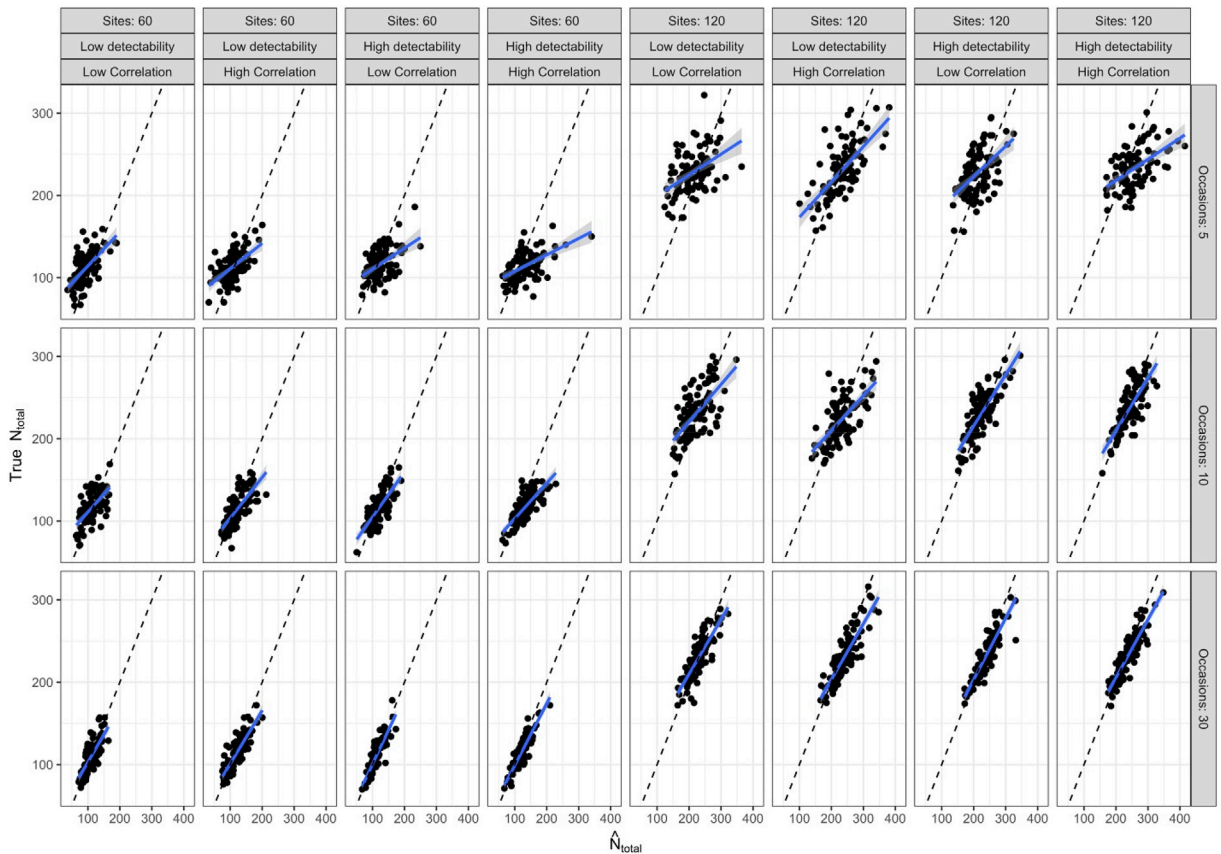
Fig. 3. Regression coefficient estimates from 24 scenarios with expected intercept = 0 and slope = 1 (dashed line). Blue line indicates model fit. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Parameter estimates and 95% credible intervals (in parentheses) for four tested models for dhole, including individual detection probability and abundance (N) from integrated count and detection/non-detection data applied to Khao Yai National Park, Dong Phayayen Forest and Kaeng Krachan National Park, Thailand.

Model	$\lambda(.)$, p(.)		λ(Prey), p(.)		λ(Park), p(.)		λ(Prey + Park), p(.)	
Parameters								
Intercept	1.384	(1.264–1.537)	−1.013	(−1.379 − -0.672)	−1.261	(−2.207 − -0.285)	−1.323	(−2.282 − -0.344)
Prey	−	−	−2.544	(−7.124 −1.128)	−	−	−3.031	(−7.804 − 0.929)
Park	−	−	−	−	0.096	(−0.704 − 0.818)	0.272	(−0.563 − 1.037)
p_{count}	0.001	(0.000−0.004)	0.001	(0.000−0.004)	0.001	(0.000−0.004)	0.001	(0.000−0.004)
$p_{detect/non-detect}$	0.015	(0.000−0.049)	0.015	(0.000−0.049)	0.014	(0.000−0.047)	0.014	(0.000−0.047)
N								
Khao Yai	23	(17−31)	25	(17−35)	23	(16−31)	24	(16−34)
Dong Phayayen	14	(10−18)	14	(9−20)	14	(10−19)	13	(8−19)
Kang Krachan	10	(8−14)	9	(5−14)	12	(5−21)	11	(5−22)
DIC	707.20		708.59		709.65		710.76	

The model we developed in this study demonstrated that parameter identifiability was not a problem. We cloned our real data with the prey covariate model Lambda(prey) p(.). The posterior standard deviation indicated all parameters were shrinking towards zero as the number of clones increased. Our results were also congruent with recent findings that with or without covariates Poisson mixture models had no identifiability problems (Kéry, 2018). However, the estimate of the correlation parameter (rho) using a beta-binomial distribution suggested there was a numerical problem as noted by Martin et al. (2011), "when the data followed a binomial distribution, the chains for the beta-binomial mixture model did not mix well". We set our correlation parameter to be relatively low as is expected with endangered species. The parameter rho can approach zero but cannot be exactly zero, otherwise, the data follow a binomial distribution (with no overdispersion). We also explored the rho_{count} and $rho_{detection}$ with scenarios 29−32 where we varied the proportion of count data. The $rho_{detections\ 29-32}$ were

similar to the first 24 scenarios which were also biased low because the data followed a binomial distribution. However, the $rho_{count,}$ where the proportion of count data was 10% (scenario29), was also biased. As expected, the individual detection probabilities of the detection/non-detection data ($p2$) was less informative with most of the data being detection/non-detection only (90% of data followed a binomial distribution). Here the mixture model caused the rho_{count} of scenario 29 to be particularly biased, but it was not biased where the count data was >30%. In general, a lower correlation parameter can cause biased estimates of rho, but it was not especially biased regarding individual detection probability. However, we did not explore the lower limits of rho, indeed, our data (Appendix 3c) indicated that a rho >0.1 was less biased than 0.05 or 0.1. Therefore, we suggest future research consider this point when analyzing data with a relatively small proportion of counts.

To illustrate the application of our model for real empirical data, we used multiple datasets across years. The limitation of combining sites across years is that the method may sometimes violate closure assumptions. We treated the data from Kaeng Krachan as one site between the 2001 and the 2003—2004 samples (similar to a multi-session analysis). Here, we were confident that our estimate did not violate closure assumptions because the actual locations between the two surveys focused on different areas within the park. The closest distance between points along the two surveys areas was 2.3 km. However, the total abundance estimated across years should be inferred carefully when combining among different areas and times.

Although, we fit separate detection probabilities, trap setup differences likely incurred differences in our ability to detect dhole. In Kaeng Krachan, the individual detection probability of dhole was probably higher because the camera trap setups were along animal trails as the objective of the survey focused on tiger and leopard. Dhole is known to extensively use trails or roads inside forests for movement (Venkataraman et al., 1995; Srivathsa et al., 2014). Camera traps in Khao Yai and Dong Phayayen were all set up off trails but were baited. Therefore, the park covariate in our data represents variation due to different camera setups rather than real site variation in individual detection probabilities.

The negative relationship between dhole and their prey in our data seems unrealistic but could reflect differences in the abundance of the two main competitors of dhole among our three main study sites, Khao Yai, Dong Phayayen, and Kaeng Krachan. Kaeng Krachan had the highest prey abundance (13.2/100 trap days), but supported three large carnivores (tiger, leopard, and dhole). Dong Phayayen had moderate prey abundance levels (8.5/100 trap days) but supported only tiger and dhole (leopard did not occur here and Khao Yai historically). In contrast, Khao Yai had only dhole present, but the lowest prey abundance (2.0/100 trap days). Tiger went locally extinct in Khao Yai sometime between 2001 and 2005, and therefore the lack of competition with other large carnivores may be at least partly responsible for the higher dhole abundance in Khao Yai despite the lower prey base (Steinmetz et al., 2013; Ngoprasert and Gale, 2019). However, the park model indicated a positive relationship between prey abundance and dhole abundance whereby dhole abundance was lower in DPKY (lambda = 0.32; 95%CrI 0.22−0.43) than Kaeng Krachan (lambda = 0.36; 95% CrI 0.17−0.64). It is also possible that the fewer sample units in Kaeng Krachan might have affected the parameter estimates as indicated by the wider 95%CrIs. Overall, comparisons between different studies should be interpreted with some caution because direct comparisons of prey relative abundance may be limited due to differences in duration of surveys and/or the different trap set-ups (Sollmann et al., 2013).

The density estimates for dhole were low in both forest complexes and a cause for conservation concern. Our densities were notably smaller than previously reported in Pakke Tiger Reserve, India (Selvan et al., 2014) 6.6 individuals per 100 km^2, although a similar density 3.3 individuals per 100 km^2 was observed in the Pench landscape of central India (Majumder et al., 2011). However, the Pench landscape was more heterogenous in terms of densities and there was probably higher food competition with other large carnivores including tiger, wolf, and hyena. In general, our estimates were much smaller than those reported for India (Majumder et al., 2011). In Thailand, dhole may be as seriously threatened as tiger as a consequence of significant declines in large ungulate prey in many protected areas (Pisdamkham et al., 2010). Furthermore, we detected domestic animals (i.e. dogs and cattle) in our study areas, these could cause additional threats to our small populations of dhole, i.e. transmission of disease from domestic dogs to dhole (Hughes and Macdonald, 2013).

In this study we have assumed that the dhole detections at each camera-trap site were independent. However, as trap spacing gets smaller, this is increasingly unlikely. A mismatch is quite possible when using by-catch from surveys designed for other species. This is currently a disadvantage of by-catch data where data would need to be discarded if sampling locations are spatially correlated. Future models that incorporate spatial correlation processes within a hierarchical spatial framework could resolve issues in detection/non-detection data such as by incorporating random effects (Johnson et al., 2013). Furthermore, spatial correlations within count data may provide further possibilities of combining models (Chandler and Royle, 2013). Chandler and Royle's unmarked model framework use explicit spatial correlations of count data to infer locations of individual activity centers in which detection probability declines with distance. Thus, the ability to account for spatial correlation is an important focus for future model development as typically prior knowledge about movement of target species will be unavailable. Therefore, care should also be given when applying our current model to species which are likely to move long distances relative to sampling occasions.

In our particular application, we used camera trapping to obtain both count and detection/non-detection data but such integrated likelihood models described here can use a variety of detection/non-detection data from almost any survey design such as tracks from transect surveys (Karanth et al., 2011; Srivathsa et al., 2014), or presence of feces/dung (Long et al., 2007). Transect surveys are relatively easily to implement for large-scale monitoring for elusive or rare species (e.g., Guillera-Arroita et al., 2011; Gopalaswamy et al., 2012). This method offers an alternative to existing data, however further work is required to maximize trap set-ups to increase the chances of determining group size from count data. Also, for detection/non-detection data, the model requires a sampling design where the spacing between detection devices is relatively larger than the home-

range radius of the species of interest. In conclusion, our model should be applicable to a wide variety of by-catch datasets available in a given region for inferences regarding large scale abundance of group-living unmarked animals.

Declaration of interests

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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Appendix 1. Simulation scenarios, percentage of estimates with True *N* within 95% CrI, and mean relative bias of estimated total *N*

| Scenario | Number of sites | Number of occasions | $p1$ | Rho1 | $p2$ | Rho2 | Covariates | | True*N* in 95%CrI | Mean relative bias |
							Prey	Park		
1	60	5	0.15	0.10	0.10	0.05	1	0	91	−0.15
2	60	10	0.15	0.10	0.10	0.05	1	0	98	−0.03
3	60	30	0.15	0.10	0.10	0.05	1	0	98	0.02
4	120	5	0.15	0.10	0.10	0.05	1	0	94	−0.07
5	120	10	0.15	0.10	0.10	0.05	1	0	97	−0.03
6	120	30	0.15	0.10	0.10	0.05	1	0	98	0.00
7	60	5	0.15	0.20	0.10	0.10	1	0	92	−0.05
8	60	10	0.15	0.20	0.10	0.10	1	0	98	0.07
9	60	30	0.15	0.20	0.10	0.10	1	0	94	0.05
10	120	5	0.15	0.20	0.10	0.10	1	0	98	0.01
11	120	10	0.15	0.20	0.10	0.10	1	0	98	0.04
12	120	30	0.15	0.20	0.10	0.10	1	0	96	0.04
13	60	5	0.30	0.10	0.20	0.05	1	0	98	0.09
14	60	10	0.30	0.10	0.20	0.05	1	0	96	0.03
15	60	30	0.30	0.10	0.20	0.05	1	0	98	0.02
16	120	5	0.30	0.10	0.20	0.05	1	0	85	−0.07
17	120	10	0.30	0.10	0.20	0.05	1	0	93	−0.03
18	120	30	0.30	0.10	0.20	0.05	1	0	95	0.03
19	60	5	0.30	0.20	0.20	0.10	1	0	93	0.16
20	60	10	0.30	0.20	0.20	0.10	1	0	91	0.12
21	60	30	0.30	0.20	0.20	0.10	1	0	95	0.06
22	120	5	0.30	0.20	0.20	0.10	1	0	98	0.11
23	120	10	0.30	0.20	0.20	0.10	1	0	96	0.03
24	120	30	0.30	0.20	0.20	0.10	1	0	93	0.03
25	120	10	0.30	0.20	0.20	0.10	1	1	96	0.06
26	120	10	0.15	0.10	0.10	0.05	1	1	93	−0.06
27	20	30	0.30	0.20	0.20	0.10	1	0	1	3.88
28	20	30	0.15	0.10	0.10	0.05	1	0	10	2.20
29	120	30	0.30	0.20	0.20	0.10	1	1	88	0.06
30	120	30	0.30	0.20	0.20	0.10	1	1	96	0.02
31	120	30	0.30	0.20	0.20	0.10	1	1	94	0.03
32	120	30	0.30	0.20	0.20	0.10	1	1	89	0.02

Appendix 2. R script used to analyze dhole data presented in this paper.

```
# Abundance estimation from multiple data types for group living unmarked animals
# Example: Dhole in Dong Phayayen-Khao Yai Forest complex and Kaeng Krachan National Park
# Load package
library(jagsUI)
# Analysis real data with prey and park covariates
# Create model file
modeltext <- "
model{
                for(i in 1:nSites){
                        N[i] ~ dpois(lambda[i])
                        log(lambda[i]) <- b0 + b1*covariate1[i] + b2*covariate2[i]
                }
                # Beta-Binomial/Poisson mixture model
                for(i in 1:nC){
                        for(j in 1:nOcc) {
                                p1[i,j] ~ dbeta(A, B)T(0.01, 0.99)
                                C[i,j] ~ dbin(p1[i,j], N[i])
                        }
                }
                # Bernoulli/Poisson mixture model
                for(i in 1:nO){
                        for(j in 1:nOcc) {
                                p1[i+nC,j] ~ dbeta(D, E)T(0.01, 0.99)
                                p2[i,j] <- 1-(1 - p1[i+nC,j])^N[i+nC]
                                Y[i,j] ~ dbern(p2[i,j])
                        }
                }
                # Priors
                b0 ~ dunif(-10, 10)
                b1 ~ dunif(-10, 10)
                b2 ~ dunif(-10, 10)

                # detection of count data
                mu1 ~ dunif(0, 1)
                theta1 ~ dgamma(10, 2)
                A <- mu1 * theta1
                B <- (1 - mu1) * theta1
                # detection of present/absent data
                mu2 ~ dunif(0, 1)
                theta2 ~ dgamma(10, 2)
                D <- mu2 * theta2
                E <- (1 - mu2) * theta2
                # derived variable
                totalN <- sum(N[])
                pAB <- A/(A+B)                  # derived detection probability
                rhoAB <- 1/(A+B+1)             # correlation coefficient
                pDE <- D/(D+E)                  # derived detection probability
                rhoDE <- 1/(D+E+1)             # correlation coefficient
        }"
writeLines(modeltext, con="dholeWith_2SiteCov.txt")
 # -----------------------------------------------------------
```

```
# Read input file

DH <- read.csv("DPKY_KK_dholeDHfinal.csv", row.names = 1, comment = "#")

dim(DH)

View(DH)

nC = 117

nO = 32

nSites = nC+nO

nOcc = 182


#Data

C <- DH[1:nC, 1:nOcc]

Y <- DH[(nC+1):nSites, 1:nOcc]

prey <- DH[,(nOcc+1)]

trapDay <- DH[,(nOcc+2)]

RAIprey <- prey/trapDay

park <- factor(DH[,(nOcc+3)])

park1 <- as.integer(park)


# Run JAGS

wanted <- c("pAB","rhoAB", "pDE", "rhoDE", "b0", "b1", "b2", "totalN", "lambda")

JAGSdata <- list(nSites = nSites, nOcc = nOcc, C = C, Y = Y, nC = nC, nO = nO, covariate1 = RAIprey, covariate2
                = park1)

str(JAGSdata)

Nhat <- apply(C[,1:nOcc], 1, max, na.rm=TRUE)+1

Noc <- rep(1, nO)

Nall <- c(Nhat, Noc)

inits <- function() list(N = Nall ,  mu1 = runif(1), mu2 = runif(1))

jagsOut <- jags(JAGSdata, inits, wanted, "dholeWith_2SiteCov.txt",

        n.chains=12, n.iter=100000, n.adapt=2000, n.burnin=40000, n.thin=5, DIC=TRUE,  parallel=TRUE)

# ------------------------------------------------------------

saveRDS(jagsOut,file = "RealdholeWith_2siteCov.rds")

# Inspect output

plot(jagsOut)
```
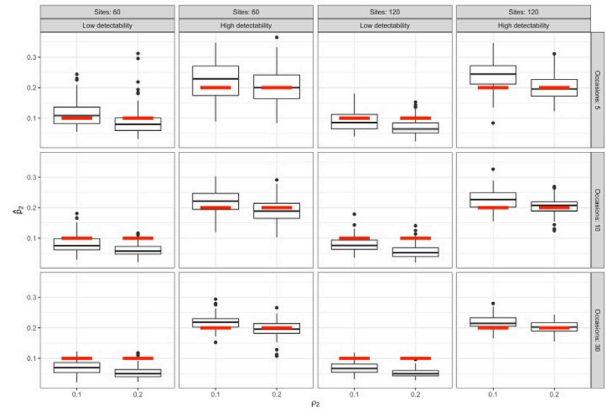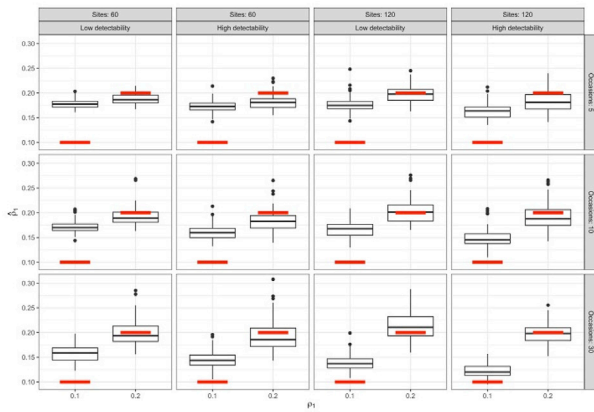
Appendix 3. Simulation results of detection probability (*p*) and correlation coefficients (*rho*) from 24 scenarios where the red line indicates the true value. Left panel: (a) *p*1 and (c) *rho*1 of count data, Right panel: (b) *p*2 and (d) *rho*2 of detection/non-detection data.
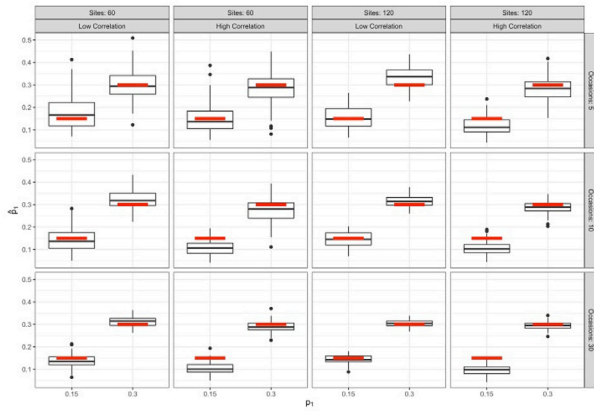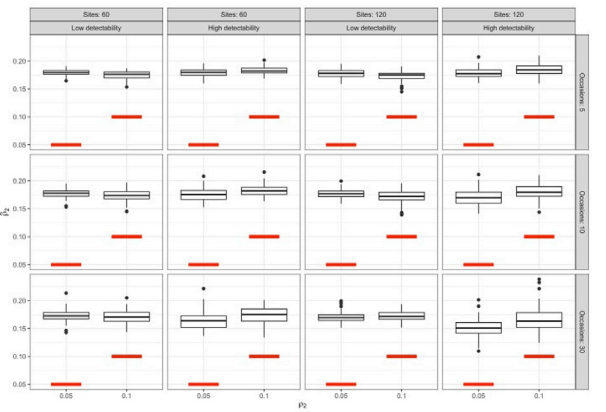
(a)

(b)

(c)

(d)

Appendix 4. Parameter estimates using data cloning to check parameter identifiability for dhole data with the prey covariate in the model. Posterior standard deviations of all parameters are shrinking as the number of copies increase indicating that the parameters are identifiable.

Number of copies	Count data		Detection data		β_0	β_1
	p	rho	p	rho		
1	0.0010	0.0060	0.0130	0.0250	0.1820	2.1140
5	0.0000	0.0020	0.0050	0.0120	0.0820	0.9380
10	0.0000	0.0010	0.0030	0.0090	0.0580	0.6660
20	0.0001	0.0009	0.0023	0.0062	0.0415	0.4703

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