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Covariates influence optimal camera-trap survey design for occupancy modelling

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Abstract

Motion-activated cameras ('camera-traps') have become indispensable for wildlife monitoring. Data from camera-trap surveys can be used to make inferences about animal behaviour, space use and population dynamics. Occupancy modelling is a statistical framework commonly used to analyse camera-trap data, which estimates species occurrence while accounting for imperfect detection. Including covariates in models enables the investigation of relationships between occupancy and the environment. Survey design studies help practitioners decide the number of cameras to deploy, deployment duration and camera positioning. However, existing assessments have generally assumed constant occupancy and detectability (i.e. no covariates were considered), which is unrealistic for most real-world scenarios. We investigated the effects of covariates on the relationship between survey effort and the combination of accuracy and precision (i.e. error) of occupancy models. Camera-trap data for a 'virtual' species were simulated as a function of randomly generated, site- and survey-specific covariates (e.g. habitat type/quality and temperature, respectively). We then assessed how varying survey design and total effort influenced estimation error with and without covariate information. Increasing the number of cameras consistently reduced error, while longer deployments were only beneficial when the covariate influenced occupancy. When both parameters were affected by covariates, omitting effects on detectability had limited impact on model performance. However, failing to account for effects on occupancy significantly increased error, and none of the predefined thresholds (root mean squared error = 0.15, 0.10 and 0.075) were achievable, even with the maximum survey effort of 9000 camera-days. These results suggest that increasing survey effort is unlikely to improve model performance unless site-level conditions are appropriately modelled. Thus, robust study design should consider total effort and the monitoring of covariates across sites to ensure efficient use of time and financial resources.

Introduction

Monitoring the distribution of species and tracking changes over time is a fundamental component of biodiversity conservation and ecological research (Burton et al., 2015; Kays et al., 2015). It provides essential information for assessing the local extinction risk of vulnerable species, understanding human-wildlife conflicts and forecasting the effects of global climate change on wildlife populations (Dirzo et al., 2014; Johnson et al., 2017). Collecting data on the behaviour and space use of wide-ranging terrestrial animals can be logistically challenging, particularly for rare or cryptic species, and may require investment of sizeable financial and human resources (Festa-Bianchet et al., 2017; Lindenmayer & Likens, 2010). Motion-activated digital cameras ('camera-traps') are one of several technologies, including Global Positioning System (GPS) devices and satellite imagery, that have advanced rapidly in recent years and provided new opportunities for scientists to monitor animals remotely over large geographic areas (Pimm et al., 2015).

Camera traps offer advantages over traditional monitoring techniques (e.g. direct counts and track surveys) as the data collection process is largely non-invasive and requires relatively less surveyor effort (Blount et al., 2021; Trolliet et al., 2014). They have been used to investigate a wide range of biological questions relating to population density (Parsons et al., 2017; Rowcliffe et al., 2008), species interactions (Gorczynski et al., 2022), temporal activity (Frey et al., 2017; Lazzeri et al., 2022) and population dynamics (Kasada et al., 2022; Trolliet et al., 2014). The reliability and utility of camera trap surveys depend on a robust study design accounting for key factors, such as animal movement and habitat preference, the influence of attractants (e.g. scent lures), as well as environmental conditions (e.g. habitat type) that may influence detection probability (Burton et al., 2015; Kays et al., 2021). A well-designed study ensures the collection of high-quality, relevant data necessary to meet research objectives (MacKenzie et al., 2017).

Occupancy modelling is a widely used framework for analysing camera-trap data that accounts for two factors: (1) species occupancy (presence/absence) and (2) detection probability (i.e. the probability of recording the species when it is present, Burton et al., 2015; MacKenzie et al., 2017). Since detection probability is often less than one, failing to account for it can bias estimates. Occupancy models correct for this by using repeated surveys across multiple sites to estimate detection probability and improve accuracy (Mackenzie et al., 2002, 2017). One of the key benefits of this framework is the potential to model each probability as a function of covariates that may be site-specific (e.g. habitat type, patch size and forage quality) and/or survey-specific (e.g. temperature and moon phase, Brubaker et al., 2014, Wevers et al., 2021). Incorporating covariates will generally improve the biological realism of estimates, as assuming equal occupancy and detectability across sites and survey days is unlikely to be reasonable (Lahoz-Monfort et al., 2014; MacKenzie et al., 2017). Furthermore, quantifying how occupancy probability and detectability vary with environmental characteristics is often the primary research focus. For example, predator–prey interactions (Widodo et al., 2022), habitat use (Lamichhane et al., 2020) and population viability (Farr et al., 2022) have been explored using occupancy–covariate relationships. These studies support conservation practitioners in directing their efforts towards landscape features crucial to the focal species (Broekhuis et al., 2022; Calderón et al., 2022).

Evaluating survey design by assessing the reliability and inference of occupancy estimates is essential to inform decisions on the number of cameras, duration and location of deployment. Increasing survey effort (i.e. camera sites and survey days) generally increases the accuracy and precision (i.e. reduces error) of occupancy estimates. However, optimal survey strategies may depend on characteristics of the target species. For example, error is most efficiently reduced for rare species that are easy to detect by increasing the number of camera sites, while for species that are difficult to detect but spatially common, error can be minimized more effectively by increasing survey days (Chatterjee et al., 2021; Kays et al., 2020; Mackenzie & Royle, 2005; Shannon et al., 2014). Camera-trap surveys are often constrained by logistical issues, including equipment costs, camera maintenance, site access and data storage. Studies on survey optimization, therefore, provide useful guidance on the relative costs and benefits of alternative camera deployment strategies (Gálvez et al., 2016; Kays et al., 2020; Shannon et al., 2014).

To date, these assessments have assumed that occupancy and detection remain constant across sites and survey days (i.e. no covariates were used in the analyses), which is seldom the case in real-world scenarios (Mackenzie et al., 2002). Consequently, the extent to which covariates affect trade-offs in effort allocation between sites and surveys remains uncertain. Optimal survey design may depend on both the magnitude of covariate effects and whether they are site- or survey-specific, as these factors determine the range and quantity of covariate data available for modelling. Indeed, forecasting the strength and direction of covariate relationships with occupancy and detection can play an important role in designing efficient surveys. However, in many cases, there is limited a priori knowledge of whether a given covariate primarily affects occupancy and/or detection. Therefore, investigating the relative costs of misidentifying covariate relationships in terms of estimation bias and wasted survey effort can provide useful information for guiding camera-trap survey design.

Assessing alternative survey designs with empirical data is challenging because differences in a wide range of conditions (e.g. habitat, weather and elevation) may exist between study sites, and their effects are likely to vary across taxa (Chatterjee et al., 2021; Kays et al., 2020; Mackenzie & Royle, 2005). Computer simulations are well suited to explore the effects of covariates on survey design trade-offs, as covariate properties (e.g. spatial extent and strength of effects) can be manipulated to facilitate the investigation (Lotterhos et al., 2022). Although simulation tools are available to explore study design (GENPRES: Bailey et al., 2007; SODA: Guillera-Arroita et al., 2010), the functionality of these programs is currently limited to comparing occupancy between predefined groups of sites (i.e. investigating the effect of a categorical covariate only).

This study aimed to investigate how covariates influence both accuracy and precision (i.e. error) of occupancy models in relation to survey effort. Using simulated detection histories of a virtual species, we assessed the effects of site- and survey-specific covariates on occupancy and detectability. We evaluated how survey design factors (camera number, deployment duration, positioning and covariate effect magnitude) impact parameter error, both with and without covariate inclusion in occupancy models. We hypothesised that optimal survey design would depend on the type (i.e. site- or survey-specific) and magnitude of covariate effects, as well as whether they primarily influenced occupancy or detectability. Additionally, we expected that, for the same level of survey effort, models correctly incorporating influential covariates would yield lower error than those omitting them. Based on our findings, we offer broad recommendations for designing camera-trap surveys to estimate species occupancy when covariate effects are expected and highlight the potential costs of suboptimal designs when such effects are unknown.

Materials and Methods

The methods are an extension of the simulation approach used by Shannon et al. (2014). Simulations were parameterised to investigate 2700 different scenarios that varied by number of cameras (sites: $N = 10, 30, 50, 70, 90$), number of survey days (occasions: $S = 20, 40, 60, 80, 100$), proportion of cameras positioned in habitat patches ($Prop = 0, 0.2, 0.4, 0.6, 0.8, 1$) and type of covariate affecting detectability ($EffectType_{(p)}$ = site- or survey-specific) as well as the magnitude of covariate effects on occupancy ($Magnitude_{(\psi)}$ = none, weak or strong) and detectability ($Magnitude_{(p)}$ = none, weak or strong).

The site-specific covariate was simulated to mimic a patchily distributed resource (e.g. woodland, water source and wetland) surrounded by a matrix of alternative, lower-quality habitat land cover types. *Prop* represents the proportion of camera sites (N) located within these habitat patches and reflects real-world scenarios, where observed heterogeneity in a covariate may arise from variation in its spatial extent, distribution or the camera deployment strategy used (Fig. 1). For example, uniform sampling is often used when the objective is to estimate habitat preferences (e.g. Estevo et al., 2017). Alternatively, non-uniform sampling may be used when assessing the relationship between occupancy and a characteristic of the habitat patch (e.g. quality, salinity and plant species richness) is the aim of the study (e.g. Hansen

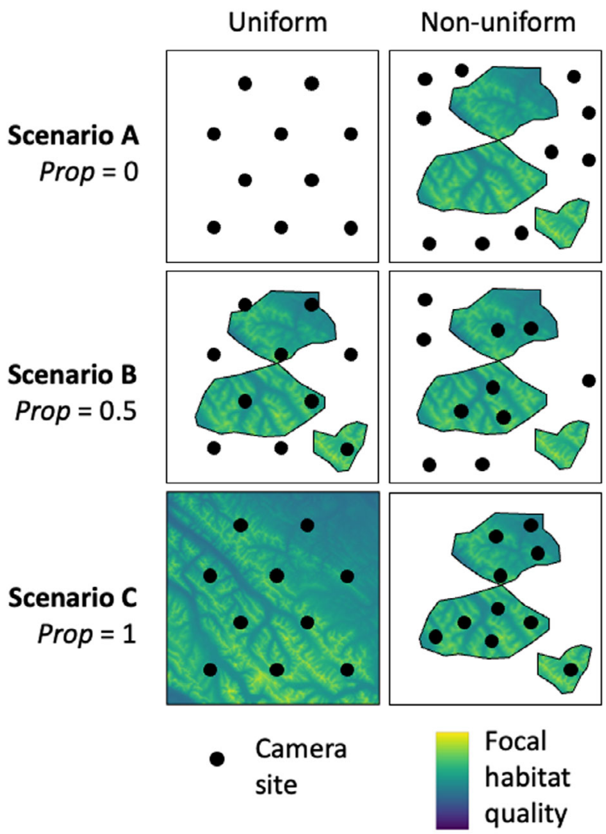

Figure 1. Camera data collection scenarios are represented by varying the proportion of camera sites (*N*) located in patches of a given habitat type (*Prop*) and quality. Scenario A: the habitat is either not present or deliberately not sampled. Scenario B: 50% of cameras are in habitat patches, either by design or distribution of the habitat. Scenario C: 100% of cameras are in patches of the habitat type, either by design or because there is contiguous habitat cover.

et al., 2020), or there is a need to stratify sampling across habitat types (Bailey et al., 2007; Kays et al., 2020; MacKenzie et al., 2017). The survey-specific covariate was simulated to represent an environmental or observational factor that varies across survey occasions but not camera sites, such as temperature, Julian day or moon phase.

Simulated detection histories

A total of 500 sets of detection histories were created for each combination of N (5 levels), S (5 levels), *Prop* (6 levels), $EffectType_{(p)}$ (2 levels), $Magnitude_{(\psi)}$ (3 levels) and $Magnitude_{(p)}$ (3 levels, $5\times5\times6\times2\times3\times3=2700$ in total). Detection histories consisted of $N \times S$ events, where each ith camera site was occupied or not (y_i) from $i=1, \ldots, N$, following a Bernoulli process with probability ψ_i. At occupied sites, it was then determined if the species was detected or not for each occasion from $j=1, \ldots, S$ following a Bernoulli process with probability p_i or p_j, when $EffectType_{(p)}$ was site- or survey-specific, respectively (Shannon et al., 2014).

Occupancy (ψ) was modelled as a function of a site-specific covariate, while detection probability (p) was modelled as a function of either a site- or survey-specific covariate, depending on $EffectType_{(p)}$ (Mackenzie & Bailey, 2004). In each simulation, sites were considered to be in patches of the focal habitat (n $= N\times$ *Prop*) or the surrounding matrix ($n=N\times$ (1-*Prop*)). For each camera site in the habitat patches, a random value between 0 and 10 was generated from a uniform distribution to represent a characteristic of the patch (e.g. habitat quality). Camera sites in the matrix were assigned habitat quality values of 0. The probability ψ was calculated using the logistic model (Equation 1) with intercept and slope terms shown in Table 1 (Mackenzie et al., 2002):

$$\mathrm{logit}(\psi_i) = \mathrm{Intercept} + (\mathrm{Slope} \times \mathrm{Covariate}_i) \qquad (1)$$

where Covariate is the habitat quality value (0–10) generated from the uniform distribution. The probability ψ was constant (0.4) at matrix sites and increased with increasing quality of the habitat patch for the camera site it contains, representing a mechanism whereby a species uses a range of habitats but prefers higher quality patches of a given type (Fig. 2). The same equation structure was used for modelling detection probability (Equation 1). For scenarios where $EffectType_{(p)}$ was site-specific, detectability p was modelled as a function of habitat type and was assumed to be lower in the matrix ($p=0.05$, Table 1), representing a scenario where the species is more detectable in habitat patches ($p=0.3$, 'patch sites' hereafter, Table 1), possibly because activity is higher, or game trails are easier to identify. For scenarios where $EffectType_{(p)}$ was survey-specific, covariate values for p were simulated using a similar procedure as for ψ. A random value between 0 and 10 was generated for each survey day from a uniform distribution to represent a dynamic environmental variable (e.g. temperature) and a survey-specific p was estimated using the logistic model (Equation 1, Table 1, Fig. 2).

The intercept and slope terms were calculated to represent a species with low-to-moderate occupancy and low detectability when covariate values were zero (e.g. in matrix sites or temperature of 0). Occupancy and detectability increased to moderate or high levels depending on the strength of the covariate effects, with weak effects leading to moderate increases and strong effects resulting in high occupancy and detectability. The parameter values used to create detection histories of the virtual species are representative of the range of values observed in empirical studies of terrestrial mammals (Chatterjee et al., 2021; Kays et al., 2020; Shannon et al., 2014).

Occupancy modelling and error estimation

Simulated detection histories were analysed using single-season single-species occupancy models (Mackenzie et al., 2002) in the 'RPresence' package, which implements the statistical models available in the software program PRESENCE (www.mbrpwrc.usgs.gov/software/presence.shtml) in R (R Core Development Team, 2024).

Table 1. Intercept and slope terms used to model occupancy (ψ) and detection probabilities (p) as a function of a randomly generated site- or survey-specific covariate (Equation 1).

Parameter	p Effect type	Effect magnitude	Intercept	Slope	Range of values: Matrix sites	Range of values: Patch sites
ψ		Weak	−0.41	0.13	0.4	0.4–0.7
ψ		Strong	−0.41	0.26	0.4	0.4–0.99
p	Site-specific	Weak	−2.94	0.75	0.05	0.1
p	Site-specific	Strong	−2.94	2.1	0.05	0.3
p	Survey-specific	Weak	−2.94	0.07	0.05–0.1	0.05–0.1
p	Survey-specific	Strong	−2.94	0.5	0.05–0.3	0.05–0.3

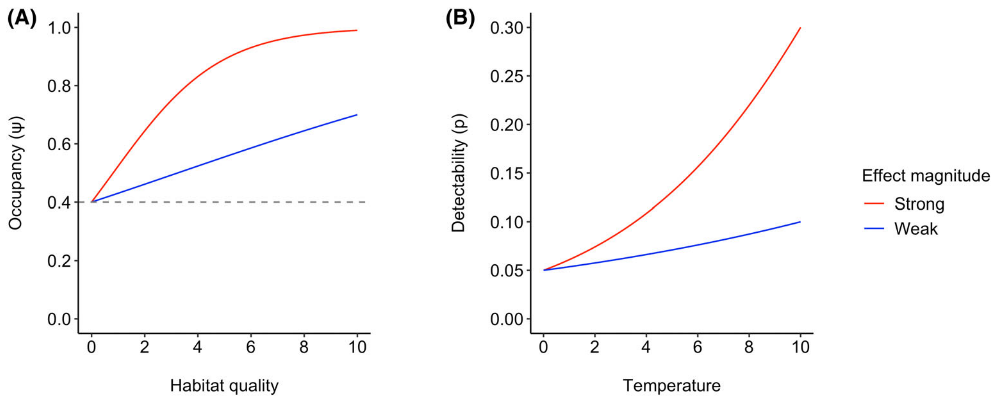

Figure 2. Relationship between (A) occupancy (ψ) and habitat quality and (B) detectability (p, when $EffectType_{(p)}$ = survey-specific) and temperature used to simulate detection histories of a virtual species. Habitat quality and temperature values were both randomly generated from a uniform distribution. The dashed line indicates ψ for matrix sites (0.4), which were assigned habitat values of 0.

It was assumed (i) sites were closed to changes in occupancy, (ii) detection of species and detection histories at each site were independent and (iii) species were correctly identified (i.e. no false positives, MacKenzie et al., 2017).

For each scenario (i.e. combination of N, S, $Prop$, $EffectType_{(p)}$, $Magnitude_{(\psi)}$ and $Magnitude_{(p)}$) from $k = 1, \ldots, 2700$, we fitted four models: (1) 'Constant': $\psi(.)p(.)$, where ψ and p were held constant, (2) 'Occupancy-only': ψ(habitat quality)$p(.)$, where ψ varied with habitat quality while p was held constant, (3) 'Detection-only': $\psi(.)p$(temperature/habitat type) where ψ was held constant and p varied with temperature or habitat type and (4) an 'Occupancy and Detection' model: ψ(habitat quality)p(temperature/habitat type), where both parameters varied in relation to covariates. Error was calculated using root mean squared error (RMSE), which is a measure of both accuracy and precision:

$$\mathrm{RMSE}_k = \sqrt{\sum\left[\left(\widehat{\psi_i} - \psi_i\right)^2\right]} \tag{2}$$

where k is the scenario and $\widehat{\psi}$ and ψ are the model-estimated and true values for occupancy at site i, respectively. To assess the effect of the covariate on the optimal survey design, three different RMSE target values (0.15, 0.10 and 0.075) were selected to represent differing levels of error. Consistent with the analyses conducted by Shannon et al. (2014), the number of occasions (S) and number of cameras (N) were weighted equally. The optimal survey design was estimated as the minimum survey effort ($N \times S$) required to estimate occupancy to a desired level of error. Finally, to evaluate the relative penalty for failing to account for covariate effects, we calculated the difference in error between optimal models (e.g. an Occupancy-only model applied when the covariate affected occupancy and not detection) and sub-optimal models that omitted one or more influential covariates ($\Delta\mathrm{RMSE} = \mathrm{RMSE}_{\mathrm{Optimal}} - \mathrm{RMSE}_{\mathrm{Sub\text{-}optimal}}$). The ΔRMSE was calculated in relation to total survey effort and effect magnitude, where negative values indicate worse model performance (i.e. an increase in error) due to covariate omission.

It should be noted that only outputs from valid models were included in the results. For a model to be valid it had to meet the following criteria: (1) converge to a minimum of three significant digits (provided in the RPresence model output), (2) no variance–covariance (VC) warnings, (3) naive occupancy > 0 and < 1 and (4) β estimates $<= 6.906755$ and $>= -6.906755$, which represents a maximum of a 0.999 change in the estimate of a parameter (ψ or p) for a 1 standard deviation unit change in the covariate (applies to covariate models only, Tables S1 and S2).

Results

Increasing the number of cameras consistently reduced the root mean squared error (RMSE) of occupancy (ψ) estimates across all simulated scenarios (Fig. 3). A key finding, however, was that increasing the number of survey days only reduced error when occupancy was influenced by a covariate and had minimal impact when covariates affected detectability (Table 2, Fig. 3). Greater total survey effort (sites and surveys) was needed when covariate effects on occupancy were weak, and a larger number of sites was required when detectability was weakly influenced by a survey-specific covariate. In contrast, effect magnitude had minimal influence when the detectability covariate was site-specific (Table 2).

Omitting the occupancy covariate substantially decreased model performance (i.e. greater error),

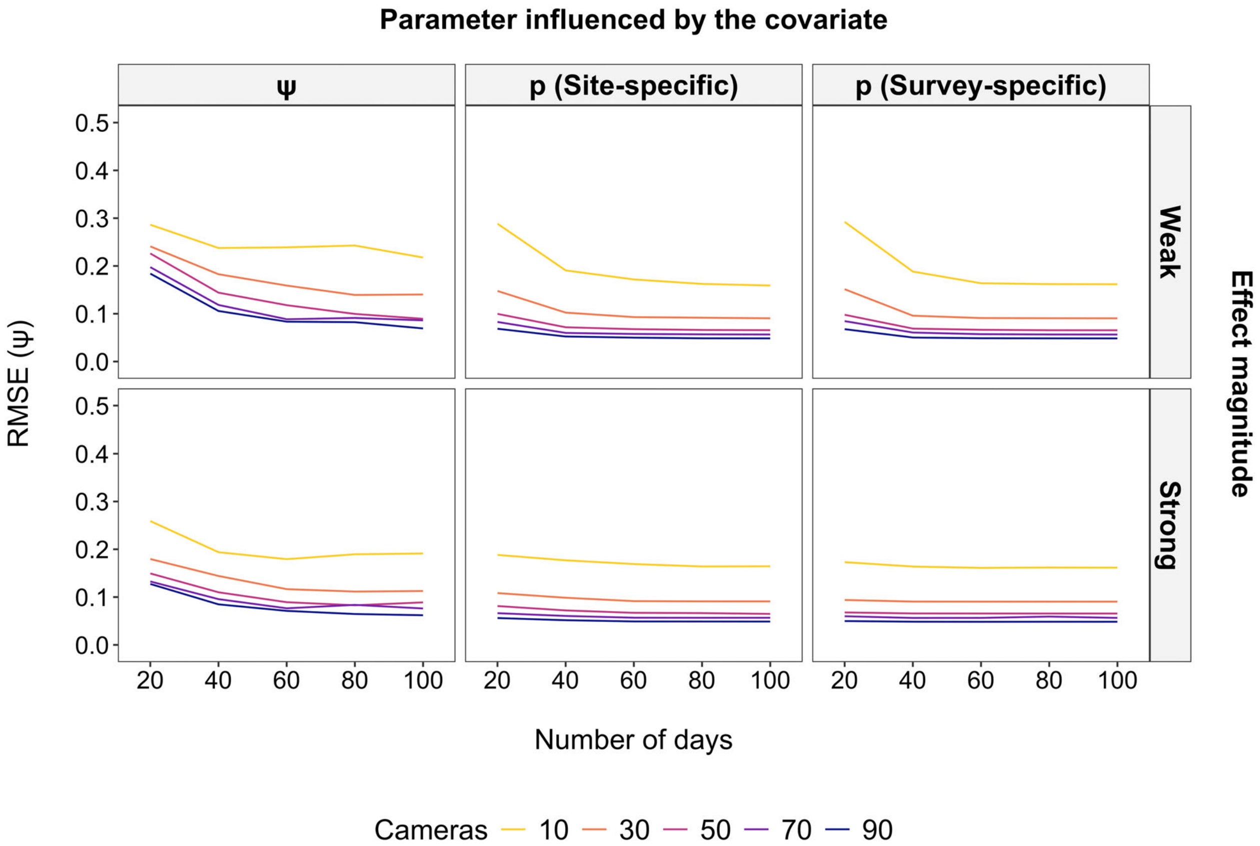

Figure 3. Root mean squared error (RMSE) for estimates of occupancy (ψ) in relation to survey effort (number of cameras and number of days of deployment) and covariate effects that varied by the parameter affected (occupancy or detectability, p), as well as effect magnitude and the type of covariate affecting p (site- or survey-specific). Results shown are for scenarios where an intermediate proportion of camera sites were in habitat patches (*Prop* = 0.6).

Table 2. Optimal survey design (number of cameras $N\times$ number of survey days S) for estimating occupancy with a minimum level of precision (root mean squared error, RMSE) of 0.15, 0.10 and 0.075 under different scenarios of covariate effects on either occupancy (ψ) or detectability (p).

		RMSE = 0. 15		RMSE = 0.1		RMSE = 0.075	
Parameter influenced by the covariate	Effect magnitude	$N \times S$	Total	$N \times S$	Total	$N \times S$	Total
None (Constant model)	—	30 × 40	1200	30 × 60	1800	70 × 40	2800
ψ	Weak	50 × 40	2000	50 × 80	4000	90 × 100	9000
	Strong	50 × 20	1000	70 × 40	2800	90 × 60	5400
p (Site-specific)	Weak	30 × 20	600	50 × 20	1000	90 × 20	1800
	Strong	30 × 20	600	50 × 20	1000	70 × 20	1400
p (Survey-specific)	Weak	50 × 20	1000	50 × 20	1000	90 × 20	1800
	Strong	30 × 20	600	30 × 20	600	50 × 20	1000

Note: We assume equal costs of cameras versus survey days (as per Shannon et al., 2014). Results are shown for models that correctly incorporated covariates when necessary and for scenarios where an intermediate proportion of camera sites were in habitat patches (*Prop* = 0.6).

particularly when the effect magnitude was strong, and an intermediate proportion of cameras were in habitat patches (Figs 4 and 5). Furthermore, in scenarios where both occupancy and detectability were influenced by covariates, models that did not account for occupancy effects achieved none of the pre-defined error thresholds, even with the maximum survey effort (9000 camera-days, Table 3). Conversely, omitting the detectability covariate

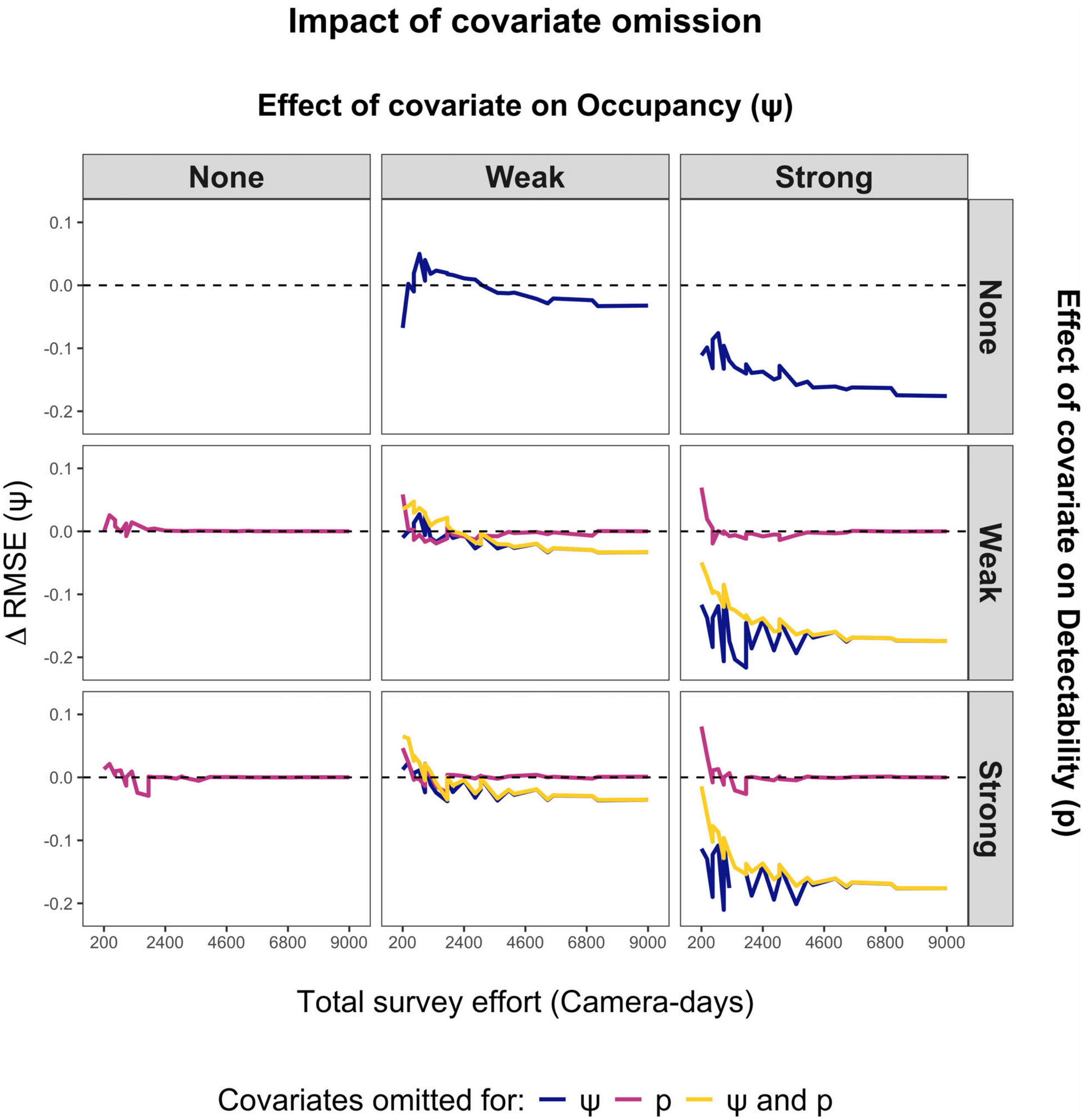

Figure 4. Difference in root mean squared error for estimates of occupancy (ψ) between optimal models and sub-optimal models that omitted one or more influential covariates ($\Delta\text{RMSE} = \text{RMSE}_{\text{Optimal}}–\text{RMSE}_{\text{Sub-optimal}}$) in relation to total survey effort (Camera-days: number of cameras × number of days of deployment) and effect magnitude. Negative values below the dashed horizontal line indicate worse performance (i.e. more error associated with sub-optimal models). Results shown are for scenarios where an intermediate proportion of camera sites were in habitat patches (*Prop* = 0.6) and $EffectType_{(p)}$ = site-specific; for survey-specific results see Figure S2.

had little impact on model performance, regardless of effect magnitude or whether the covariate was site- or survey-specific (Fig. 4, Table 3). In scenarios where occupancy covariates were absent or weakly influential, omitting covariates occasionally improved performance at lower levels of survey effort, most likely because of uncertainty in estimating effects (i.e. regression coefficients, Fig. S1).

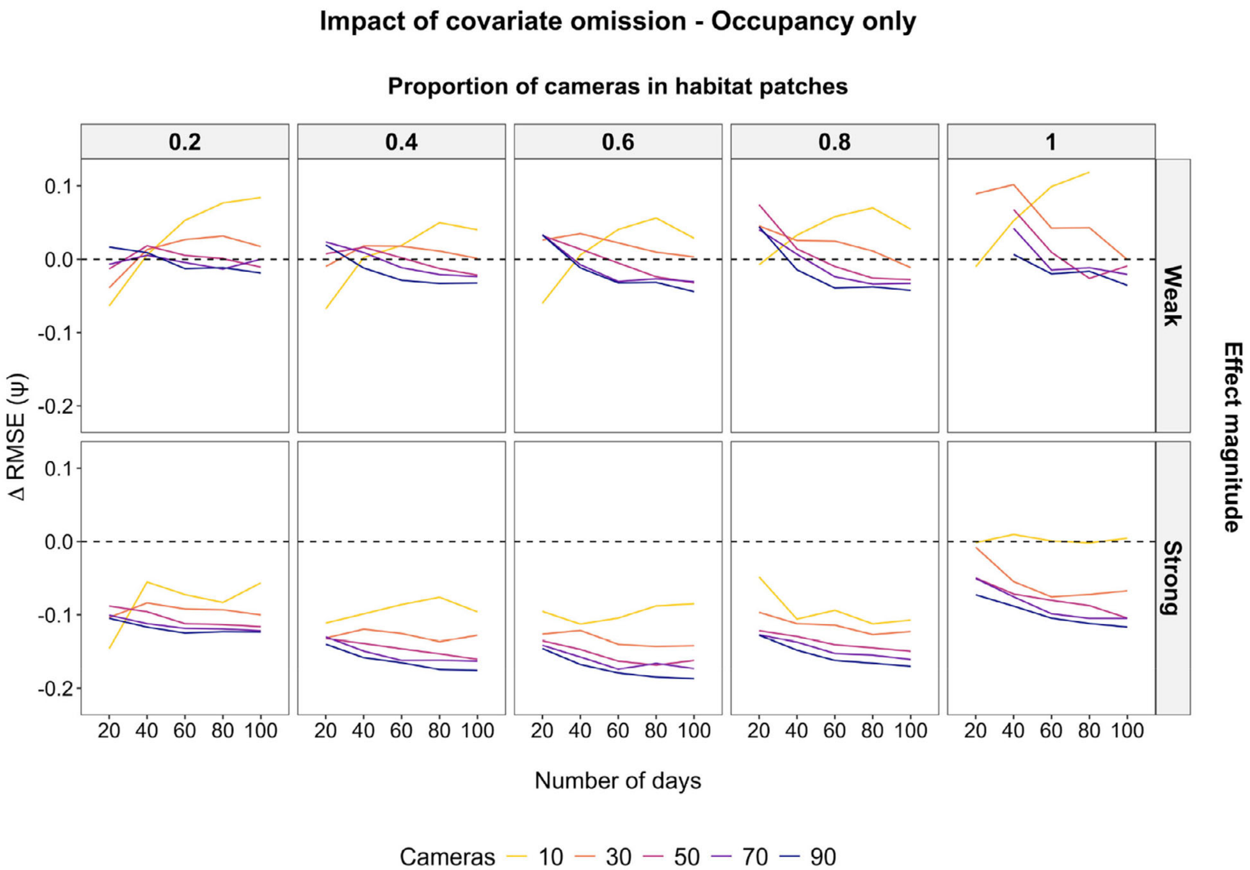

Figure 5. Difference in root mean squared error for estimates of occupancy (ψ) between optimal 'Occupancy-only' models and 'Constant' models that omitted the occupancy covariate ($\Delta RMSE = RMSE_{Occupancy\text{-}only} – RMSE_{constant}$) in relation to survey effort (number of cameras and number of days of deployment), effect magnitude and the proportion of camera sites in habitat patches. Negative values below the dashed horizontal line indicate worse performance (i.e. more error associated with the Constant model).

Table 3. Impact of covariate omission when occupancy (ψ) and detectability (p) are both strongly influenced by covariates in terms of optimal survey design (number of cameras N x number of survey days S) for estimating occupancy with a minimum level of precision (root mean squared error, RMSE) of 0.15, 0.10 and 0.075.

	Covariates omitted							
	ψ and p		ψ		p		None (Correct)	
Minimum precision threshold (RMSE)	$N \times S$	Total	$N \times S$	Total	$N \times S$	Total	$N \times S$	Total
p (Site-specific)								
0.15	F	F	F	F	30 × 20	1000	30 × 20	600
0.1	F	F	F	F	50 × 40	2800	70 × 20	1400
0.075	F	F	F	F	90 × 40	5400	90 × 40	3600
p (Survey-specific)								
0.15	F	F	F	F	30 × 20	600	30 × 20	600
0.1	F	F	F	F	50 × 20	1000	50 × 20	1000
0.075	F	F	F	F	90 × 20	1800	90 × 20	1800

Note: We assume equal costs of cameras versus survey days (as per Shannon et al., 2014). Results are shown for scenarios where an intermediate proportion of camera sites were in habitat patches ($Prop = 0.6$). 'F' indicates failure to achieve the precision threshold with the maximum possible survey effort (9000 camera-days).

Discussion

We used a simulation approach to assess the effects of covariates on the precision and accuracy (i.e. error) of occupancy models in relation to camera-trap survey effort. The results showed that increasing the number of cameras consistently decreased error. However, the relative benefit of longer deployments and the total survey effort required to achieve precision targets depended on which model parameter (occupancy or detectability) was influenced by the covariate and the magnitude of the effects. Furthermore, we found that increased survey effort only reduced error when the effects of occupancy-related covariates were properly accounted for in the model. In contrast, failing to include covariates influencing detectability had minimal impact. Our findings highlight the importance of prioritising biologically relevant covariates during survey design to ensure efficient monitoring and precise occupancy estimation.

The benefits of maximising the number of cameras and accounting for covariate effects on occupancy were clear across all survey design scenarios. Covariates are used to satisfy the assumption that heterogeneity in occupancy and detection probabilities across sites and surveys is accounted for in the modelling of each parameter (Mackenzie et al., 2002, 2017). In scenarios where a spatial covariate (e.g. habitat type or quality) is the source of heterogeneity, deploying more cameras expands the range and coverage of data available for modelling. This, in turn, improves the estimation of effects and the efficacy of models to discriminate between competing hypotheses (e.g. to assess habitat preferences, Bailey et al., 2007; Guillera-Arroita & Lahoz-Monfort, 2012; MacKenzie et al., 2017). Importantly, our results suggest that unless site-level heterogeneity is appropriately quantified and modelled using covariates, increasing survey effort is unlikely to provide any benefit for model performance. Identifying and accounting for potentially influential covariates at the earliest stages of study design is therefore an efficient way to improve estimation precision and prevent the wasteful use of additional cameras or extended deployments.

In real-world scenarios, occupancy and detectability can be influenced by a variety of spatially variable factors, the effects of which may be unknown. Furthermore, environmental features may vary at multiple hierarchical levels, as exemplified by the habitat variable used in our study, which varied by type (e.g. forest and grassland) and quality (low-high). Our findings show that, while standardising site selection (e.g. by selecting all sites of the same habitat type, represented by $Prop = 1$ in our simulations) can eliminate one source of spatial heterogeneity, assuming constant occupancy may be inappropriate due to the unmodelled effects of additional factors. This underscores the need to consider the study's primary objectives when selecting sites relative to covariate gradients. Simple random sampling is well-suited to identifying habitat preferences across broad habitat types (e.g. Donini et al., 2025; Nagy-Reis et al., 2017). However, for habitat specialist species—whose preferences are known a-priori—targeting these habitats and distributing cameras evenly across the value-ranges of secondary factors such as quality or forage availability (e.g. Bitani et al., 2023; Bowler et al., 2017) may provide more useful data. Combining these strategies can be useful for surveying rare or understudied species, where limited prior knowledge of habitat use is available to inform site selection (e.g. Khwaja et al., 2019). Initially, cameras can be deployed in a uniform grid followed by redeployment to preferred habitats (e.g. van Berkel et al., 2022).

When the source of heterogeneity is a temporally dynamic factor (e.g. moon phase or temperature), it may seem intuitive that increasing deployment duration would benefit model performance, since longer surveys allow for the observation of a wider range of covariate values to estimate effects. However, our results do not support this hypothesis. Increasing deployment length only reduced error when detectability was held constant (i.e. not influenced by the covariate). Longer camera deployments help distinguish whether non-detection at a given site is due to true absence (i.e. the site is unoccupied) or low detectability by increasing the cumulative detection probability (i.e. the probability of detecting the species at least once over the entire survey period, p^*, for the equation formula see Fig. S3 and Shannon et al., 2014). As p^* approaches a value of 1, detectability ceases to influence the occupancy estimate and additional surveys become redundant. In the absence of covariate effects, the baseline detection probability ($p = 0.05$) used in our study resulted in a p^* that ranged from 0.65 for the shortest deployment ($S = 20$ days), to 0.98 for deployments of 80 days or longer. The simulated covariate increased the average detection probability (i.e. mean p across sites and surveys) from the 0.05 baseline to a minimum of 0.08 and 0.18 for weak and strong effects, respectively (Fig. S3). These values for p correspond to p^* estimates of 0.81 and 0.98 for the shortest deployment, which only marginally increased with additional survey days (Fig. S3). This likely explains why extending deployment duration had little effect on model performance when detectability was influenced by covariates, and why excluding these covariates had substantially less of an impact than omitting those affecting occupancy.

In situations where baseline detectability is very low (i.e. $p < 0.05$), detectability is strongly reduced by environmental factors, or deployments are less than 20 days, deployment duration—and the impact of omitting detectability covariates—may exert a stronger influence on estimation error (Wright et al., 2019). For example, occupancy studies of herpetofauna typically rely on non-camera-based survey methods that are often logistically limited to very low numbers (<10) of repetitions. In these circumstances, incorporating covariates for detectability may be equally as important as accounting for factors influencing occupancy (Baumgardt et al., 2021; Oropeza-Sánchez et al., 2021). Nevertheless, a 20-day deployment reflects the shorter end of durations typically used in camera-based occupancy studies (Kays et al., 2020). Furthermore, the values for baseline detectability and effect magnitude in our simulations are representative of those observed in empirical studies (Chatterjee et al., 2021; Kays et al., 2020; Shannon et al., 2014) and the findings should therefore be applicable to a wide range of taxa and situations where camera-traps are used to study patterns of site occupancy.

For convenience, we parameterised our simulations so that detectability was entirely site- or survey-specific. However, there are many real-world cases where factors influencing detectability vary both spatially and temporally. For example, temperature may fluctuate day-to-day but also across sites at different elevations. In such conditions, longer-duration deployments are likely to be beneficial due to the additional spatial heterogeneity in detectability. This could be explored by adapting our code (Data S1 and S2) to simulate a covariate that is both site- and survey-specific. Our analyses could also be expanded to explore how seasonal variation in occupancy/detectability influences survey optimization. For example, if a species is more active in the summer than in the winter because environmental conditions are more favourable, detection probability may be higher during the summer, meaning fewer repeated surveys would be required to achieve the same level of estimation accuracy/precision. Furthermore, camera-traps are often used to monitor multiple species, each of which may respond differently to environmental factors. Using multi-species and/or multi-season models (see MacKenzie et al., 2017) within our simulation framework may be useful to evaluate survey optimisation under these more complex conditions.

As with the design of any ecological study, the potential benefits of a given survey strategy must be weighed against the practical costs of implementation. When calculating the minimum survey effort required to achieve error below a target value, the number of cameras and number of survey days were weighted equally in the present study. In real-world scenarios, each survey component may have different human and financial costs that need to be considered to find an efficient solution within the logistical constraints of a study. There are also costs associated with collecting covariate data, which can vary greatly depending on the type of data required, as well as the ecological context and scale of the study. Remotely-sensed environmental data have been collected for many countries worldwide and are free to access from sources such as the European Space Agency (https://worldcover2020.esa.int/) and Copernicus Global Land Service (https://land.copernicus.eu/global/products/). However, data on finer-scale (e.g. habitat structure) or dynamic (e.g. prey availability) covariates may be more challenging and expensive to collect. Real-world costs have been evaluated in previous assessments of camera-trap surveys (Gálvez et al., 2016; Guillera-Arroita et al., 2010; Shannon et al., 2014), which could be expanded to include the collection of covariate data.

Conclusions

Our study demonstrates the fundamental importance of considering covariate effects on occupancy and detection probabilities in camera-trap survey design. While the results show that extended camera deployments may partially compensate for unmodelled detectability covariates, the impact of neglecting effects on occupancy is unlikely to be mitigated by any level of increased survey effort. Therefore, we recommend that researchers clearly define study objectives and prioritise the identification of key covariates early in the design process. When spatial heterogeneity is a concern, increasing camera coverage across covariate gradients is likely to enhance model performance. Furthermore, characteristics (e.g. quality) of an apparently homogenous covariate (e.g. habitat type) may vary spatially and should be accounted for where possible. In contrast, temporal covariates may not justify longer-duration deployments unless the species is especially rare and/or the effects on detectability are negative.

Although simulation studies provide useful theoretical guidance, it will be important to validate our results with empirical data. Modelling covariates adds a dimension of complexity that makes validation with empirical data very challenging as a wide range of factors may influence the observed relationship between covariates and occupancy/detectability, including spatial and temporal scale, ecological context, community composition and species abundance (Heino & Tolonen, 2018; Hofmeester et al., 2019; Morán-López et al., 2022; Steenweg et al., 2018). Initiatives such as Wildlife Insights powered by Google (Thau et al., 2019), Snapshot (Europe, USA, Japan and Brazil, https://snapshot-global.org/) and the eMammal repository (McShea et al., 2016) have collated camera-trap data for a wide range of species from around the world. These large, centralised datasets may facilitate appropriately detailed analyses, from which the results may be transposed to a range of species, ecological contexts and survey scenarios.

Author Contributions

OB: Conceptualization (equal); Investigation (lead); Formal analysis (lead); Methodology (lead); Writing—Original Draft Preparation (lead); Writing—Review and Editing (equal). BDG: Formal analysis (supporting); Methodology (supporting); Writing—Review and Editing (supporting). LSC: Supervision (supporting); Writing—Review and Editing (supporting); Visualization (supporting). JRH: Supervision (supporting); Writing—Review and Editing (supporting). GS: Supervision (lead); Conceptualization (equal); Investigation (supporting); Methodology (supporting); Writing—Original Draft Preparation (supporting); Writing—Review and Editing (equal). All authors contributed critically to the manuscript and gave final approval for submission.

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Conflict of Interest

The authors declare that no competing interests exist.

Data Availability Statement

Code to create the data used in this study is available as supplementary material (Data S1 and S2). Data files will also be made available upon written request to the corresponding author(s).

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Mean proportion of invalid models (n invalid/number of detection histories (500)) across all scenarios of number of cameras, number of days, *Prop*, $EffectType_{(p)}$, $Magnitude_{(psi)}$ and $Magnitude_{(p)}$ for optimal models, where covariates were incorporated correctly (e.g. an Occupancy-only model applied when the covariate influenced occupancy ψ and not detectability p). For a model to be valid it had to meet the following criteria: (1) converge to a minimum of 3 significant digits, (2) no variance–covariance (VC) warnings, (3) naive occupancy > 0 and < 1 and (4) coefficient estimates $<= 6.906755$ and $>= -6.906755$, which represents a maximum of a 0.999 change in the estimate of a parameter (ψ or p) for a 1 standard deviation unit change in the covariate.

Table S2. Mean proportion of invalid models (n invalid/number of detection histories (500) across all scenarios of number of cameras, number of days, *Prop*, $EffectType_{(p)}$, $Magnitude_{(psi)}$ and $Magnitude_{(p)}$) for sub-optimal models, where one or more influential covariates were omitted. For a model to be valid it had to meet the following criteria: (1) converge to a minimum of 3 significant digits, (2) no variance–covariance (VC) warnings, (3) naive occupancy > 0 and < 1 and (4) coefficient estimates $<= 6.906755$ and $> = -6.906755$, which represents a maximum of a 0.999 change in the estimate of a parameter (ψ or p) for a 1 standard deviation unit change in the covariate.

Figure S1. Mean standard error of regression coefficients estimates (β) describing the relationship between a randomly-generated site-specific covariate (habitat quality) and occupancy (ψ) from optimal 'Occupancy-only' models (i.e. occupancy covariates were used and detectability was constant) in relation to survey effort (number of cameras and number of days of deployment), effect magnitude and the proportion of camera sites in habitat patches. Means were estimated from 500 replicate models.

Figure S2. Difference in root mean squared error for estimates of occupancy (ψ) between correctly-specified models and alternative models that omitted one or more influential covariates ($\Delta\mathrm{RMSE} = \mathrm{RMSE}_{\mathrm{correct}} - \mathrm{RMSE}_{\mathrm{alternative}}$) in relation to total survey effort (Camera-days: number of cameras $\times$ number of days of deployment) and effect magnitude. Negative values below the dashed horizontal line indicate worse performance (i.e. more error associated with alternative models). Results shown are for scenarios where an intermediate proportion of camera sites were in habitat patches ($Prop = 0.6$) and $p.EffectType =$ survey-specific.

Figure S3. Cumulative detection probability $\left(p^* = 1-(1-p)^S\right.$, where p is detection probability and S is the number of survey days, Shannon et al. (2014) in relation to the number of survey days used for camera deployment, type of covariate affecting detectability ($EffectType_{(p)}$) and the magnitude of effects ($Magnitude_{(p)}$). The solid black line represents the $p = 0.05$ baseline detection probability. Results shown are for scenarios where an intermediate proportion of camera sites were in habitat patches ($Prop = 0.6$).

Data S1.

Data S2.