Inferring wildlife poaching in Southeast Asia with multispecies dynamic site-occupancy models

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Abstract

Determining the range dynamics of co-occurring species is crucial to assess the extinction risk of species threatened by poaching. Multi-species site-occupancy models allow the examination of distribution patterns of species while accounting for imperfect detection. These models can be extended to describe species interactions explicitly, by considering the extinction and colonisation probabilities of a species conditional on the presence or absence of the others. Here, we develop a hidden Markov modelling formulation of dynamic two-species site-occupancy models that provides a flexible framework to decompose complex species interaction patterns. We apply our model to a case study on wildlife poaching in the Eastern plains of Cambodia. We used 4 years of survey on locations of snares and wildlife, provided by the SMART partnership to study the distribution dynamics between poachers and six ungulate species regarded as main prey of tigers. Our results showed that a substantial proportion of sites occupied by ungulate species went extinct over the years of the study while the proportion of sites colonised by poachers increased. We also showed that spatio-temporal heterogeneity in the patrolling effort explains a great deal of the variation in the detection of poachers and ungulates. To ensure that our estimates were unbiased, we also performed a simulation study considering the presence/absence of species co-occurring across fictive study sites. Our approach provides practitioners with a robust tool to assess conservation status and extinction risk of wildlife populations. It can assist managers in better evaluating, learning and adapting the patrolling strategies of rangers.

Keywords

Banteng, Hidden Markov models, poaching, site-occupancy models, species interactions, tiger

1. Introduction

Scientists are acknowledging the importance of biotic interactions for understanding the spatial distribution of species across large spatial extents and broad scales (Wisz et al., 2013). Assessing the role of biotic interactions in the partitioning of niches provides insights into the mechanisms of speciation, species coexistence, and habitat selection (Boulangeat et al., 2012) as well as into pressing conservation issues in the context of global change, poaching threats, pathogen or species invasion (Brooker, Travis, Clark & Dytham, 2007).

However, identifying mechanisms of interactions such as predation, competition, mutualism and quantifying their contribution to species links with their habitats is quite challenging given the paucity of co-occurrence data on sympatric species.

In their review, Wisz et al. (2013) thoroughly described a range of methods to assess multispecies distribution in relation to their environment. One may apply single species distribution models (SDM) separately and infer species interactions by exploring the correlation structure in the residuals of the regression between species occurrence and the abiotic variables (Pellissier et al., 2013). Preferably, one can also use joint SDM in which the distributions of several species are modelled simultaneously, hence quantifying the relationship between these species and their environment while formally considering biotic interactions (Ovaskainen et al., 2010; Pollock et al., 2014).

Joint SDM make, however, two strong assumptions that may not be always valid: perfect species detection and static species distribution (Guillera-Arroita et al., 2017). When a species is not observed in a habitat, standard SDM predict that the habitat is unsuitable for the species whereas actually it might be because the species did not have the opportunity to colonise yet,

because of local extinction due to poaching for instance or because the species was missed due to insufficient survey effort, cryptic species behaviour. Treating species non-detections as false absences can strongly underestimate the true species distribution and lead to over-estimation of precision, flawed species-habitat associations, and wrong predictions of the trends of species range and risk of extinction (Kéry and Chandler, 2012; Tyre et al., 2003).

Over the last 15 years, the site-occupancy modelling framework has been proposed and extended to interacting species to address both the issues of imperfect species detection and static distribution (MacKenzie, 2017). Using species co-occurrence detections and non-detections collected at several spatial units on repeated occasions over several years, one can estimate the detection and occupancy probabilities of a species in a given site conditional on the occurrence of other species with which they interact, and assess the dynamics of interactions simultaneously (Fidino et al., 2018).

Here, we propose a new formulation of dynamic site-occupancy models for interacting species using hidden Markov models (HMM). HMM are well known for their flexibility to capture complex processes (Zucchini, MacDonald, & Langrock, 2016), including in occupancy models (Gimenez et al., 2014). More specifically, each relevant process (e.g., occupancy, transition between occupancy states) can be broken up into simpler steps that match the underlying ecological events, making the model more transparent and its outputs easier to interpret (Louvrier et al., 2018).

We illustrate the novelty of our approach to study interactions between poachers and wildlife, which are by nature dynamic and difficult to detect, through a HMM which directly estimates site-specific extinction probabilities of wildlife conditional on the presence of snares. Poaching is an important cause of species extinction in the world (Plumptre et al., 2014). Yet,

assessing the risk of extinction of a species due to poaching remains challenging mostly because of the difficulty to detect poachers and to assess the consequences of poaching (Moore et al., 2018). Naturally, poachers and wildlife can be compared to a predator-prey system in which interactions fluctuate over time in a “landscape of fear” (Laundre, Hernandez, & Ripple, 2010). As tracking poachers with GPS devices, commonly done in predator-prey interactions studies, is highly unlikely, rangers often use indirect methods based on observations of snares, hunting camps, and social surveys to detect their presence (Milner-Gulland & Leader-Williams 1992). As such, these observations suffer from imperfect detection of poachers. A recent study applied a novel approach to assess poaching by fitting an occupancy model on detection/non-detection of poaching signs but not wildlife (Moore et al., 2018). The authors noted that rangers observed in the field the steady increase of count data of poaching signs. Nevertheless, after fitting a site-occupancy model, they found that detection probability of poaching-related threats increased during the study period, probably owed to the improvement of patrolling effort and that the true occupancy of poachers was actually declining. Their study highlights the importance of accounting for detection probability for site-based anti-poaching management programs (Moore et al., 2018). Here by adding the wildlife component, we aim at addressing simultaneously the issues related to imperfect detection of poachers and animals and their dynamic interactions, through a multi-season, two-species site-occupancy models.

We applied our new model to a case study of poaching in North-East Cambodia, where one of the last and largest populations of the endangered banteng (*Bos javanicus*) in the world occurs. We used detection/non-detection information collected by rangers looking for snares and signs of four threatened ungulate species occurring in the area: the banteng, the gaur (*Bos gaurus*), the sambar deer (*Rusa unicolor*), the eld's deer (*Rucervus eldii*) and two least-concern

species, the wild boar (*Sus scrofa*) and the barking deer, also called red muntjac (*Muntiacus muntjak*). Those six species selected in our study represent the common prey of the tiger (*Panthera tigris*), a globally endangered species that was declared functionally extinct in Cambodia since 2016, mainly because of poaching (IUCN, 2016). WWF is collaborating with scientists to understand the poaching threats and anti-poaching response to those threats so it can provide strategic interventions.

2. Material and methods

2.1 Study area

Our study was conducted in two protected areas. Both study sites are located within the eastern Plains Landscape of Cambodia, the Phnom Prich Wildlife Sanctuary (PPWS), covering more than 2,000 km^2, and the Serepok Wildlife Sancturary (SWS), covering over 3,700 km^2 of the Lower Mekong Dry Forest Eco-region. Both sites are among the 200 most important eco-regions of the world due to the high level of biodiversity facing myriad threats (Rostro-Garcia et al., 2018).

A total of 11 patrol stations are in the sanctuaries (5 in PPWS & 6 in SWS) from which rangers depart by motorbike (95% of the data), boats or vehicle, in order to inspect for illegal activities and monitor wildlife. Patrolling for illegal activity mainly consists of locating snares

and removing them. It also aims at intercepting poachers. Rangers therefore fulfil both wildlife monitoring and poachers surveillance.

2.2 Data collection

The data we used for the analysis was obtained from the Spatial Monitoring And Reporting Tool (SMART), a tool that has been developed by the consortium of conservation organizations to measure, evaluate and improve the effectiveness of wildlife law enforcement patrols and site-based conservation activities (smartconservationtoools.org). SMART has also been identified as a key tool for the recovery of the populations of tiger and other keystone species (CA|TS manual 2018).

We extracted all the dates and geolocations of information collected by rangers from January 2013 to December 2016. We gathered 1647 GPS waypoints reported by rangers associated with the 11 patrolling stations. During each patrolling session, rangers recorded several observations on specific landscape features (e.g., roads and rivers), illegal activity (e.g., snaring, logging, fishing) and presence of animal species (e.g., track, scats or calls, carcasses) or when no activity was detected.

For the wildlife data in the model, we used direct observations and presence signs of the six tiger prey species mentioned above. We assumed rangers always managed to identify the species correctly during their field survey. That said, we removed signs of carcasses from the data to avoid possible misidentifications on the localisation of animals intentionally displaced by humans or other animals. We used snares as relevant indicators of the presence of poachers and of their interactions with wildlife, as they represent a non-targeted catching technique for small

and large wildlife species. Rangers collected the date and the GPS location of snares during their anti-poaching patrol route. Hereafter, we use the term “site occupied by poachers” to refer to the sites that are expected to have snares.

We plotted all the GPS data points collected in the two study areas, and used 10 x 10 km cells to partition the study areas, resulting in 42 sites for PPWS and 56 for SWS (Figure 1). We chose this cell size to represent sample sites in order to achieve a compromise between ecological and monitoring assumptions. We made sure the site was large enough to meet the closure assumption upon which occupancy models rely on (see section below), meaning that wildlife would not move out of the site between sampling occasions. On the other hand, we ensured the scale of the cells was sufficiently fine to ensure that a fair proportion of each cell was prospected and avoid considering sites that were actually never sampled. Finally, we combined information on poaching-related threats and wildlife in a table composed of 81 rows representing the sites prospected by rangers and 48 columns representing the monthly occasions during the four years of the study. We removed 17 sites that were never prospected by rangers (Figure 1); seven cells were from the PPWS grid and ten from the SPS one.

2.3 Hidden Markov formulation of multi-season two-species occupancy model

2.3.1 Definition of states and observations

We developed a multi-season two-species site-occupancy model (MacKenzie et al., 2004) in a hidden Markov modelling (HMM) framework (Gimenez et al., 2014). The ecological process was defined as follows as a latent variable indicating at each sampling occasion whether a site is: “unoccupied by poachers and wildlife” (U), “occupied by poachers only” (OP), “occupied by

wildlife only" (OW), and "occupied by wildlife and poachers" (WP). Site-occupancy models rely on the main assumption known as "population closure", whereby sites are supposed to remain in the same occupancy states and only detection can vary between repeated surveys called secondary occasions. Sites can then change from one state to another between successive primary occasions through extinction and colonisation processes. The observation process is characterized by a known variable showing time series of detection/non-detection of species for each site (MacKenzie 2006). Here, the variable takes values 1 when snares only were detected, 2 when only wildlife were detected, 3 when both snares and at least one of the 6 wildlife species were detected in the same site, and 0 when neither evidence of wildlife or poacher was found.

We adopted the Waddle et al. (2010) parameterization for occupancy and detection because it is more appropriate to describe poacher-wildlife interactions and identify the effects of covariates described above on species occupancy. This parameterization states that the initial occurrence of one species depends on the occurrence of the common species but the reciprocate regarding the common species is not true. Such parameterization is used to model host-parasites, predator-prey, and other asymmetric interactions such as poaching (Waddle et al., 2010). We used the MacKenzie (2006) parameterization for the transition of sites from one state to another which is appealing because it considers reciprocal responses between species following their interactions, meaning that extinction, colonisation probabilities of a species was conditional on the presence or absence of the other. It also considered the probability that a species replaced another in a given site from one primary occasion to another (Fidino et al., 2018).

2.3.2 Occupancy

To build the model, we first defined whether a site was initially occupied or not, and in which state, which was conveniently captured by the initial state probabilities of HMM (Gimenez et al., 2014). We proceed in two steps for clarity. The first step represents whether a site is occupied or not by wildlife regardless of the presence or absence of poachers. The following vector shows the probability of being in an unoccupied site U or a site occupied by W:

$$\begin{array}{cc} U & W \\ \end{array}$$

$$\Pi_1 = [1 - \psi_W \quad \psi_W]$$

with ψ_W the occupancy probability by wildlife and its complementary the probability of a site being unoccupied. The second matrix represents whether poachers, depending on the presence or absence of wildlife, occupy a site:

$$\begin{array}{cc} & \begin{array}{cccc} U & OP & OW & WP \end{array} \\ \Pi_2 = \begin{array}{c} U \\ W \end{array} & \begin{bmatrix} 1 - \psi_{P/\overline{W}} & \psi_{P/\overline{W}} & 0 & 0 \\ 0 & 0 & 1 - \psi_{P/W} & \psi_{P/W} \end{bmatrix} \end{array}$$

with $\psi_{P/W}$ the occupancy probability by poachers, conditional on the presence of wildlife and the complementary $1 - \psi_{P/W}$ that a site is not occupied by poachers, conditional on the presence of wildlife. Parameter $\psi_{P/\overline{W}}$ is the occupancy probability by poachers, conditional on the absence of wildlife and the complementary $1 - \psi_{P/\overline{W}}$ is the probability that poachers do not occupy a site conditional on the absence of animals.

2.3.3 Transitions

Once we have assessed whether a site is initially occupied, we describe how its status changes over time, which define a Markovian process. We define the transition matrix *T* for a given site between the states U, OP, OW, WP from primary occasion *t* to the next primary occasion *t* + 1 as follows:

$$
\mathrm{T} = \begin{array}{c} \\ U \\ OP \\ OW \\ WP \end{array}
\begin{array}{c}
\begin{array}{cccc} U & OP & OW & WP \end{array} \\
\begin{bmatrix}
1-\gamma_P-\gamma_P+\gamma_{WP} & \gamma_P-\gamma_{AP} & \gamma_A-\gamma_{AP} & \gamma_{WP} \\
\epsilon_{P/\bar{W}} & 1-\epsilon_{P/\bar{W}}-\omega_{AP}-\gamma_{W/P} & \omega_{AP} & \gamma_{W/P} \\
\epsilon_{W/\bar{P}} & \omega_{WP} & 1-\epsilon_{W/\bar{P}}-\omega_{WP}-\gamma_{P/W} & \gamma_{P/W} \\
\epsilon_{WP} & \epsilon_W-\epsilon_{WP} & \epsilon_P-\epsilon_{WP} & 1-\epsilon_P-\epsilon_W+\epsilon_{WP}
\end{bmatrix}
\end{array}
$$

Each element of the matrix *T* is the transition probability from one of the occupancy states during a given year to another or the same occupancy state in the next year. The matrix describes four main processes: colonisation, extinction, replacement, and fidelity (MacKenzie 2006) that are detailed in Table 1.

These transitions occur at the beginning of each year (January). Within each primary occasion, the transition matrix *T* is simply a diagonal matrix of 1's because the status of a site does not change from one secondary occasion to the other according to the closure assumption. Here, we defined the secondary occasions on a monthly-based time interval (from February to December).

2.3.4 Observations

The last step of the HMM consists of linking the observation process to the partially

observed latent states (U, WO, PO, WP) describing the dynamic of the species occupancy. The observation process is captured by four events: nothing was detected (ND), only wildlife were detected (WD), only poachers were detected (PD), or both were detected (WPD). For the sake of simplicity, we described detection probabilities of a species (poachers or wildlife) not conditionally on the presence/absence of the other (Fidino et al., 2018). We therefore defined the observation matrix as:

$$\mathbf{B} = \begin{array}{c} \\ U \\ OP \\ OW \\ WP \end{array} \begin{array}{c} \begin{array}{cccc} ND & PD & WD & WPD \end{array} \\ \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1-p_P & p_P & 0 & 0 \\ 1-p_W & 0 & p_W & 0 \\ 1-p_{WP} & 0 & 0 & p_{WP} \end{bmatrix} \end{array}$$

with p_P the probability of detecting poachers in a site given that only poaching-related threats occur, p_W the probability of detecting wildlife in a site where only wildlife occur and p_{WP} the probability of detecting poachers and wildlife conditional on the presence of both.

2.4 Analyses

2.4.1 Covariates

We accounted for the patrolling effort defined as the number of survey carried out on each site at each sampling occasion and standardized to a scale from 0 when a site was not prospected on a given occasion, to 1 where the most GPS waypoints were recorded on a sampling occasion. We also considered the nearest distance to a ranger station as another site-specific covariate reflecting spatial variation in the patrolling effort. We defined the shortest distance of each site to a road to account for effects of road access on the monitoring effort of rangers but also on the distributions of wildlife and poachers. Finally, we assessed the stream length crossing in each cell as another potential determinant of species detection and occupancy.

2.4.2 Model selection and parameter estimation

We performed model selection on the poacher-wildlife occupancy and tested different hypotheses to determine the biotic (species interactions) and abiotic drivers (effects of roads, rivers, spatial-temporal effects of patrolling effort) of species detection, occupancy and transition probabilities. This was done in three steps. First, we accounted for the different effects on the detection. Second, we used the best model structure on detection selected in step 1, and accounted for different effects on occupancy. Third, we kept the best structure on occupancy selected in step 2, and tested varying hypotheses regarding the transition processes. In this step, we particularly tested for one-year delayed effects of patrolling effort on parameter transition (See Appendix A for more details on the hypotheses tested).

For each step of the model selection, we used the Akaike information criterion (AIC, Burnham & Anderson 2003) to determine which effects best explain the variation in the data. We considered the model having the lowest AIC to be best supported by the data. We used R.3.5.0. (R Core Team 2017) for all analyses. The maximum likelihood estimates were obtained using

the quasi-newton method of the optim function in R. We provide the data and R codes in GitHub at https://github.com/oliviergimenez/poaching_occupancy.

2.4.3 Occupancy dynamics

From the estimated probabilities of initial occupancy and the estimated transition matrix, we assessed temporal changes in the probability of occupancy in the four states over the study period. We obtained confidence intervals using a parametric bootstrap (Davison & Hinkley 1997).

2.5 Simulations

A key aspect of designing occupancy studies relies on the choice of the number and the size of sites as well as on the number of repeated surveys (i.e., the number of secondary occasions) that should be conducted and the length of the study period (i.e., the number of primary occasions) (MacKenzie & Royle 2005). To validate the premises of our model, we assess the bias and precision in parameter estimates using two simulation studies focusing on 1) variation in the occupancy design and 2) variation inherent to the data owed to different monitoring efficiency, species ecology and interactions.

First, we investigated the bias and mean squared error (MSE) for different study designs with varying number of sampling units and time intervals of repeated measures. We considered a fictive study area decomposed into 35, 50, 100, or 150 sites monitored during 3, 5 or 10 years (number of primary occasions) every month, trimester or semester (so with 3, 6 or 12 repeated surveys). For each combination of occupancy-design, we simulated 1000 data sets describing the

co-occurrence of the two species based on the estimated parameters obtained from the best model of the joint analysis.

Second, we investigated the bias and MSE along a range of values for the occupancy and detection probabilities and for different transition parameter combinations. We first considered fictive populations for the two species from rare to abundant ($\psi_{P/W}, \psi_W, \psi_{P/\bar{W}}$ = {0.1, 0.25, 0.5}) from easily detectable to very discrete ($p_P = p_W = p_{WP}$ = {0.1, 0.25, 0.5}). For the sake of simplicity and computation time, we assumed detection probability was the same between poachers and wildlife. We set the transition parameters constant and at equivalent values to the estimates obtained from the best model of the joint analysis. We simulated 1000 occupancy datasets, designed with only 35 sites. We chose a small number of sites to investigate what could be the bias in estimates if we analyze the PPWS study area only.

3. Results

3.1 Occupancy data

Over the study period, we collected 322 presence signs of our six key wildlife species (119 of banteng, 119 of barking deer, 9 of gaur, 65 of wild boar, 2 of eld's deer and 8 of sambar deer) and 377 presences of snares from the two study areas. Our final occupancy table was composed of 195 detections of sites occupied by poachers only. Wildlife only (i.e., no poachers recorded) were detected at 213 sites. We counted 38 detections of both poachers and wildlife in the same sites (Fig. 1). Finally, the occupancy table was also composed of 3442 non-detections (Appendix Table A.1).

3.2 Model selection

The model best supported by our data showed that detection probability was species-specific and related to the spatial and temporal variations of patrolling effort whereas poachers' occupancy was independent of wildlife distribution and unrelated to rangers' patrolling effort (AIC = 3105.28, Table 1). We found that poachers' transition probabilities were not affected by wildlife distribution or by patrolling effort, meaning that poacher extinction and colonisation was independent of wildlife distribution regardless of where and how often rangers were patrolling. Conversely, we found that extinction probability of wildlife was positively related to the presence of poachers and colonisation probability of wildlife negatively related to presence of poachers.

The initial occupancy probability of poachers (0.06 ±0.11) was lower than the initial occupancy of wildlife (0.46 ±0.11) (Figure 2). We found that the extinction probability of wildlife in a given year in sites occupied by poachers ($\epsilon_{W/P}$ = 0.80 ± 0.14) was more than double than in sites where poachers were absent ($\epsilon_{W/\bar{P}}$ = 0.36 ± 0.11). The probability of poacher extinction was unrelated to wildlife occurrence ($\epsilon_{P/\bar{W}}$ = $\epsilon_{P/W}$ = 0.20 ± 0.14). The probability of wildlife colonisation was greater in absence of poachers ($\gamma_{W/\bar{P}}$= 0.28 ± 0.02 with γ_{WP} ~ 0) than in their presence ($\gamma_{W/P}$=0.05 ± 0.02). The probability that a site occupied by wildlife was replaced by poachers (ω_{WP}=0.44 ± 0.11) was more than three times the probability that a site occupied by poachers was replaced by wildlife (ω_{PW}=0.12 ± 0.11). Poachers were three times more likely than wildlife to remain in a site (site fidelity of 0.63 ± 0.09 for poachers vs 0.20 ± 0.11 for wildlife). The probability that poachers colonise sites was independent of wildlife present and was very low ($\gamma_{P/\bar{W}}$= $\gamma_{P/W}$ = 0 ± 0.11 with γ_{WP} ~ 0) (Fig. 2).

The estimated probability of sites being occupied by wildlife only was initially high (0.43 +/- 0.02) then decreased by about 50% over the years of the study to 0.22 +/- 0.01. The probability of sites occupied by poachers only exceeded the probability of wildlife occupancy on the second year of the study. More specifically, it increased from 0.04 +/- 0.01 to 0.30 +/- 0.05 during the study period. The probability of sites occupied by both wildlife and poachers remained relatively constant over the study period (from 0.04 to 0.02 +/- 0.01) (Fig. 3).

Detection probability of poachers and wildlife was greater than detection of poachers only or wildlife only, and increased rapidly with patrolling effort. The detection probability of wildlife and poachers at a given occasion where both co-occurred was perfect where the patrolling effort was above 0.4, meaning sites, in which the number of survey was above 40% the maximum number of GPS waypoints per site recorded. The detection probability of *poachers only* increased from 0.04 to 0.96 and was consistently greater than the detection of *wildlife only*, which increased from 0.04 to 0.62 also with patrolling effort (Appendix Fig.A.1 and A.2).

3.3 Simulations

3.3.1 Overview

Results from the two simulation analyses revealed that bias tended to be more sensitive to occupancy design than to the parameters values used to simulate the data. Minimum squared error was consistently low across both simulation analyses (MSE < 10^{-2}). Overall, our results showed that it is better to increase the number of repeated survey (secondary occasions) rather than increasing the number of sampled sites. When this condition is fulfilled, estimates are unbiased regardless of the occupancy and detection probabilities, except the occupancy probability of the poachers in absence of the wildlife with which they interact.

3.3.2 Designing a two-species occupancy study

In the first simulation analysis, aiming to explore the optimal occupancy design for two-species, we found that increasing survey effort by 4 (conducting 12 repeated survey instead of 3) decreased the mean bias by 20% whereas increasing the spatial coverage by 7 (sampling 250 sites rather than 35) decreased the mean bias by only 8%. Our results showed that the parameters most likely to be biased (more than 10% on average) were the occupancy probabilities, and the probability that a site occupied by wildlife become extinct (which tended to be underestimated), but the bias diminished with increasing number of repeated surveys. The mean bias for any other estimate remains invariant to the number of sampled sites. Results from these simulations showed that the design we used for our analysis of poacher and wildlife interactions should not generate any bias greater than 15% (Appendix Table A.2 and A.3).

3.3.3 Sensitivity to occupancy and detection probabilities

Results from the second simulation analysis with varying occupancy probabilities revealed that the biases in the estimates of all parameters were consistently lower than 5% and the associated MSE lower than 0.01 except for the occupancy probability of poachers in absence of wildlife (Figure 5). This latter parameter was underestimated (min(Bias$\psi_{P/\overline{W}}$) = - 0.3 MSE=0.01) when the probability of poachers occupancy in absence of wildlife was higher than in presence of them and overestimated (max(Bias$\psi_{P/\overline{W}}$) =0.3 MSE=0.002) when the occupancy probability of poachers was higher in presence of wildlife than in their absence. However, the bias disappeared when occupancy probability of both poachers and wildlife were independent from each other, which was the case in our empirical analysis. This symmetrical trend observed in the bias of occupancy of poachers in absence of wildlife was consistent across the gradient of detection probabilities and probability of occupancy of wildlife (Appendix Figure A.3).

4. Discussion

4.1 Impact of poaching

The spread of wildlife hunting through time and space and its impact on wildlife species remains poorly known even in surveillance systems handled by rangers (Milner-Gulland and Leader-Williams, 1992). Here, we developed a two-species occupancy model to study inter-specific interactions, namely poacher-wildlife systems and their range dynamics. We found that while the proportion of sites occupied by wildlife was initially high in 2013, there has been a steady and dramatic decline of the spatial coverage by wildlife mainly due to an expanding poaching pressure. Indeed, over just 4 years we found a substantial increase in the proportion of sites occupied only by poachers (approximately from 80 km^2 to 600 km^2 in PPWS and from 148 to 1110 km^2 in SWS), which concurred with a decline of the proportion of sites occupied by wildlife while the proportion of sites occupied by both remained relatively constant. The occupancy range of wildlife, initially covering 42% of the two study areas, could slowly recover from 400 km^2 to 580 km^2 in PPWS and from 740km^2 to 1073 km^2 in SWS if poaching was reduced by half.

We also found that the initial occupancy, the extinction and colonisation of poachers were independent of wildlife occurrence, which can be owed to poachers setting snares without targeting specific species (Critchlow et al., 2015). Because poaching in our two study sites was not selective, intense and widespread, wildlife range dynamics did not affect the distribution of snares.

Our results also suggest that the patrolling effort in the PPWS and SWS study areas of Cambodia are currently inadequate, in both the spatial coverage and the time allocation of rangers' forces. Patrolling effort was improving detection but not occupancy or transition probabilities of poachers, meaning that increasing the frequency of survey within a site was effective for detecting snares but not for preventing poaching. For many sites, poachers were likely to colonise and extirpate wildlife before rangers even had time to realize that wildlife used to be there, as probability that poachers replaced a site occupied by wildlife very high while the detection probability of wildlife only by rangers was very low.

When patrolling effort was sufficiently high, the detection probability of both poachers and wildlife was perfect and could be explained by higher species abundance in those sites where wildlife and poachers co-occur. Poachers tend to put more snares in sites where wildlife is abundant in order to maximize the likelihood of catching an animal, which in the same time increases the chance of their snares being detected and removed by rangers (Hines et al., 2010). Rangers should then invest less in monitoring those sites and probably focus more on finding new sites where only poaching-related threats occur especially as more poachers might invade more sites while wildlife disappears.

4.2 Optimizing the occupancy design

Choosing the optimal sampling design for the monitoring of species in their natural habitat is highly recommended before building and fitting occupancy models. MacKenzie and Royle (2005) performed a simulation study to advise the users of occupancy models on how to design their monitoring scheme. They recommend standardized and planned surveys in order to collect informative data on the detection/non-detections of species in the most effective way to decrease the problems of imperfect detection. When detection probability is high, they advocate an

increase in the number of sampled sites rather than repeating the number of secondary occasions. As the detection probability decreases, more repeated survey should be conducted. In line with previous analysis on this trade-off between spatial coverage and survey effort conducted only in the single-species occupancy models, we also found that it was more effective to allocate effort on sampling few sites intensively rather than many sites cursorily in the two-species occupancy model (Guillera-Arroita et al., 2011). The results from our simulation study confirm that our sampling design composed of more than 50 cells monitored intensively every month during 4 years, provides robust parameter estimates, even for the study of species with relatively low occupancy and detection probabilities.

Choosing the spatial scale of the cells is also an important step when designing an occupancy study (Dia et al., 2017). Here we chose the best compromise between cells that are large enough to make sure there is no transient movement of wildlife and fine enough to ensure that a fair proportion of the cell was prospected (Berigan et al., 2018). This is important especially if we want to establish relationships between distribution of wildlife with population trend and status and further to assess which sites are suitable for tiger reintroduction with respect to prey availability and poaching risk (Carter et al., 2012). The problem of individuals moving out of the cell between occasions is similar to the one of having false positives in the data set, which means that it can overestimate the wildlife distribution range and leading to insufficient management intervention. Among the six ungulate species composing our data set, the gaur, with a home range of 107 km^2 for adult male, was more likely to move out of a site than the other species with much smaller home ranges (Chaiyarat et al., 2017).

4.3 Model limitations

Besides population closure, our model relies on several assumptions, which under certain

circumstances, can be violated. First, we did not account for spatial autocorrelation among detections and occupancy states, which is likely to occur in interacting species, monitored with transects (Hines et al., 2010). Our model also assumes spatial independence in the process governing the range dynamics of species. This assumption can be relaxed via Bayesian methods using estimated occupancy of neighboring sites in the previous time step as a covariate to predict extinction/colonisation processes in the current step (Green et al., 2018; Heard et al., 2013).

Finally, the last methodological issue we are coping with lies in the difficulty to assess the quality of fit of occupancy models accounting for imperfect detection. In standard species distribution models, AUC metrics are used in routine for model evaluation and predictive performance. AUC metrics can still be computed in site-occupancy models under imperfect detection, but they no longer assess how well it predicts true occupancy but rather how well it predicts detection (Lahoz-Monfort et al., 2014). MacKenzie and Bailey (2004) developed a goodness-of-fit test for single-season occupancy models for one species only but no test has so far been developed for two-species occupancy models. The simulations we performed in a two-fold validation process, demonstrated that our model was appropriate for the sampling design and the community dynamics in our case study.

4.4 Adaptive management

To our knowledge, this study is one of the few applications of a two-species occupancy model extended to a multi-season version (see also Fidino et al., 2018). Our analysis revealed how important it is to model the processes governing interacting species through their range dynamics (Guillera-Arroita, 2017 ; Ranjan, 2018). It is particularly important in the context of wildlife conservation in conflictual areas of the world, which involves socio-ecological systems that are not at an equilibrium (Carter et al., 2017). Poacher-wildlife and ranger interactions are

dynamic by nature, where each agent is expected to consistently adapt its strategy according to the activity of the other (Ranjan 2018, Plumptre et al., 2014). Therefore, we believe that studying the spatial dynamics of poacher-wildlife interactions in relation to the variation in patrolling effort is a crucial preliminary step for defining the optimal strategy of ranger patrol within an adaptive management framework to efficiently reduce poaching (Keane et al., 2008). Moreover, our model helps quantify the rate at which poaching pressure shrinks the occupied range of wildlife species, as well as wildlife communities, in relatively data-poor systems. Range contraction has been shown to be an important indicator of species extinction risk (Burgess et al. 2017). Thus, methods for evaluating wildlife range dynamics that account for the impacts of illegal hunting, as with our model, can enable better prediction of how different poaching interdiction strategies will influence wildlife recovery in space and time.

One such species that this would be extremely useful for is the tiger, which is undergoing a serious decline worldwide (Carter et al., 2012). Once the cause of its extirpation has been identified and counteracted, reintroduction is a possible solution for tiger conservation (Hayward and Somers, 2009). Despite few exceptions of successful reintroduction of carnivores, the reintroduction of large carnivores is generally more challenging than that of large ungulates. Many attempts have actually failed, probably because of a lack of post-monitoring but mostly because the socio-ecological system prior of the reintroduction are often under-studied (Reading and Kellert, 1993). Understanding the mechanisms explaining the distribution and trends in the poaching of the main tiger prey species is necessary before considering the reintroduction of tigers. Our study is a proof of concept for a science-based conservation program in the wildlife sanctuaries of Cambodia and could be a pioneer study for further application of our multi-species dynamic occupancy model on SMART data from other system. It provides rangers a flexible tool

for assessing occupancy of poachers and wildlife, to evaluate the effectiveness of their ongoing patrolling on the detection of both poachers and wildlife and on how rangers can alter their interactions.

Acknowledgments

We are grateful to SMART partnership, WWF Cambodia, the ministry of Environment Cambodia, along with the rangers who have planned and collected the data from the Phnom Prich wildlife sanctuary and Serepok Sanctuary and the collaboration of the Asia Poaching prevention group of WWF. LM and OG were funded by the French National Research Agency (grant ANR-16-CE02-0007).

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Table 1: Description of the ecological parameters used in the multi-season two-species occupancy model.

Processes	Symbol	Description by site
Occupancy		
OW	$\psi_{P/W}$	occupancy probability of poachers in presence of wildlife
OP	$\psi_{P/\bar{W}}$	occupancy probability of poachers in absence of wildlife
WP	ψ_{W}	occupancy probability of wildlife regardless of poachers
Colonisation		
from U to OW	$\gamma_{W/\bar{P}} = \gamma_W - \gamma_{WP}$	probability that wildlife colonise an unoccupied site
from U to OP	$\gamma_{P/\bar{W}} = \gamma_P - \gamma_{WP}$	probability that poachers colonise an unoccupied site
from U to WP	γ_{WP}	probability that both colonise an unoccupied site
from OP to WP	$\gamma_{W/P}$	probability that a site is colonised by wildlife given the presence of poachers
from OW to WP	$\gamma_{P/W}$	probability that a site is colonised by poachers given the presence of wildlife
Extinction		
from WP to OP	$\epsilon_{W/P} = \epsilon_W - \epsilon_P$	extinction probability of wildlife given presence of poachers
from WP to OW	$\epsilon_{P/W} = \epsilon_P - \epsilon_{WP}$	extinction probability of poachers given presence of wildlife
from WP to U	ϵ_{WP}	extinction probability of both in a site
from OP to U	$\epsilon_{P/\bar{W}}$	extinction probability of poachers conditional on the absence of wildlife
from OW to U	$\epsilon_{W/\bar{P}}$	extinction probability of wildlife conditional on the absence of poachers
Replacement		
from OW to OP	ω_{WP}	probability that a site occupied by wildlife only is replaced by poachers
from OP to OW	ω_{PW}	probability a site occupied by poachers only is replaced by wildlife

Fidelity		
from OP to OP	$1 - \gamma_{W/P} - \omega_{PW} - \epsilon_{P/\bar{W}}$	a site stays occupied by poachers only from one year to another
from OW to OW	$1 - \gamma_{P/W} - \omega_{WP} - \epsilon_{W/\bar{P}}$	a site stays occupied by wildlife only from one year to another
from WP to WP	$1 - \epsilon_P - \epsilon_W - \epsilon_{WP}$	a site stays occupied by both from one year to another

Table 2: Model selection results for detection, occupancy and transition processes. The model names describe the effects of patrolling effort, of roads, rivers and stations, and species interaction (reciprocal or directional) on detection, occupancy and transition probabilities. The number of parameter, the deviance, AIC and ΔAIC the difference of AICs between the best model and any other candidate models of each step of the model selection procedure (detection, occupancy, transition). The best model supported by the data is the one with the lowest AIC.

Model names	# parameters	Deviance	AIC	ΔAIC
Detection				
Spatio-temporal effect of patrolling effort on both poachers and wildlife	**21**	**1527.21**	**3112.085**	**0**
Constant	16	1563.34	3167.189	55.11
Spatial effect of patrolling effort on both	21	1563.66	3167.824	55.74
Species interaction effect	18	1566.38	3173.264	61.18
Temporal effect of patrolling effort on both	21	1568.71	3177.928	65.84
Stream length effect on both	21	2101.64	4257.838	1145.35
Distance to road effect on both	21	2126.57	4307.311	1195.23
Distance to station effect on both	21	2126.58	4310.81	1198.72
Occupancy				
No wildlife effect on poachers	**20**	**1528.787**	**3111.574**	**0**
Species interaction effect	21	1536.912	3112.085	0.51
Spatial effect of patrolling effort on poacher only	21	1528.587	3114.836	3.262
Spatial effect of patrolling effort on poacher only	23	1527.082	3119.533	7.959
Spatial effect of patrolling effort on both	24	1527.077	3123.583	12.009
Distance to road effect on both	24	1620.35	3140.27	28.69

Stream length effect on both	24	1575.97	3212.86	101.28
Distance to station effect on both	24	1805.45	3680.34	467.48
Transition				
No wildlife effects on poachers	**18**	**1529.12**	**3105.276**	**0**
Temporal effect of patrolling effort on both	23	1523.272	3111.913	6.63
Poacher performance*	18	1532.535	3112.115	6.84
Temporal effects of patrolling effort on poachers	23	1526.38	3118.136	12.86
Spatial effect of patrolling effort on both	23	1527.083	3119.77	14.49
Spatial effect of patrolling on poachers	23	1528.703	3122.773	17.49
Delayed effect of patrolling on both	23	1532.787	3130.942	25.66
Spatio-temporal effect of patrolling on both	31	1516.28	3135.066	29.79
Delayed effect of ranger on poachers	23	1537.501	3140.371	35.09

* poachers' extinction and wildlife colonisation parameters are unrelated to poacher-wildlife interactions

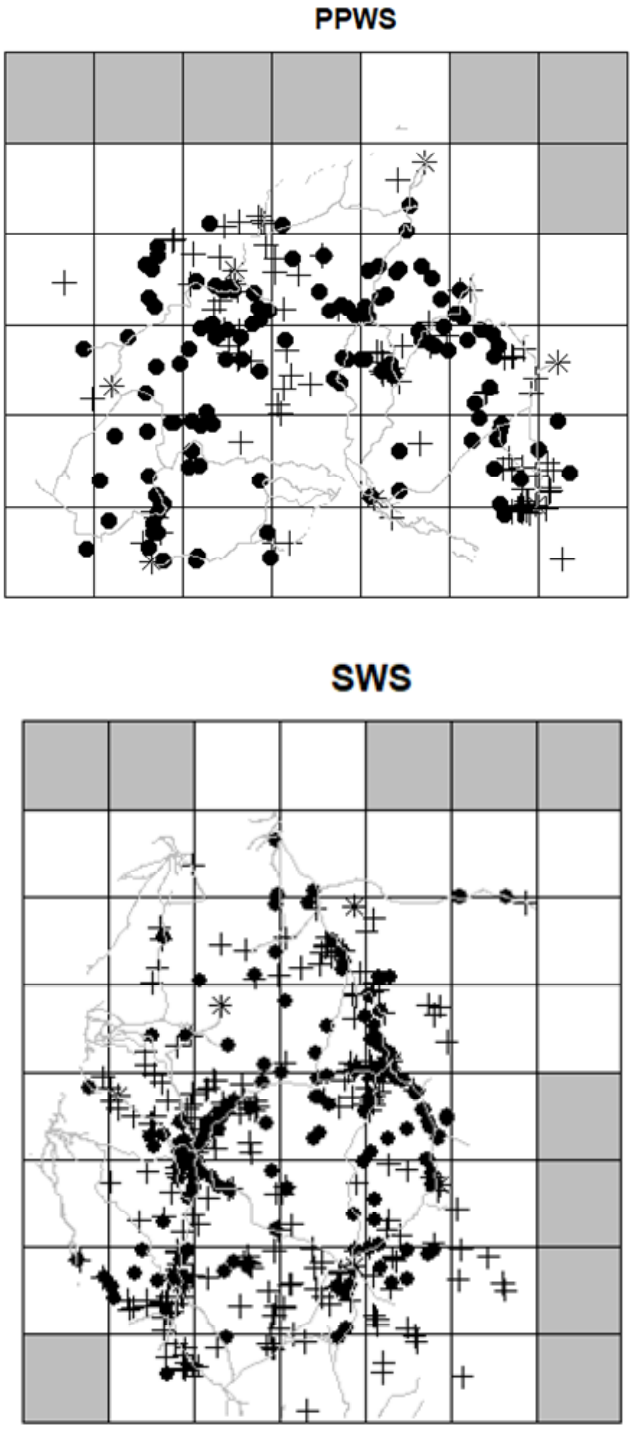

Figure 1: Map of the study areas in Cambodia, the Phnom Prich Wildlife Sanctuary (PPWS) and Serepok Wildlife Sanctuary (SWS). Sampling sites were defined as 10x10 km cells. We show the occurrence patterns of poachers (crosses) and wildlife species (black dots). Grey lines the road network, stars represent the ranger stations as well as temporary ranger's campsites. Grey cells represents sites that were never sampled and removed from analysis.

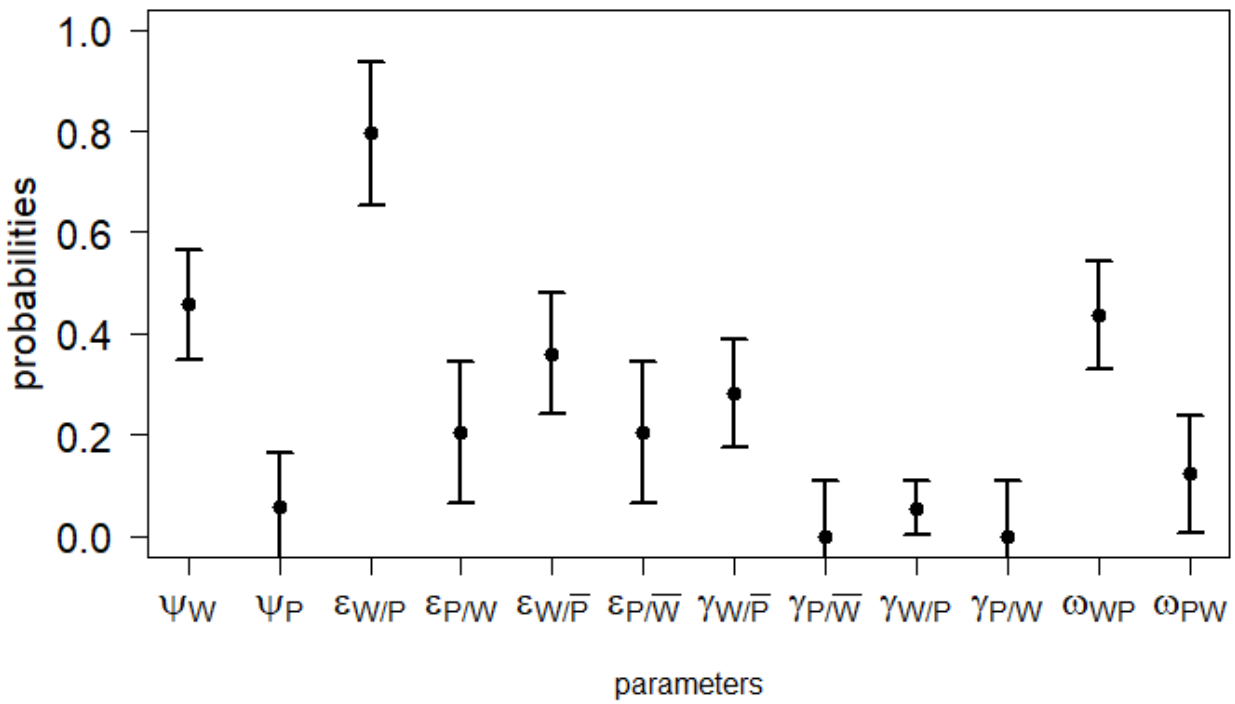

Figure 2: Estimated ecological parameters with associated 95% confidence intervals. We provide the estimated occupancy probability for wildlife (□) regardless of the presence/absence of the other, the extinction probability (ε) of a species (wildlife denoted by W or poachers noted by P) given the presence (without an upper bar) or absence (denoted by an upper bar) of the other (W or P) , the colonisation probability of a species (γ) conditional on the presence/absence of the other, the replacement probability of one species by another (ω). Estimates were obtained from the best model displayed in Table 1 with no effects of wildlife on the transition parameters of the poachers nor on their initial occupancy and spatiotemporal effect of the patrolling efforts on the detection probability of poachers and wildlife.

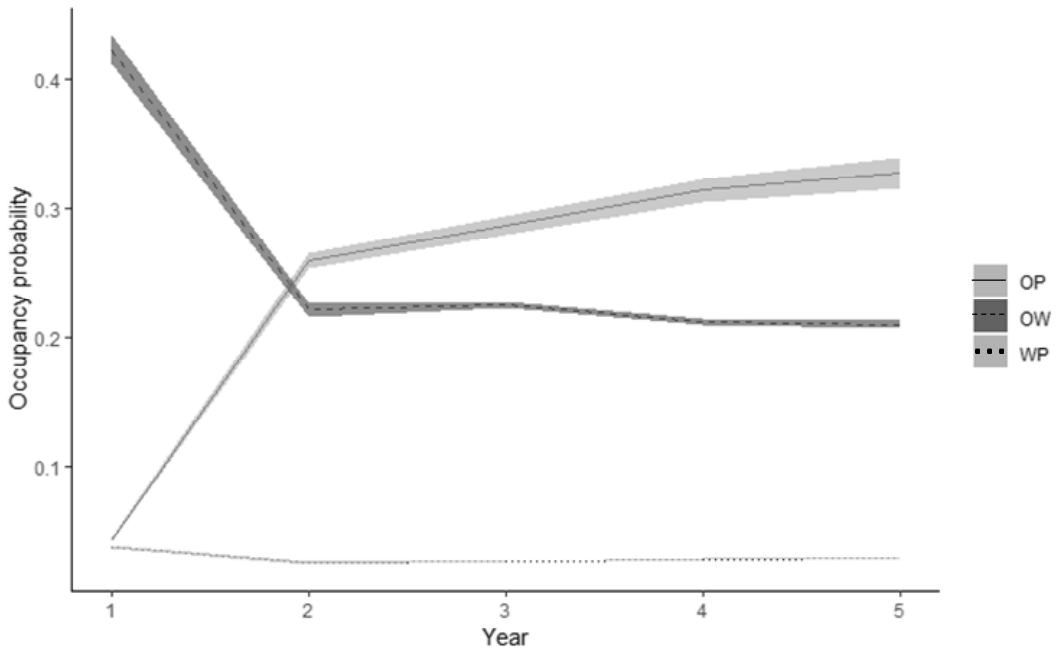

Figure 3: Temporal changes in the probability that a site is occupied by poachers only (OP, solid line) and occupied by wildlife only (OW, dashed line), or occupied by both, poacher and wildlife (WP, dotted line), estimated over the study period.

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Appendix A

Inferring wildlife poaching in Southeast Asia with a hidden Markov multispecies dynamic occupancy model

Supplementary information on the SMART data analyses

We performed model selection on the poacher-wildlife occupancy and tested different hypotheses regarding effects of biotic (species interactions) and abiotic variables (roads, rivers, spatial-temporal effects of patrolling effort) on species detection, occupancy and transition probabilities. This was done in three steps.

First, we accounted for the different effects on the detection process and tested the following hypotheses:

i) poachers and species of the wildlife are similarly detectable so they have the same detection probabilities (*constant*)

ii) detection of poachers only or wildlife only, vary from the detection of both (called *species interactions effects* in table 2 of the manuscript)

iii) patrolling effort influences the detection of a species in time or space or both.

i) spatial variation in detection of poachers only, wildlife only, and both were explained by distance to road (the minimum distance between the center of each site and the road)

ii) spatial variation in detection of poachers only, wildlife only, and both were explained by distance to ranger station (the minimum distance between the center of each site and a patrolling station)

iv) linear effects of stream length per site on the detection probability of poachers only,

wildlife only, and both.

Second, we used the best model structure on detection selected in step 1, and accounted for different effects on occupancy. testing the following hypotheses:

iii) no wildlife effect on occupancy of poachers

iv) spatial effect of patrolling effort on poacher occupancy only

v) spatial effect of patrolling effort on the occupancy of poachers and the occupancy of wildlife conditional on presence/absence of poachers

vi) occupancy of poachers and wildlife conditional on presence/absence of poachers defined as a function of distance to the road

vii) occupancy of poachers and wildlife conditional on presence/absence of poachers defined as a function of distance to station

viii) occupancy of poachers and wildlife conditional on presence/absence of poachers defined as a function of stream length per site

Third, we kept the best structure on occupancy selected in step 2, and tested the following hypotheses regarding the transition processes :

i) poachers' transition parameters are independent on the occurrence of wildlife ("*no wildlife effects*")

ii) poachers' extinction and wildlife colonization parameters are unrelated to poacher-wildlife interactions ("*poachers performance*")

iii) the transitions parameters specific to poachers depend on temporal or spatial variation or both in patrolling effort

iv) the transitions parameters of the two species depend on the temporal or spatial variation or both in patrolling effort

v) one-year delayed effects of patrolling effort on transition parameters transition.

Supplementary information on the results

The simultaneous extinction probability of both poachers and wildlife in a site on a give year, as well as the colonisation of both poachers and wildlife and the colonisation probability of poachers in presence of wildlife were all estimated at almost 0. We considered them not estimable, as the number of observed transitions associated to those probabilities was less than three (one from U to WP, one from WP to U and three from PO to PW) (Table A.1).

Table A.1 : How site occupancy events were assigned. Sample size in terms of number of detection of wildlife only, poachers only, both and none by year and number of transition from one state to another observed in the occupancy table

Events in occupancy states	Total # of events	Sample size per year				OW	OP	WP	U
OW	213	70	56	68	19	27	19	13	22
OP	195	16	35	71	73	4	10	3	8
WP	38	7	5	14	12	11	4	4	1
U	3442	879	876	819	868	14	13	1	89

Table A.2: Values used to simulate the data in the first part of the simulation study wherein we investigated the bias in parameter estimates emerging from different occupancy. The input parameter used to simulated the data were fixed to the values obtained from the empirical analysis.

Symbol	Probability	Estimates from the best occupancy model
$\Psi_{P/W}$	Occupancy probability of poachers in presence of animals	0.06
$\Psi_{P/\bar{W}}$	Occupancy probability of poachers in absence of animals	0.06
ψ_W	Occupancy probability of animals	0.46
$\gamma_W - \gamma_{WP}$	probability that an unoccupied site is colonized by animals	0.28

	only	
$\gamma_P - \gamma_{WP}$	probability that an unoccupied site is colonized by poachers only	0.001
γ_{WP}	probability that an unoccupied site is colonized by both	0.001
$\gamma_{W/P}$	probability that a site is colonized by animals given the presence of poachers	0.05
$\gamma_{P/W}$	probability that a site is colonized by poachers given the presence of animals	0.001
$\epsilon_W - \epsilon_{WP}$	probability that animals are going extinct given the presence of poachers in a site	0.80
$\epsilon_P - \epsilon_{WP}$	probability that poachers are going extinct given the presence of animals in a site	0.20
ϵ_{WP}	the probability that poachers and animals are going extinct in a site	0.001
$\epsilon_{P/\bar{W}}$	the extinction probability of poachers conditional on the absence of animals	0.20
$\epsilon_{W/\bar{P}}$	the extinction probability of animals conditional on the absence of poachers	0.41
ω_{WP}	probability that a site occupied by animals is replaced by poachers	0.44
ω_{PW}	probability a site occupied by poachers only is replaced by animals	0.12

Regarding the results from the simulation specifically, our model tended to underestimate the probability that a site occupied by wildlife become extinct by more than 10%, regardless of the number of primary occasions, the number of repeated surveys or of sampled sites. The mean bias on occupancy estimates were 19% when only three secondary occasions were considered, 13% when six secondary occasions were recorded, down to only 3% in studies with 12 secondary occasions. The mean bias for any other estimate remains invariant to the number of sampled sites and was around 9%. Results from these simulations showed that the design we used for our analysis of poacher and wildlife interactions should not generate any bias greater than 15% (Appendix 1).

Table A.3: Bias in the 18 parameter estimates of the two-species dynamic occupancy model calculated from 1000 simulations run for 36 different occupancy design : with number of sites ranging from 35, 100, 250, 500 monitored during 3, 5, 10 primary occasions with 3, 6, or 12 secondary occasions. We calculated the bias as the mean difference between the parameter values estimated and the values used to simulate the data across 1000 simulations. Yellow colored cells represent a positive bias greater than 0.1 and blue colored cell a negative bias lower than -0.1. The framed row corresponds to the bias in estimates for the occupancy design the closest to ours. The value used to simulated the data are presented in table 1 of the appendix (See table 1 for the signification of each parameter symbol).

Site	Occasions		Mean Bias in parameter estimates																	
#	1ary	2ary	ψ_W	$\psi_{P/\bar{W}}$	$\psi_{P/W}$	γ_{WP}	γ_P	γ_W	$\varepsilon_{P/\bar{W}}$	ω_{AP}	$\gamma_{P/W}$	$\varepsilon_{W/\bar{P}}$	ω_{PA}	$\gamma_{W/P}$	ε_{WP}	ε_W	ε_P	p_W	p_P	p_{WP}
35	3	3	0.18	0.12	0.12	0.21	0.20	0.03	0.09	-0.04	0.07	0.08	-0.07	-0.01	0.53	-0.59	0.01	0.03	0.03	-0.02
100	3	3	0.27	0.31	0.18	0.25	0.08	0.06	0.02	-0.03	0.06	-0.09	-0.02	0.10	0.46	-0.49	-0.04	0.01	0.01	-0.01
250	3	3	0.12	0.08	0.10	0.05	0.01	-0.01	0.00	0.01	0.01	-0.10	-0.01	0.09	0.29	-0.34	-0.01	0.00	0.01	0.00
500	3	3	0.21	0.17	0.20	0.29	-0.05	0.02	-0.01	0.01	0.01	-0.27	-0.01	0.27	0.38	-0.37	-0.05	0.00	0.00	-0.03
35	5	3	0.27	0.19	0.22	0.10	0.22	0.03	0.02	-0.02	0.09	0.00	-0.05	0.03	0.42	-0.59	0.03	0.02	0.01	-0.02
100	5	3	0.17	0.17	0.11	0.11	0.05	0.01	-0.02	0.00	0.05	-0.09	0.00	0.08	0.33	-0.45	0.01	0.00	0.01	0.00
250	5	3	0.25	0.25	0.21	0.30	0.03	0.04	-0.04	0.02	0.03	-0.21	-0.02	0.22	0.37	-0.46	-0.05	0.00	0.00	-0.03
500	5	3	0.06	0.04	0.07	0.03	0.00	0.00	-0.02	0.00	0.01	-0.10	-0.01	0.10	0.13	-0.17	-0.01	0.00	0.00	0.00
35	10	3	0.32	0.18	0.25	0.21	0.05	0.06	-0.04	0.02	0.06	-0.03	-0.03	0.06	0.45	-0.54	-0.01	0.01	0.01	-0.02
100	10	3	0.29	0.26	0.22	0.18	0.19	0.02	-0.06	0.03	0.05	-0.19	-0.02	0.20	0.25	-0.48	-0.04	0.00	0.00	-0.02
250	10	3	0.11	0.10	0.10	0.03	0.05	-0.01	-0.03	0.01	0.02	-0.12	-0.01	0.12	0.14	-0.23	-0.02	0.00	0.00	0.00
500	10	3	0.27	0.32	0.24	0.10	0.16	0.04	-0.06	0.02	0.04	-0.25	-0.02	0.26	0.19	-0.37	-0.05	-0.01	0.00	-0.03
35	3	6	0.11	0.12	0.03	0.06	0.06	0.02	0.04	-0.02	0.01	-0.04	0.00	0.03	0.29	-0.38	0.03	0.00	0.00	0.05
100	3	6	0.08	0.05	0.06	0.05	-0.01	0.00	-0.01	-0.01	0.02	-0.07	0.00	0.07	0.22	-0.25	-0.01	0.00	0.00	0.00
250	3	6	0.11	0.12	0.09	0.05	-0.01	0.00	-0.03	0.02	0.00	-0.12	0.00	0.12	0.19	-0.18	-0.04	0.00	0.00	-0.01
500	3	6	0.06	0.05	0.06	0.01	0.01	-0.01	-0.04	0.02	0.00	-0.06	0.00	0.06	0.07	-0.10	-0.01	0.00	0.00	0.00

35	5	6	0.16	0.14	0.04	0.05	0.08	0.02	-0.02	0.02	0.02	-0.03	-0.02	0.04	0.23	-0.40	0.04	0.00	0.00	0.09
100	5	6	0.21	0.24	0.12	0.02	0.13	0.02	-0.04	0.03	0.01	-0.12	-0.02	0.13	0.14	-0.32	-0.03	-0.01	0.00	0.00
250	5	6	0.15	0.17	0.12	0.00	0.11	-0.02	-0.05	0.04	0.01	-0.09	-0.02	0.10	0.06	-0.22	0.00	-0.01	0.00	-0.01
500	5	6	0.24	0.33	0.17	0.02	0.12	0.04	-0.04	0.04	0.01	-0.16	-0.02	0.16	0.09	-0.26	-0.03	-0.01	0.00	-0.02
35	10	6	0.17	0.11	0.12	0.02	0.07	-0.01	0.04	0.00	0.03	-0.03	-0.05	0.07	0.18	-0.41	0.03	-0.01	-0.02	0.01
100	10	6	0.13	0.12	0.12	0.01	0.10	-0.01	-0.01	0.02	0.02	-0.08	-0.03	0.10	0.11	-0.28	-0.02	0.00	-0.01	-0.01
250	10	6	0.16	0.17	0.12	0.01	0.13	0.00	-0.04	0.03	0.02	-0.10	-0.02	0.11	0.07	-0.23	-0.01	-0.01	0.00	-0.01
500	10	6	0.14	0.19	0.10	0.01	0.13	0.00	-0.03	0.02	0.02	-0.08	-0.02	0.08	0.07	-0.19	-0.02	-0.01	-0.01	-0.02
35	3	12	0.04	0.02	0.01	0.02	-0.02	0.01	0.00	0.00	0.01	-0.04	0.03	0.02	0.13	-0.20	0.02	0.00	0.00	0.10
100	3	12	0.09	0.07	0.05	0.01	0.04	-0.01	-0.02	0.02	0.00	-0.07	0.00	0.06	0.11	-0.15	-0.01	-0.01	0.00	0.00
250	3	12	0.08	0.02	0.08	0.00	-0.04	-0.03	-0.04	0.02	0.01	-0.07	-0.01	0.07	0.03	-0.12	0.05	-0.01	0.00	-0.02
500	3	12	0.10	0.04	0.07	0.00	0.01	-0.02	-0.02	0.01	0.01	-0.06	-0.01	0.06	0.05	-0.12	0.02	-0.01	0.00	-0.01
35	5	12	0.02	0.01	0.01	0.01	0.01	0.00	0.03	0.01	0.02	0.03	-0.02	-0.02	0.20	-0.36	0.06	-0.01	-0.02	0.22
100	5	12	0.07	0.04	0.05	0.00	0.01	-0.01	0.00	0.02	0.01	-0.01	-0.02	0.02	0.09	-0.22	0.02	-0.01	-0.01	0.05
250	5	12	0.08	0.06	0.08	0.01	0.05	-0.01	-0.03	0.02	0.01	-0.06	-0.02	0.07	0.04	-0.15	0.01	0.00	-0.01	-0.01
500	5	12	0.11	0.11	0.06	0.00	0.05	-0.02	-0.03	0.03	0.01	-0.04	-0.01	0.04	0.05	-0.23	0.06	-0.01	-0.01	-0.02
35	10	12	0.10	0.06	0.04	0.01	-0.07	0.01	0.14	0.07	0.02	0.04	-0.08	-0.08	0.24	-0.53	0.10	-0.01	-0.05	0.41
100	10	12	0.01	0.06	0.16	0.00	-0.14	-0.04	0.38	-0.03	0.04	0.12	-0.18	-0.05	0.22	-0.57	0.10	-0.06	-0.11	0.35
250	10	12	-0.32	-0.03	0.07	0.00	-0.17	-0.04	0.76	-0.15	0.01	0.52	-0.37	-0.15	0.28	-0.58	0.12	-0.10	-0.16	0.40
500	10	12	-0.36	-0.05	-0.03	0.00	-0.17	-0.04	0.80	-0.17	0.00	0.55	-0.38	-0.16	0.31	-0.58	0.10	-0.10	-0.16	0.31

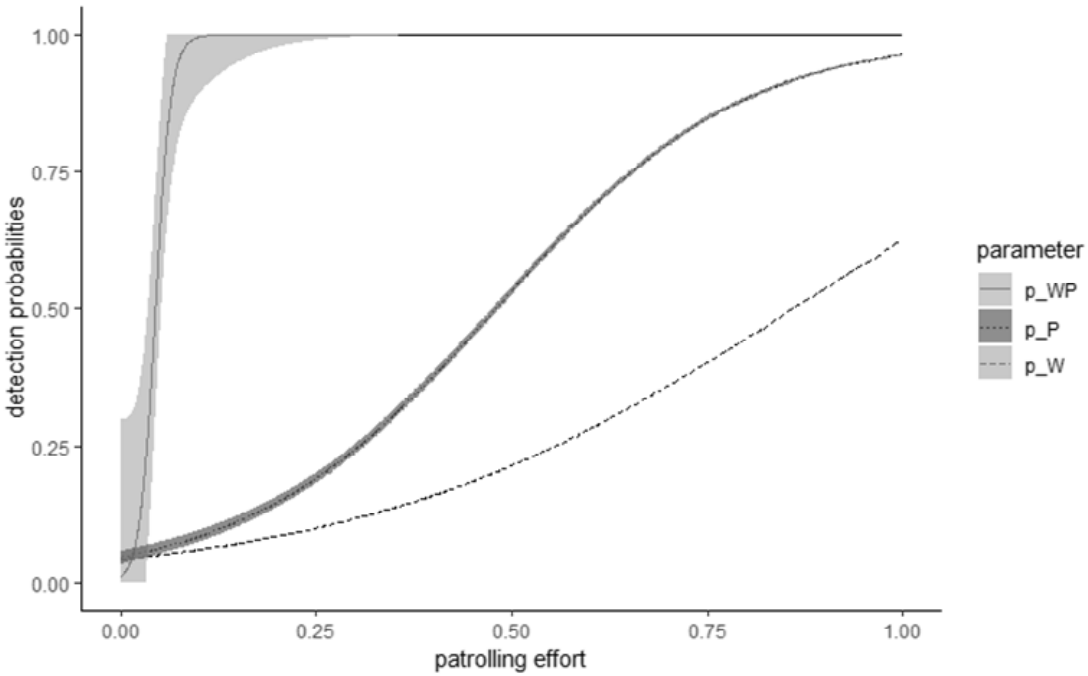
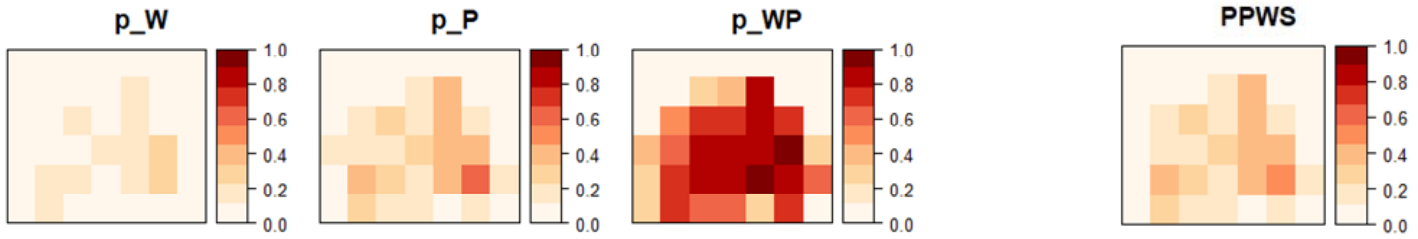


Figure A.1: Estimated site-specific detection probabilities and their 95% confidence intervals as a function of patrolling effort. The figure represents detection of both wildlife and poachers (solid line), detection probability of poacher (dashed line), detection probability of wildlife (dotted line). Estimates were obtained from the model best supported by the data, see Table 1.

a)



b)

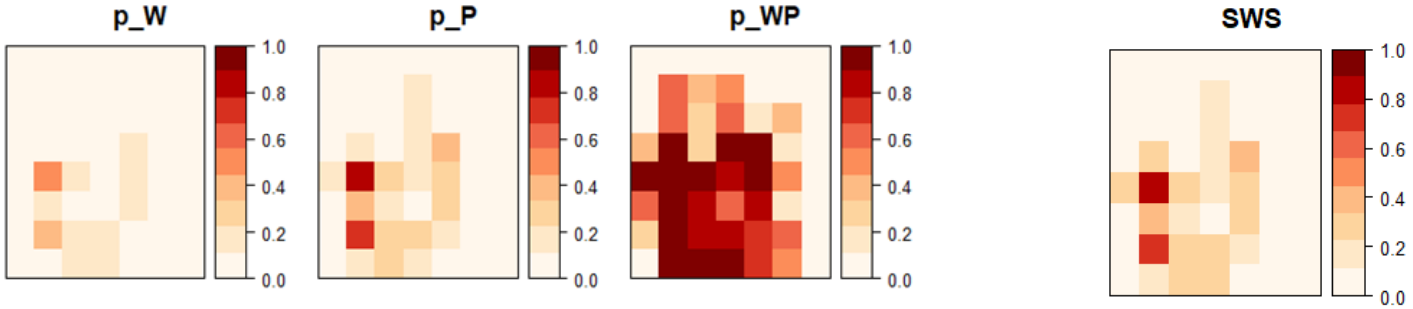


Fig. A2: Spatial variation in the probability of detection of wildlife only p_W, poachers only p_P, and the detection probability of both wildlife and poachers p_WP in a) Phnom Prich Wildlife Sanctuary (PPWS) b) Srepock Wildlife sanctuary (SWS) and the spatial representation of spatial effort (averaged over the sampling occasions) in those two study areas (two panels PPWS and SWS on the right).

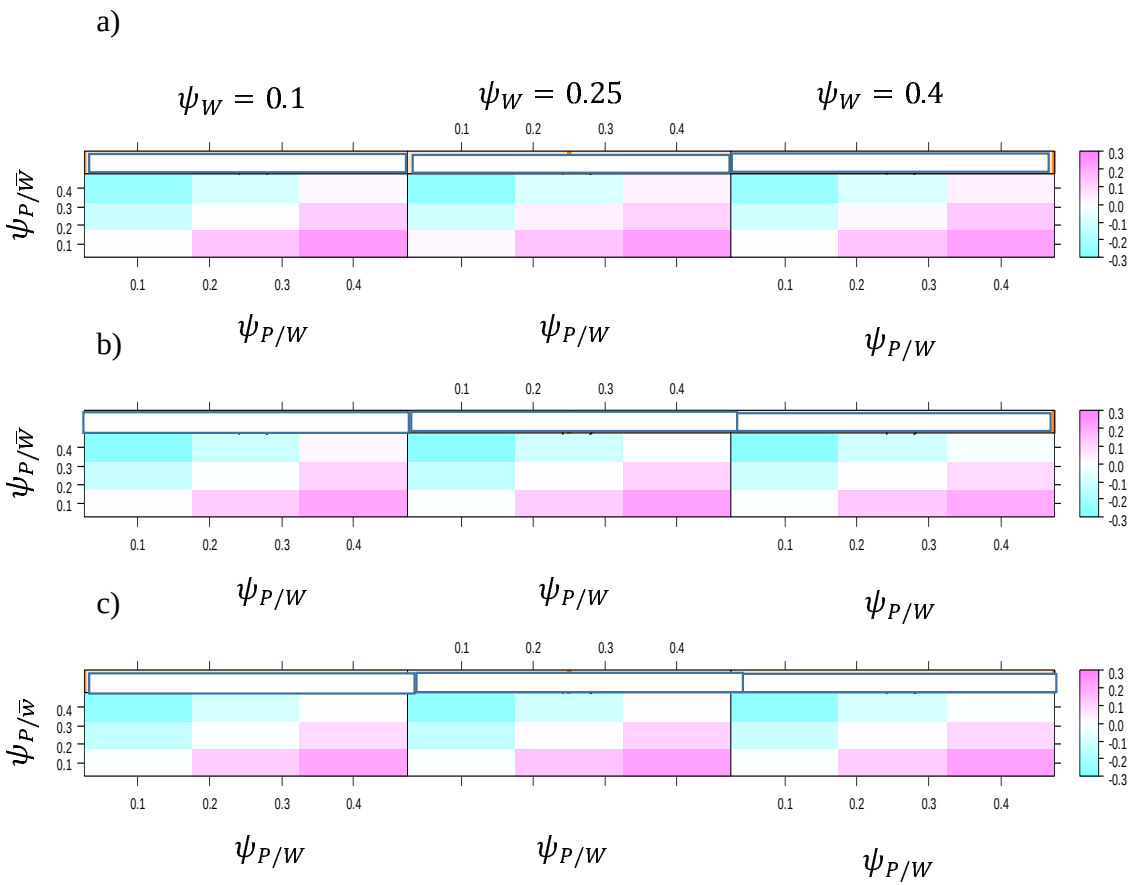


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Figure A.3: Bias in the occupancy probability of poachers in absence of wildlife in relation to varying input values used to simulate data. We varied the occupancy probability of poachers in absence of wildlife (y-axis), the occupancy probability of poachers in presence of wildlife (x-axis), the occupancy probability of wildlife regardless of the occurrence of poachers (from the left to the right). The detection probability varied from a) 0.1, b) 0.25 to c) 0.4 and was assumed the same between poachers and wildlife.