

## Accounting for misidentification and heterogeneity in occupancy studies using hidden Markov models



Julie Louvrier<sup>a,b,\*</sup>, Thierry Chambert<sup>a</sup>, Eric Marboutin<sup>c</sup>, Olivier Gimenez<sup>a</sup>

<sup>a</sup> CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

<sup>b</sup> Office National de la Chasse et de la Faune Sauvage, CNERA prédateurs et animaux déprédateurs, Parc Micropolis, 05000 Gap, France

<sup>c</sup> ONCFS, Gières, France

### ARTICLE INFO

#### Keywords:

Occupancy models  
Detection heterogeneity  
Species imperfect detection  
False-positives  
Finite-mixture models

### ABSTRACT

Occupancy models allow assessing species occurrence while accounting for imperfect detection. As with any statistical models, occupancy models rely on several assumptions amongst which (i) there should be no unmodelled heterogeneity in the detection probability and (ii) the species should not be detected when absent from a site, in other words there should be no false positives (e.g., due to misidentification). In the real world, these two assumptions are often violated. To date, models accounting simultaneously for both detection heterogeneity and false positives are yet to be developed. Here, we first show how occupancy models with false positives can be formulated as hidden Markov models (HMM). Second, benefiting from the HMM framework flexibility, we extend models with false positives to account for heterogeneity with finite mixtures. First, using simulations, we demonstrate that, as the level of heterogeneity increases, occupancy models accounting for both heterogeneity and misidentification perform better in terms of bias and precision than models accounting for misidentification only. Next, we illustrate the implementation of our new model to a real case study with grey wolves (*Canis lupus*) in France. We demonstrate that heterogeneity in wolf detection (false negatives) is mainly due to a heterogeneous sampling effort across space. In addition to providing a novel modeling formulation, this work illustrates the flexibility of HMM framework to formulate complex ecological models and relax important assumptions that are not always likely to hold. In particular, we show how to decompose the model structure in several simple components, in a way that provides much clearer ecological interpretation.

### 1. Introduction

Occupancy models (Mackenzie et al., 2006) are commonly used to infer species occurrence while accounting for imperfect detection (Bailey et al., 2014; Guisera-Arroita, 2017). These models rely on species detections and non-detections recorded during surveys repeated across time and across several spatial sampling units (sites). As with any statistical models, inferences made from occupancy analyses heavily rely on several assumptions that should be checked and validated (Mackenzie et al., 2003, 2006), although in reality this is rarely done (see however, Mackenzie et al., 2004; Warton et al., 2017).

Here, we focus on two important assumptions. First, there should be no unmodelled heterogeneity in species detection. In other words, all heterogeneity should be accounted for with covariates. If ignored, heterogeneity in detection leads to underestimating occupancy (Royle

and Nichols, 2003; Royle, 2006). Detection heterogeneity can be due to a heterogeneous sampling effort in space (Louvrier et al., 2018), variation in animal abundance (Royle and Nichols, 2003) or variation in site characteristics (Mackenzie et al., 2011). Often, site-level covariates can be measured on the field and incorporated in occupancy models to account for detection heterogeneity. However, unexplained variation may remain or measuring the relevant covariates may simply be impossible in the field. When we suspect substantial unmodelled heterogeneity to occur, we should consider modeling it, either with continuous latent variables (through normally distributed site random effects, e.g. Gimenez et al., 2014). Modelling heterogeneity using normally distributed random effect has long been studied in the field of theoretical biology (e.g., Perc, 2011). Alternatively, modelling heterogeneity can be done using finite mixtures. In finite-mixture models, a latent variable is defined to assign sites to a mixture components (i.e.,

*Abbreviations:* MMO, model accounting for misidentification only; MMH, model accounting for misidentification and heterogeneity in the detection probabilities; MMS, model accounting for misidentification only and sampling effort as a covariate on the detection probability; MMHS, model accounting for misidentification and heterogeneity in the detection probabilities and sampling effort as a covariate on the detection probabilities

\* Corresponding author at: Centre d'Écologie Fonctionnelle et Évolutive, CNRS, 1919 route de Mende, 34090 Montpellier, France.

E-mail address: [julie.louvrier@cefe.cnrs.fr](mailto:julie.louvrier@cefe.cnrs.fr) (J. Louvrier).

<https://doi.org/10.1016/j.ecolmodel.2018.09.002>

Received 4 January 2018; Received in revised form 6 August 2018; Accepted 3 September 2018

0304-3800/ © 2018 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

groups of heterogeneity) characterized by specific parameters (Royle, 2006; Pledger and Phillpot, 2008). While heterogeneity in detection probability using mixture models has been long studied in the capture-recapture (CR) literature (review in Gimenez et al., 2017), less attention has been given to this issue in occupancy models (Gimenez et al., 2014; Miller et al., 2015).

A second important assumption of occupancy models is that the species should not be detected when absent from a site (i.e. no false positives). False positives occur when the species of interest is detected at sites where it did not occur, usually as a result of misidentification (Miller et al., 2013). Several studies have underlined the importance of accounting for false positives on species distribution (Royle and Link, 2006; Miller et al., 2011, 2013; Chambert et al., 2015). Ignoring false positives and counting them as true positives causes important biases, such as overestimating occupancy and colonization probabilities, and underestimating extinction probability (Royle and Link, 2006; McClintock et al., 2010). Miller et al. (2011, 2013) developed static and dynamic occupancy models that accommodate both false negatives and false positives. As example of applications, these models have been used to estimate occurrence of amphibians (Miller et al., 2011), bats (Clement et al., 2014), and several large vertebrates in India (Pillay et al., 2014), as well as occurrence dynamics of wolves in Montana (Miller et al., 2013).

While several studies have accounted for heterogeneity in occupancy models with false positives by using site-level covariates (McClintock et al., 2010; Ferguson et al., 2015; Miller, 2015), methods that simultaneously account for both unmodelled heterogeneity through finite mixtures and false positives have yet to be developed. Here, we fill this gap and illustrate the use of hidden Markov modelling (HMM) framework as a powerful tool for further developments aiming at relaxing occupancy models' assumptions.

Standard occupancy models can be formulated as HMMs describing two time-series running in parallel. The first time-series captures the dynamics of the latent states with the state process following a Markovian sequence (e.g. site occupied vs. unoccupied); the other time series models the observation process consisting in detections conditional on the underlying but possibly unknown states (Gimenez et al., 2014). The originality of our approach is twofold. First, we show how occupancy models with false positives can be formulated as HMMs. Second, benefiting from the HMM framework flexibility, we extend models with false positives to account for unmodelled heterogeneity using a finite-mixture approach.

To assess the performance of our approach, we performed a simulation study comparing parameter bias and precision in a model accounting for misidentification and heterogeneity vs. a model accounting for misidentification only. To do so, we considered scenarios with an increasing level of heterogeneity in the probability of false positive detection. We also used a case study on the grey wolves' (*Canis lupus*) distribution in France to illustrate implementation of the method in a real-world scenario. Our objectives were (i) to investigate how detection heterogeneity, when ignored, affects the accuracy of occupancy estimation and (ii) assess the extent at which this heterogeneity might be explained by sampling effort variability across space.

## 2. Methods

In the statistical literature, there are three main problems of interest when using HMM (Rabiner, 1989). In what follows, we review each of these problems in the context of occupancy models. In the *evaluation* problem, we ask what the probability that the observations are generated by our model is – see Section 2.1. In the *decoding* problem, we ask what the most likely state sequence in the model that produced the observations is – see Section 2.5. In the *learning* problem, we ask how we should adjust the model parameters to maximize the likelihood – see Section 2.3.

### 2.1. HMM formulation of occupancy models with misidentification

Occupancy models can be viewed as HMM whereby the ecological states are considered as partially hidden states, i.e. imperfectly observed (Gimenez et al., 2014). Occupancy models incorporating false positives can also be framed within this approach. The HMM formulation allows flexibility in the model formulation. By decomposing the occupancy approach into simpler steps, the HMM formulation allows better understanding of the ecological and observation processes. To account for false positives, we followed the multi-season dynamic model formulation of Miller et al. (2013). For occupied sites, three observations can be made: (i) an unambiguous detection which is a true detection that has been validated, (ii) an ambiguous detection which is also a true detection but that could not be validated and (iii) no detection. At unoccupied sites, by definition, unambiguous detections cannot occur, thus, only two possible observations can be made: an ambiguous detection, which in this case is a false positive detection due to species misidentification, or no detection. The parameters of interest are  $\psi_1$  the probability of initial occupancy, the probability of local extinction  $\epsilon$  and of colonization  $\gamma$ , the probability of correctly detecting the species at an occupied site  $p_{11}$ , the probability to falsely detect the species at an unoccupied site  $p_{10}$ , and the probability  $b$  to classify a true-positive detection as unambiguous (Miller et al., 2011). The specification of a HMM is divided in three steps: the vector of initial state probabilities, the matrix of transition probabilities linking states between successive sampling occasions and the matrix of observation probabilities linking observations and states at a given occasion (Gimenez et al., 2014). We define  $z_{i,k}$  the latent state of a site  $i$  during the primary occasion (e.g., season or year)  $k$ . At the first primary occasion,  $k = 1$ , a site can only be in one of two states ('unoccupied' or 'occupied'), with probabilities in the vector of initial state probabilities:

$$\psi = \begin{matrix} \text{unoccupied} & \text{occupied} \\ [1-\psi_1 & \psi_1] \end{matrix}$$

Then, the states are distributed as a first-order Markov chain governed by a transition matrix of the form:

$$T = \begin{matrix} & \text{unoccupied at } k+1 & \text{occupied at } k+1 \\ \begin{matrix} \text{unoccupied at } k \\ \text{occupied at } k \end{matrix} & \begin{bmatrix} 1-\gamma & \gamma \\ \epsilon & 1-\epsilon \end{bmatrix} \end{matrix}$$

where rows describe states at occasion  $k$  in, and columns describe states at  $k + 1$ .

Next, we describe the observation process, which is conditional on occupancy states. We define  $y_{i,j,k}$  the observation of a site  $i$  during the secondary occasion (e.g. visit or survey)  $j$  during the primary occasion  $k$ . For unoccupied sites, unambiguous detections ( $y_{i,j,k} = 1$ ) do not occur while ambiguous detections ( $y_{i,j,k} = 2$ ) or no detections ( $y_{i,j,k} = 0$ ) may occur. For occupied sites, unambiguous detections, ambiguous detections and no detection can all occur. For the sake of clarity, it is more convenient to write the observation process as the product of two matrices. The first matrix summarizes the detection state process conditional on occupancy state (rows) 'unoccupied' and 'occupied' at  $k$ . Columns describe the following intermediate latent detection states: 'no detection', 'true positive detection' and 'false positive detection':

$$P = \begin{matrix} & \text{no detection} & \text{true positive detection} & \text{false positive detection} \\ \begin{matrix} \text{unoccupied} \\ \text{occupied} \end{matrix} & \begin{bmatrix} 1-p_{10} & 0 & p_{10} \\ 1-p_{11} & p_{11} & 0 \end{bmatrix} \end{matrix}$$

It is important to keep in mind that the true, underlying state (i.e., false or true positive) of the detections is unknown. At this stage of the modeling, we are still dealing with latent state, not with actual data. The second matrix then summarizes the classification of a true-positive detection as unambiguous or ambiguous, with probability  $b$  and  $1-b$ , respectively. In this matrix, rows represent the above intermediate

latent detection states ('no detection', 'true-positive detection', 'false positive detection') while columns correspond to actual observations (data), i.e., 'no detection' ( $y_{i,j,k} = 0$ ), 'unambiguous detection' ( $y_{i,j,k} = 1$ ) and 'ambiguous detection' ( $y_{i,j,k} = 2$ ):

$$B = \begin{matrix} & \begin{matrix} \text{no detection} & \text{unambiguous detection} & \text{ambiguous detection} \end{matrix} \\ \begin{matrix} \text{no detection} \\ \text{true positive detection} \\ \text{false positive detection} \end{matrix} & \begin{bmatrix} 1 & 0 & 0 \\ 0 & b & 1-b \\ 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

We reemphasize that, by definition, false detections can only occur in the form of ambiguous detection. This last process only deals with the classification of true detection as certain or ambiguous, depending on the level of confidence in the observation. The overall observation process can then be written in the form of a simple matrix product,  $O = PB$ , which gives:

$$O = \begin{matrix} & \begin{matrix} \text{no detection} & \text{unambiguous detection} & \text{ambiguous detection} \end{matrix} \\ \begin{matrix} \text{unoccupied} \\ \text{occupied} \end{matrix} & \begin{bmatrix} 1-p_{10} & 0 & p_{10} \\ 1-p_{11} & bp_{11} & (1-b)p_{11} \end{bmatrix} \end{matrix}$$

Note that for simplicity we assume observation parameters to be constant, but these could be specified as survey-specific ( $j$ ), season-specific ( $k$ ), site-specific ( $i$ ) or any combination of these effects. We can then write the general probability of any detection history  $h$  such as:

$$P(h) = \overbrace{\Psi D[O(\cdot, y_{1,1} + 1)] T_0 D[O(\cdot, y_{2,1} + 1)] \dots T_0 D[O(\cdot, y_{j,1} + 1)]}^{\text{first primary occasion}} \times \overbrace{TD[O(\cdot, y_{1,2} + 1)] T_0 D[O(\cdot, y_{2,2} + 1)] \dots T_0 D[O(\cdot, y_{j,2} + 1)]}^{\text{second primary occasion}} \times \dots \times \overbrace{TD[O(\cdot, y_{1,k} + 1)] T_0 D[O(\cdot, y_{2,k} + 1)] \dots T_0 D[O(\cdot, y_{j,k} + 1)]}^{\text{last primary occasion}} \mathbf{1}_N$$

where for the sake of simplicity we have dropped the index  $i$  for site,  $D(\theta)$  is the diagonal matrix with diagonal elements equal to the elements of the arbitrary vector  $\theta$ ,  $O(\cdot, y_{j,k})$  is the column vector corresponding to the observation  $y$  at the secondary occasion  $j$  during primary occasion  $k$ ,  $A_0$  is the transition matrix with  $\varepsilon = \gamma = 0$  and  $\mathbf{1}_N$  is the column vector of  $N$  ones, with  $N$  the number of occupancy states. The likelihood is then the product of the probabilities of all the site histories (Zucchini et al., 2016).

$$T = \begin{matrix} & \begin{matrix} \text{unoccupied (A)}k+1 & \text{unoccupied (B)}k+1 & \text{occupied (A)}k+1 & \text{occupied (B)}k+1 \end{matrix} \\ \begin{matrix} \text{unoccupied (A)}k \\ \text{unoccupied (B)}k \\ \text{occupied (A)}k \\ \text{occupied (B)}k \end{matrix} & \begin{bmatrix} 1-\gamma_A & 0 & \gamma_A & 0 \\ 0 & 1-\gamma_B & 0 & \gamma_B \\ \varepsilon_A & 0 & 1-\varepsilon_A & 0 \\ 0 & \varepsilon_B & 0 & 1-\varepsilon_B \end{bmatrix} \end{matrix}$$

In our study on wolves, we focused on static (single-season) models, such that extinction and colonization events do not occur. The probability of any site history  $h$  can thus be simplified to:

$$P(h) = \Psi D[O(\cdot, y_1 + 1)] T_0 D[O(\cdot, y_2 + 1)] \dots T_0 D[O(\cdot, y_j + 1)]$$

## 2.2. Occupancy model with heterogeneity in the detection probability

We now show how to incorporate site-to-site (i.e., spatial) heterogeneity in the detection process through the addition of a probabilistic process that assigns any site to a finite number of latent classes (Royle, 2006; Miller et al., 2015). For the sake of clarity, here we only consider two classes of heterogeneity (class A and B), but more classes could easily be considered. Like group effects, membership to a heterogeneity class is a constant feature of a site (i.e., it does not change over time), so the assignment process occurs at the first modelling step, describing initial states:

$$\Pi = \begin{matrix} \text{class A} & \text{class B} \\ [\pi & 1-\pi] \end{matrix}$$

where  $\pi$  (respectively  $1-\pi$ ) is the probability for any site to be assigned to class A (resp. to class B). This is the main difference with the model described above. The following processes, and the associated parameters remain the same, except that parameters are now allowed to vary according to the two classes of sites. We now define four occupancy states: occupied (A), occupied (B), unoccupied (A) and unoccupied (B). In terms of model parameters, in addition to  $\pi$ , we now have:  $\psi_{1A}$  (resp.  $\psi_{1B}$ ) the probability of initial occupancy for sites of class A (resp. B),  $\varepsilon_A$  (resp.  $\varepsilon_B$ ) the probability of local extinction for sites of class A (resp. B) and  $\gamma_A$  (resp.  $\gamma_B$ ) the probability of local colonization for sites of class A (resp. B);  $p_{A11}$  (resp.  $p_{B11}$ ) the probability of correctly detecting the species at an occupied site of class A (resp. B),  $p_{A10}$  (resp.  $p_{B10}$ ) the probability to falsely detect the species at an unoccupied site A and the probability  $b$  to classify a true-positive detection as unambiguous (Miller et al., 2011).

The next process describes whether a site is initially occupied or not, but now conditionally on the site's class membership (A or B). The pattern matrix that links class membership to the four class-specific occupancy states is:

$$\Phi = \begin{matrix} & \begin{matrix} \text{unoccupied (A)} & \text{unoccupied (B)} & \text{occupied (A)} & \text{occupied (B)} \end{matrix} \\ \begin{matrix} \text{class A} \\ \text{class B} \end{matrix} & \begin{bmatrix} 1-\psi_{1A} & 0 & \psi_{1A} & 0 \\ 0 & 1-\psi_{1B} & 0 & \psi_{1B} \end{bmatrix} \end{matrix}$$

Here, rows correspond to the two conditioning states ('class A' and 'class B') and columns represent all possible initial states: 'unoccupied (A)', 'unoccupied (B)', 'occupied (A)' and 'occupied (B)' in columns.

The final vector of initial state probabilities is therefore the product of the row vector of class-assignment proportions and the matrix of occupancy probabilities:

$$\Psi = \Pi \Phi$$

Because we were interested in incorporating heterogeneity in the detection process only, here we assume  $\psi_{1A} = \psi_{1B} = \psi_1$ . The state transi-

tion process remains the same but is distinguished according to the two heterogeneity classes A and B. This leads us to define the following matrix for state transition from  $k$  to  $k+1$ :

The conditional observation process then happens independently at A sites and B sites. As above, rows describe occupancy states while

columns represent intermediate latent detection states ‘not detection’, ‘true positive detection’, ‘false positive detection’:

$$P = \begin{matrix} & \begin{matrix} \text{no detection} & \text{true positive detection} & \text{false positive detection} \end{matrix} \\ \begin{matrix} \text{unoccupied (A)} \\ \text{unoccupied (B)} \\ \text{occupied (A)} \\ \text{occupied (B)} \end{matrix} & \begin{bmatrix} 1-p_{A10} & 0 & p_{A10} \\ 1-p_{B10} & 0 & p_{B10} \\ 1-p_{A11} & p_{A11} & 0 \\ 1-p_{B11} & p_{B11} & 0 \end{bmatrix} \end{matrix}$$

Finally, the matrix describing the classification process of true positives as unambiguous or ambiguous detections remains unchanged (see matrix B above). Overall, the observation process can be described by the matrix product  $O = P B$  with the occupancy states in rows and the observations in columns:

$$O = \begin{matrix} & \begin{matrix} \text{no detection} & \text{unambiguous detection} & \text{ambiguous detection} \end{matrix} \\ \begin{matrix} \text{unoccupied (A)} \\ \text{unoccupied (B)} \\ \text{occupied (A)} \\ \text{occupied (B)} \end{matrix} & \begin{bmatrix} 1-p_{A10} & 0 & p_{A10} \\ 1-p_{B10} & 0 & p_{B10} \\ 1-p_{A11} & b p_{A11} & (1-b)p_{A11} \\ 1-p_{B11} & b p_{B11} & (1-b)p_{B11} \end{bmatrix} \end{matrix}$$

The likelihood, for both static and dynamic models, is written in the same way as for the model without heterogeneity, only the composition of the matrices changes. Again, in the rest of this paper, we focus on static (single-season) models, so that  $\epsilon_A = \epsilon_B = \gamma_A = \gamma_B = 0$ .

### 2.3. Implementation

Occupancy models formulated as HMMs can be implemented in the software E-SURGE (Choquet et al., 2009), which allows for the decomposition of the observation and state processes in multiple steps, providing more flexible, and often more easily interpretable parameterization (Gimenez et al., 2014). We provide in Appendix A and Appendix B two detailed step-by-step procedure to implement occupancy models accounting for false positives with and without heterogeneity in E-SURGE. We also refer to the E-SURGE manual (Choquet and Nogue, 2011) as well as Choquet (2008) and Choquet et al. (2009) for additional details. We also provide in Appendix C and Appendix D the R (R. Core Team, 2013) codes to fit the models described above.

### 2.4. Simulations

We conducted a simulation study to assess performance of two models: one accounting for misidentification only and one accounting for both misidentification and heterogeneity. First, we simulated occupancy data, including both unambiguous and ambiguous detections, assuming two classes of heterogeneity for false positive probability  $p_{10}$ . To characterize and compare heterogeneity among the scenarios considered, we define a heterogeneity coefficient as:

$$\eta = \frac{\sigma^2}{\mu(1-\mu)}$$

with the mean value of the heterogeneity parameter  $\mu = \pi p_{A10} + (1-\pi) p_{B10}$  and the variance between components  $\sigma^2 = \pi(p_{A10} - \mu)^2 + (1-\pi)(p_{B10} - \mu)^2$  (Dorazio and Royle, 2003; Cubaynes et al., 2012). We

**Table 1**

Results of the simulation study to assess the performance of the misidentification occupancy model accounting for heterogeneity (MMH) vs. the model without heterogeneity (MMO). The first column corresponds to the heterogeneity coefficient calculated with  $\pi$  the proportion of sites of class A and  $p_{A10}$  the probability of making false positive on sites of class A and  $p_{B10}$  the probability of making false positive on sites of class B. The differences of AIC ( $\Delta AIC$ ) between the two models, obtained from 200 simulations for each scenario, are provided. Estimation accuracy (RMSE) and relative bias for the occupancy probability are both provided as measures of model performance.

Heterogeneity coefficient	$\pi$	$p_{A10}$	$p_{B10}$	$\Delta AIC$	Sd ( $\Delta AIC$ )	RMSE( $\psi_1$ ) <sub>MMH</sub>	RMSE( $\psi_1$ ) <sub>MMO</sub>	Relative bias( $\psi_1$ ) <sub>MMH</sub>	Relative bias( $\psi_1$ ) <sub>MMO</sub>
0.24	0.2	0.1	0.7	6.66	8.62	0.09	0.05	6.35	4.28
0.49	0.5	0.1	0.8	28.15	13.61	0.05	0.10	3.04	12.00
0.53	0.8	0.1	0.9	45.59	19.58	0.05	0.12	2.43	12.23

considered three scenarios with increasing heterogeneity coefficient, by varying parameters  $\pi$  and  $p_{B10}$  (Table 1). Other parameters were held constant:  $p_{A10}$  was set at 0.1; the initial occupancy probability  $\psi_1$  was set at 0.8; probabilities of true positive  $p_{A11}$  and  $p_{B11}$  were both set at 0.5 and  $b$  was set at 0.7. For all simulation runs, we used 100 sites with 3 and 10 occasions. For each scenario, we simulated  $S = 200$  datasets, and for each dataset, fitted both models. Simulation and analyses were done in the software R (see Appendix C and Appendix D). We compared the two models’ performance using averaged AIC differences, calculated from the 200 repeated runs. We chose the AIC because it has been shown to be effective at selecting the number of classes in finite-mixture capture-recapture models (Cubaynes et al., 2012). For each model, we also calculated the relative bias defined as:

$$\frac{1}{S} \sum_{s=1}^S \frac{(\hat{\theta}^{(s)} - \theta)}{\theta}$$

and root mean square error (RMSE) for occupancy probability estimates:

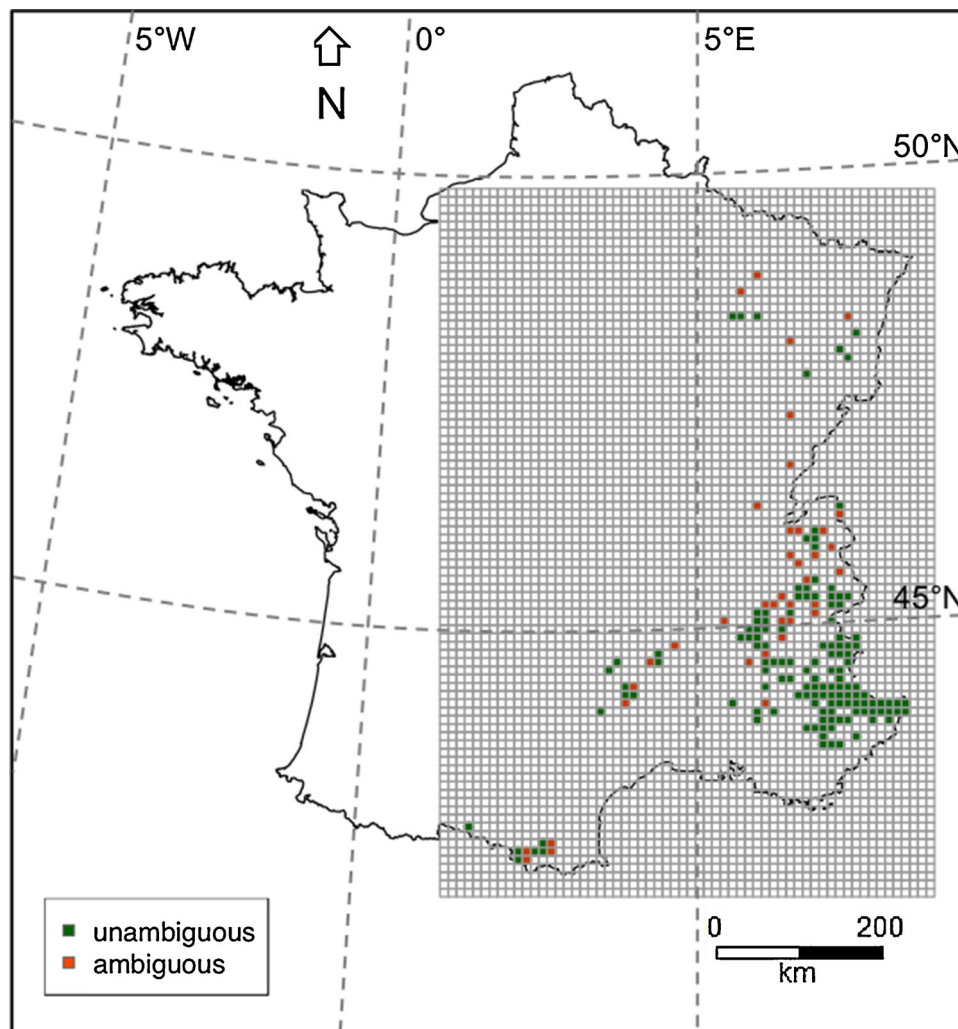
$$\sqrt{\frac{1}{S} \sum_{s=1}^S (\hat{\theta}^{(s)} - \theta)^2}$$

We performed a second simulation study, considering the same form and levels of heterogeneity, but applied to the true detection parameter  $p_{11}$  instead of the false positive detections parameter  $p_{10}$ . We tested three scenarios with increasing heterogeneity coefficient by varying parameters  $\pi$  and  $p_{B11}$ . Every other aspect of this simulation study was the same as in the first simulation study (Appendix E).

### 2.5. Application: wolf data

To illustrate use of our model accounting for both misidentification and heterogeneity, we analyzed wolves’ detection/non-detection data collected in France during the year 2013 (Louvrier et al., 2018). Signs of presence of the species such as tracks, scats, prey remains, dead wolves, camera trap photos or sightings are being collected thanks to a network of professional and non-professional observers (Duchamp et al., 2012). The data consisted of 250 unambiguous detections, 54 ambiguous detections and 12540 non-detections spread over a grid of 3211  $10 \times 10$  km cells (Fig. 1). To respect the closure assumption, sites were visited between December and March, which corresponds to a period between the two peaks of dispersal events, in spring and fall (Mech and Boitani, 2010). In a previous study, we found that variability in occupancy probabilities was mostly explained by site’s altitude, while detection probability was primarily driven by sampling effort, defined as the number of observers per site and per year (Louvrier et al., 2018). Here, we compared four different models, all of which included altitude as a covariate on occupancy parameter. A first model accounted for misidentification only without heterogeneity in the detection process (MMO); a second model accounted for misidentification with heterogeneity in both detection probabilities (MMH); in the last model, we accounted for some detection heterogeneity using the sampling effort covariate (on both  $p_{11}$  and  $p_{10}$ ) (MMS), instead of including a finite-mixture heterogeneity process. Sampling effort was indeed quite





**Fig. 1.** Map of the unambiguous detections (green) and ambiguous detections (red) cumulated for the year 2013. Sites were defined as  $10 \times 10$  km cells within a grid covering all detections (Louvrier et al., 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

heterogeneous across space, with areas around the Alps subject to much higher sampling effort than the rest of the study area. We expected sampling effort to capture most of the heterogeneity in the detection parameters, which would translate in close AIC values for MMH and MMS and a lower AIC value for MMO. Finally, we fitted a fourth model, including both the finite-mixture process (for unobserved heterogeneity) and the sampling effort covariate (MMHS). This last model allowed assessing the relative fraction of heterogeneity due to sampling effort.

Using the parameter estimates from MMH, we finally built a map depicting the estimated assigned classes of heterogeneity for the 3211 sites of the study area. This was done with the Viterbi algorithm (Rouan et al., 2009), an approach that allows estimation of latent states from HMMs. Although the Bayes' theorem could be used in this situation where no time series structure is involved, the Viterbi algorithm is a general approach that can be used in a dynamic occupancy framework.

### 3. Results

#### 3.1. Simulations

Results from the simulations with 10 occasions showed that when heterogeneity in false positive probability increased (coefficient  $\eta$  going from 0.24 to 0.53), the  $\Delta$ AIC between MMO and MMH ( $\Delta$ AIC = AIC<sub>MMO</sub>

– AIC<sub>MMH</sub>) increased from 6.66 (–10.23; 23.55) to 45.59 (7.21; 83.97). While both models showed low RMSE, in terms of occupancy estimation, MMH clearly outperformed MMO as heterogeneity increased. MMO produced increasingly biased parameters when heterogeneity increased while the bias in MMH always remained low (Table 1). We found similar results when we considered heterogeneity in the true detection probability  $p_{11}$ . MMH clearly outperformed MMO in terms of AIC, bias and RMSE as heterogeneity increased. The bias for MMO did not increase but remained important across the range of heterogeneity coefficients (Appendix E). Finally, with 3 occasions, MMH appeared to perform worse than MMO, highlighting the need to consider a minimal sampling effort to distinguish false positives and heterogeneity (Appendix F).

#### 3.2. Wolf case study

We found evidence for heterogeneity in the detection process (Table 2), with MMO having a much larger AIC (2209.49) value than MMH (2084.14). Most of this heterogeneity was explained by spatial variation in sampling effort, as suggested by the fact that MMS had a lower AIC value (2071.51) than MMH, but, even after accounting for sampling effort, there remained some unobserved heterogeneity, as evidenced by the fact that MMHS still had a lower AIC value (1953.26) than MMS.

**Table 2**

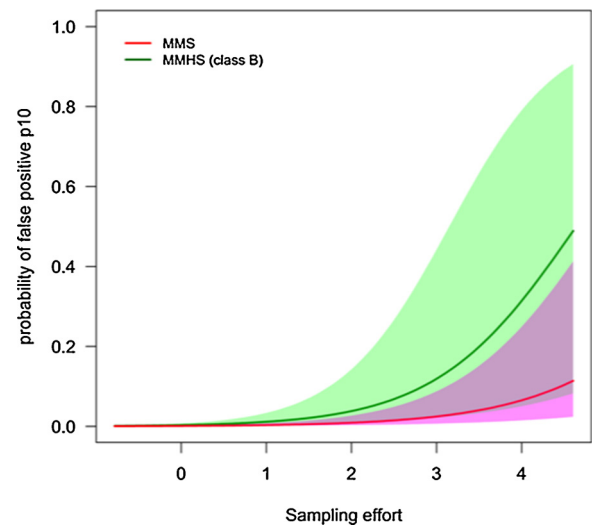
Estimated parameters for the model with misidentification and heterogeneity and sampling effort on detection probabilities ( $p_{A11}$ ,  $p_{B11}$ ,  $p_{A10}$  and  $p_{B10}$ ) (MMHS), the model with misidentification only with sampling effort on both detection probabilities ( $p_{11}$  and  $p_{10}$ ) (MMS), for the model with misidentification and heterogeneity (MMH) and the model with misidentification only (MMO). The Akaike Information Criterion (AIC) value is given for each model as well as the lower (CI-) and upper (CI+) limits of the 95% confidence interval.

Model with misidentification and heterogeneity with sampling effort on detection probabilities (MMHS)	AIC	1953.26	
<i>Parameter</i>	<i>Value</i>	<i>CI-</i>	<i>CI+</i>
Proportion of sites in class A $\pi$	0.70	0.62	0.78
Probability of occupancy $\psi$	0.05	0.03	0.10
Probability to classify a true-positive detection as unambiguous $b$	0.89	0.84	0.92
Model with misidentification only with sampling effort on both detection probabilities (MMS)	AIC	2071.51	
<i>Parameter</i>	<i>Value</i>	<i>CI-</i>	<i>CI+</i>
Probability of occupancy $\psi$	0.06	0.04	0.08
Probability to classify a true-positive detection as unambiguous $b$	0.91	0.87	0.94
Model with misidentification and heterogeneity (MMH)	AIC	2084.14	
<i>Parameter</i>	<i>Value</i>	<i>CI-</i>	<i>CI+</i>
Proportion of sites in class A $\pi$	0.81	0.75	0.86
Probability of occupancy $\psi$	0.03	0.02	0.06
Probability of false-positive detection in sites A $p_{A10}$	0.00	0.00	0.00
Probability of false-positive detection in sites B $p_{B10}$	0.00	0.00	0.00
Probability of true-positive detection in sites A $p_{A11}$	0.04	0.02	0.06
Probability of true-positive detection in sites B $p_{B11}$	0.56	0.47	0.64
Probability to classify a true-positive detection as unambiguous $b$	0.86	0.81	0.90
Model with misidentification only (MMO)	AIC	2209.49	
<i>Parameter</i>	<i>Value</i>	<i>CI-</i>	<i>CI+</i>
Probability of occupancy $\psi$	0.03	0.02	0.03
Probability of false-positive detection $p_{10}$	0.00	0.00	0.00
Probability of true-positive detection $p_{11}$	0.42	0.37	0.47
Probability to classify a true-positive detection as unambiguous $b$	0.91	0.86	0.94

Overall, all four models estimated a low occupancy probability (Table 2). All four models estimated a very low probability of false-positive detection  $p_{10}$  (Fig. 2). MMHS estimated that for 70% of sites,  $p_{10}$  was equal to zero, while for the remaining 30%  $p_{10}$  strongly increased with sampling effort. MMS results also suggested that  $p_{10}$  strongly increased with sampling effort. According to MMH, 81% of the sites had a value of  $p_{10}$  similar to the one estimated from MMO. For the remaining 19%  $p_{10}$  was equal to zero, indicating that virtually no false-positive errors occurred at these sites. As we could expect, both MMS and MMHS results suggested that true detection probability  $p_{11}$  strongly increases with sampling effort for both classes of sites. MMH estimated  $p_{11}$  quite low, at around 0.04 (0.02; 0.06) for 81% of the sites and high in 19% of the sites (Fig. 3). Finally, the sites with high detectability corresponded to sites with high sampling effort (Fig. 4).

#### 4. Discussion

While heterogeneity in detection probability has long been studied in the capture-recapture literature (review in Gimenez et al., 2017), less attention has been given to this issue in occupancy modeling (Miller et al., 2015). We developed single- (static) and multi-season (dynamic) occupancy models that account for both heterogeneity and false-positives, benefiting from the flexibility of HMM frameworks to decompose a complex likelihood structure in multiple simpler components more amenable to biological interpretation (Zucchini et al., 2016). Using simulations, we showed that, when ignored, detection heterogeneity induces biases in occupancy estimators. On a case study on wolves, we also found that finite-mixture models of detection could be used to



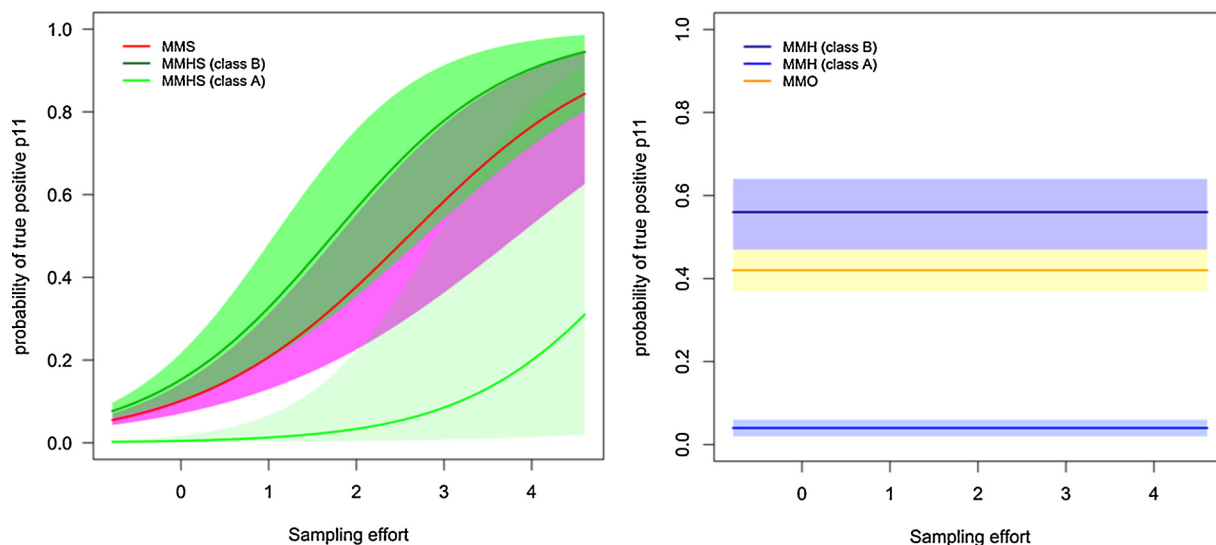
**Fig. 2.** Estimates of false positive detection from the model accounting for misidentification and sampling effort on the detection probability (MMS; red line) and the model accounting for misidentification and heterogeneity with sampling effort on detection probabilities (MMHS; green line); Lighter shades represent the estimated 95% confidence interval. The estimate of  $p_{10}$  for sites of class A was on average zero in the MMHS. In both models (MMHS and MMS) sampling effort had a positive effect on  $p_{10}$  in the MMS and on  $p_{B10}$  in the MMHS. When the sampling effort increased,  $p_{B10}$  increased but remained below 0.5. The probability  $p_{10}$  in the MMS model increased as well when sampling effort increased but  $p_{10}$  remained below  $p_{B10}$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

capture part of the heterogeneity due to variable sampling efforts. We note that, although such mixture models are very useful to account for unobserved detection heterogeneity, the associated parameters remain difficult to interpret (Gimenez et al., 2017).

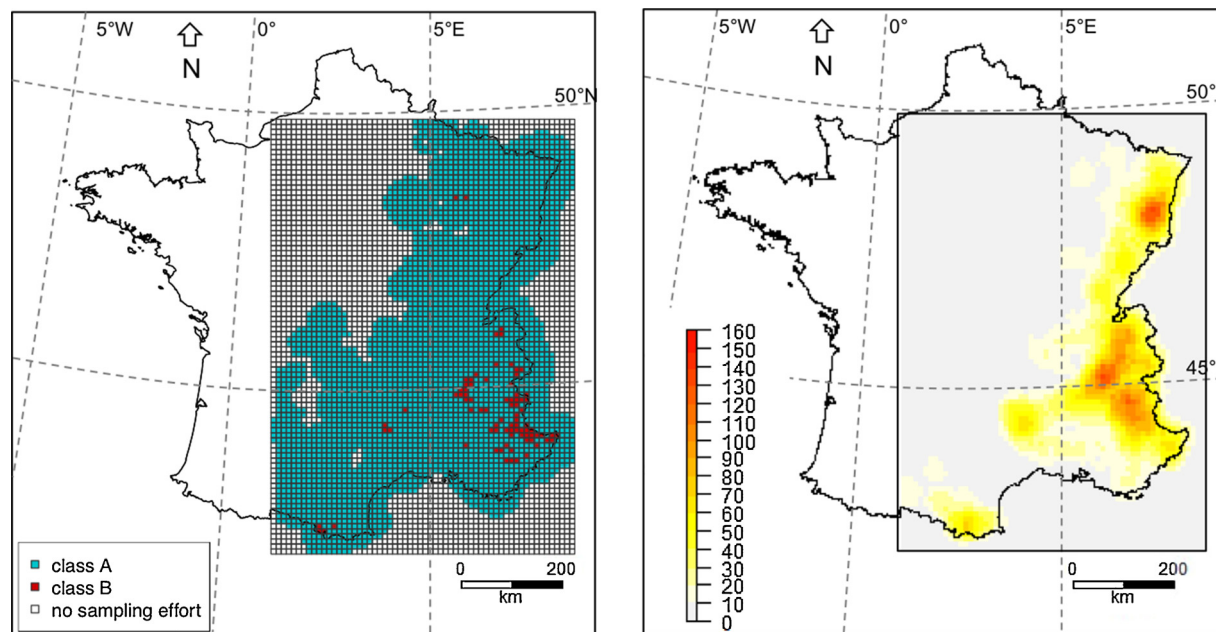
#### 4.1. Advantages of the HMM framework

The HMM formulation of occupancy models provides a great flexibility in the way detection heterogeneity and misidentification can be specified. First, the HMM formulation provides a straightforward mean to modelling the ecological and the observation processes separately (Pradel, 2005). Besides, each process can be split in multiple steps that match exactly the underlying, relevant ecological or observation events, making the modeling exercise and interpretation more intuitive to the biologist. This latter feature has been illustrated in several capture-recapture studies (Pradel, 2005; Sanz-Aguilar et al., 2011; Avril et al., 2012) but it is fairly new for occupancy models (Gimenez et al., 2014).

In this study, we focused on issues of heterogeneity in the detection process, but the framework provided can equally be used to model heterogeneity in occupancy probabilities (Gimenez et al., 2014). We may also allow a site to change heterogeneity status by introducing a transition parameter from class A to class B (Pradel, 2009; Gimenez et al., 2012). This model could be useful in the wolf case study to accommodate an increase in sampling effort over time and the possibility for some sites with low detectability to get a higher detectability. The use of finite mixtures allows capturing relevant levels of heterogeneity without the need to include a large number of explanatory covariates. It is however important to keep in mind that parameter redundancy can become an issue as we add more classes of heterogeneity and/or choose to apply finite mixtures on several parameters (Gimenez et al., 2014). For instance, if we wanted to consider classes of heterogeneity for all parameter (occupancy, true detection and false detection), our model could quickly become too complex (Gimenez et al., 2014). If parameter redundancy is suspected, it could be assessed using the methods that



**Fig. 3.** Estimates of true positive detection from the model accounting for misidentification and the standardized sampling effort (number of observers per site per year) on the detection probability (MMS; red line) and the model accounting for misidentification and heterogeneity with sampling effort on detection probabilities (MMHS; green lines) (left panel), the model accounting for misidentification and heterogeneity with sampling effort on detection probabilities for misidentification only (MMO; yellow line). Lighter shades represent the estimated 95% confidence interval. Sampling effort was defined as the number of observers per cell per year. In both models (MMHS and MMS) sampling effort had a positive effect on  $p_{11}$  in the MMS and on  $p_{A11}$  and  $p_{B11}$  in the MMHS. When sampling effort increased,  $p_{B11}$  increased as well, before almost reaching a plateau for the maximum values of sampling effort.  $p_{A11}$  increased as well but remained below 0.4 when sampling effort is at the maximum value. With (left panel) or without (right panel) sampling effort as a covariate on this probability,  $p_{A11}$  was much lower than  $p_{B11}$ . On the right panel, no covariate was used in the detection probabilities, which explains the flat lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



**Fig. 4.** Visualizing heterogeneity. Left: Map depicting the class of heterogeneity to which each site belongs to (obtained through the use of the Viterbi). Sites within the study area that are colored in white correspond to sites where sampling effort was null. Sites colored in blue are sites affiliated to class A, and sites colored in red are sites affiliated to class B. Right: Map of the sampling effort defined as the number of observers per site per year for the year 2013. The grey rectangle represents the study area where we defined our 10 x 10 km sites (Louvrier et al., 2018). Sites of class A, which correspond to the ones with a null false positive probability  $p_{A10}$  and a very low true detection probability  $p_{A11}$  are the sites represented in light blue where sampling effort is very low as well. In opposition, sites of class B seemed to be mainly where sampling effort was important. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

have been developed for this purpose (Choquet and Cole, 2012).

#### 4.2. Simulations

We considered three scenarios in which the heterogeneity coefficient increased with the proportion of sites of class A and the probability of false-positive detections in sites B. As expected, models ignoring heterogeneity produced biased and imprecise occupancy estimates when heterogeneity was actually increasing. Those results are the same whether heterogeneity occurs in probabilities of false positive detections or true detections. Previous studies have emphasized the importance of incorporating covariates, when available, on the true positive probability to avoid underestimating occupancy parameters (Miller et al., 2015). In absence of measurable candidate covariates, we recommend using the finite-mixture approach described in this paper. An alternative to finite mixtures is to consider a site random effect (Gimenez et al., 2014). An advantage of finite-mixture models is that they can easily be fitted in a frequentist or a Bayesian framework. In contrast, site random effects are naturally fitted in a Bayesian framework, but at the cost of higher computational burden; in the frequentist framework, site random effects require a specific, non-trivial treatment of the likelihood (e.g., Gimenez and Choquet, 2010).

#### 4.3. Wolf case study

We found strong evidence of among-site heterogeneity in the detection probability of wolves. This heterogeneity was mostly explained by spatial variation in sampling effort. As expected, the probability of true positive detection increased with sampling effort. In this study, more sampling effort occurs at the core of the species' distribution, around the Alps and in the North-Eastern part of France (Fig. 1). This variable effort is explained by the fact that in France, the first recolonizing wolves were detected in the Alps, before they started spreading out (Valière et al., 2003).

Average values of detection parameters estimated by the MMH were close to the average values estimated by the MMS and the MMHS, highlighting the similarities between these models. However, the MMH and MMS provided slightly different estimates of occupancy probability. AIC comparison between these two models revealed that sampling effort explains most of the variation in detection probabilities. A previous study (Louvrier et al., 2018) had also found strong support for this covariate, and the authors had shown that ignoring the effect of sampling effort leads to underestimating occupancy probabilities, especially at sites with low effort. Results from the MMHS confirm this hypothesis as the estimate of occupancy probability was close to the one provided by the MMS. Sampling effort is thus an important covariate to account for, but the fact that MMHS had the lowest AIC suggests that some unobserved detection heterogeneity remains. If sampling effort cannot easily be measured, models accounting for unobserved heterogeneity could be used as an alternative to control for detection variability and avoid estimation biases. Such an approach should prove especially useful for analyses of opportunistic monitoring data collected by large networks of citizens, which rely on protocols that rarely include explicit measures of sampling effort.

The fact that the estimated probability of false positive detection was low suggests that the continuous training, over the years, of the observers of the network (Duchamp et al., 2012) has been efficient. The low value of the false positive detection could also mean that the filtering process of observations was effective. Part of this filtering process consisted in rejecting detections that could be identified as false positives to avoid noise in the data. We can conclude that most false positives may very well have already been rejected during this filtering process. Based on this fact and the value of the probability to classify a true detection as unambiguous  $b$  we could conclude that most of the ambiguous data were actually true positive detections, which could be considered as unambiguous detections and analyzed with standard

occupancy models. However, running the model accounting for false positives would still be a necessary step to ensure that false positive probability is extremely low, before we decide to treat ambiguous data as true detections.

In our wolf study, winter observations consisted mostly of tracks found in the snow, scats, carcasses and camera trap photographs (Duchamp et al., 2012), which were all observations that could easily be verified. However, on the colonization front, a larger proportion of detections consisted of visual sightings, and because these types of data could not be verified they were therefore classified as ambiguous. Here, integrating these ambiguous data is especially interesting because it brings new information about the wolf distribution on the colonization front. These data could thus provide new insights in the context of managing an expanding protected species where new identified sites could help understanding the processes underlying the recolonization of wolves (Guillera-arroita et al., 2015).

We found from the Viterbi algorithm that the sites having the higher true positive probability were those where the sampling effort was high. However, the fact that the estimated number of sites of class B from the Viterbi algorithm is lower than what the MMH estimated can be due to the low value of the occupancy probability. This low occupancy estimate can lead to a greater uncertainty in assessing the class of a site (Rouan et al., 2009). Despite this fact, it is possible to see the link between sampling effort and the two classes of heterogeneity. Sites belonging to the heterogeneity class A, which were primarily found on the colonization front of the species (Louvrier et al., 2018), had a lower detection probability  $p_{11}$  than sites of class B. This strongly suggests that the species is less likely to be detected on the colonization front, where new conflicts with human activities can arise.

In conclusion, we recommend devoting efforts in the monitoring process to minimize heterogeneity across sites, and possibly identifying and measuring covariates that may affect detection probability such as the sampling effort. If not possible, we recommend using occupancy models accounting for detection heterogeneity if covariates possibly explaining site-to-site variation cannot be measured in the field. The HMM formulation we propose allows an easy implementation of these models.

#### Data accessibility

We provide the scripts to simulate the data in the Appendix B and Appendix C as well as the wolf data in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.g9s1d>

#### Acknowledgements

We gratefully acknowledge the help of people who have collaborated with the wolf monitoring network supervised by the French game and wildlife agency (ONCFS). We warmly thank Christophe Duchamp for his help and for making the data available to us. We thank the Montpellier University and the ONCFS for a PhD grant to the first author.

#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2018.09.002>.

#### References

- Avril, A., Letty, J., Pradel, R., Léonard, Y., Santin-Janin, H., Pontier, D., 2012. A multi-event model to study stage-dependent dispersal in radio-collared hares: when hunting promotes costly transience. A multi-event model to study stage-dependent dispersal in radio-collared hares : when hunting promotes costly transience. *Ecology* 93, 1305–1316.
- Bailey, L.L., Mackenzie, D.L., Nichols, J.D., 2014. Advances and applications of occupancy



- models. *Methods Ecol. Evol.* 5, 1269–1279.
- Chambert, T., Miller, D.A.W., Nichols, J.D., 2015. Modeling false positive detections in species occurrence data under different study designs. *Ecology* 96, 332–339.
- Choquet, R., 2008. Automatic generation of multistate capture-recapture models. *Can. J. Stat.* 36, 43–57.
- Choquet, R., Cole, D.J., 2012. Mathematical Biosciences A hybrid symbolic-numerical method for determining model structure. *Math. Biosci.* 236, 117–125.
- Choquet, R., Nogue, E., 2011. E-SURGE 1.8 User's Manual. CEFÉ, Montpellier, France.
- Choquet, R., Rouan, L., Pradel, R., 2009. Program E-surge: a software application for fitting multievent models. In: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds.), *Modeling Demographic Processes in Marked Populations*. Springer US, Boston, MA, pp. 845–865.
- Clement, M.J., Rodhouse, T.J., Ormsbee, P.C., Szwczak, J.M., Nichols, J.D., 2014. Accounting for false-positive acoustic detections of bats using occupancy models. *J. Appl. Ecol.* 51, 1460–1467.
- Cubaynes, S., Lavergne, C., Marboutin, E., Gimenez, O., 2012. Assessing individual heterogeneity using model selection criteria: how many mixture components in capture-recapture models? *Methods Ecol. Evol.* 3, 564–573.
- Dorazio, R.M., Royle, J.A., 2003. Mixture models for estimating the size of a closed population when capture rates vary among individuals. *Biometrics* 59, 351–364.
- Duchamp, C., Boyer, J., Briaudet, P.E., Leonard, Y., Moris, P., Bataille, A., Dahier, T., et al., 2012. A dual frame survey to assess time- and space-related changes of the colonizing wolf population in France. *Hystrix* 23, 14–28.
- Ferguson, P.F.B., Conroy, M.J., Hepinstall-Cymerman, J., 2015. Occupancy models for data with false positive and false negative errors and heterogeneity across sites and surveys. *Methods Ecol. Evol.* 6, 1395–1406.
- Gimenez, O., Choquet, R., 2010. Individual heterogeneity in studies on marked animals using numerical integration : capture – recapture mixed models. *Ecology* 91, 951–957.
- Gimenez, O., Lebreton, J., Gaillard, J., Choquet, R., Pradel, R., 2012. Estimating demographic parameters using hidden process dynamic models. *Theor. Popul. Biol.* 82, 307–316.
- Gimenez, O., Blanc, L., Besnard, A., Pradel, R., Doherty, P.F.J., Marboutin, E., Choquet, R., 2014. Fitting occupancy models with E-SURGE : hidden Markov modelling of presence – absence data. *Methods Ecol. Evol.* 5, 592–597.
- Gimenez, O., Cam, E., Gaillard, J., 2017. Individual heterogeneity and capture-recapture models: what, why and how? *Oikos* 127 (5), 664–686.
- Guillera-arroita, G., Lahoz-monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., Mccarthy, M.A., et al., 2015. Is my species distribution model fit for purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.* 24, 276–292.
- Guillera-Arroita, G., 2017. Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography* 40, 281–295.
- Louvrier, J., Duchamp, C., Lauret, V., Marboutin, E., Cubaynes, S., Choquet, R., Miquel, C., et al., 2018. Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data. *Ecography* 41, 647–660.
- Mackenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207.
- Mackenzie, D.I., Bailey, L.L., Nichols, J.D., 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *J. Anim. Ecol.* 73, 546–555.
- Mackenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. *Occupancy Estimation and Modeling*. Academic Press.
- Mackenzie, D.I., Bailey, L.L., Hines, J.E., Nichols, J.D., 2011. An integrated model of habitat and species occurrence dynamics. *Methods Ecol. Evol.* 2, 612–622.
- McClintock, B.T., Bailey, L.L., Pollock, K.H., Simons, T.R., 2010. Unmodeled observation error induces bias when inferring patterns and dynamics of species occurrence via aural detections. *Ecology* 91, 2446–2454.
- Mech, L.D., Boitani, L., 2010. *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.
- Miller, J.R.B., 2015. Mapping attack hotspots to mitigate human–carnivore conflict: approaches and applications of spatial predation risk modeling. *Biodivers. Conserv.* 24, 2887–2911.
- Miller, D.A., Nichols, J.D., McClintock, B.T., Grant, E.H.C., Bailey, L.L., Weir, L.A., 2011. Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. *Ecology* 92, 1422–1428.
- Miller, D.A.W., Nichols, J.D., Gude, J.A., Rich, L.N., Podruzny, K.M., Hines, J.E., Mitchell, M.S., 2013. Determining occurrence dynamics when false positives occur: estimating the range dynamics of wolves from public survey data. *PLoS One* 8.
- Miller, D.A.W., Bailey, L.L., Grant, E.H.C., McClintock, B.T., Weir, L.A., Simons, T.R., 2015. Performance of species occurrence estimators when basic assumptions are not met: a test using field data where true occupancy status is known. *Methods Ecol. Evol.* 6, 557–565.
- Perc, M., 2011. Does strong heterogeneity promote cooperation by group interactions? *New J. Phys.* 13, 123027.
- Pillay, R., Miller, D.A.W., Hines, J.E., Joshi, A.A., Madhusudan, M.D., 2014. Informant interviews. *Divers. Distrib.* 20, 223–235.
- Pledger, S., Phillpot, P., 2008. Using mixtures to model heterogeneity in ecological capture-recapture studies. *Biometr. J.* 50, 1022–1034.
- Pradel, R., 2005. Multievent : an extension of multistate capture – recapture models to uncertain states. *Biometrics* 61, 442–447.
- Pradel, R., 2009. The stakes of capture–recapture models with state uncertainty. *Modeling Demographic Processes in Marked Populations*. Springer, Boston, MA, pp. 781–795.
- Rabiner, L.R., 1989. A tutorial on hidden Markov models and selected applications in speech recognition. *Proc. IEEE* 77, 257–286.
- Rouan, L., Gaillard, J.-M., Guédon, Y., Pradel, R., 2009. Estimation of lifetime reproductive success when reproductive status cannot always be assessed. *Modeling Demographic Processes in Marked Populations*. Springer, pp. 867–879.
- Royle, J.A., 2006. Site occupancy models with heterogeneous detection probabilities. *Biometrics* 62, 97–102.
- Royle, J.A., Link, A.W., 2006. Generalized site occupancy models allowing for false positive and false negative errors. *Ecology* 87, 835–841.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84, 777–790.
- Sanz-Aguilar, A., Tavecchia, G., Genovart, M., Igual, J.M., Oro, D., Rouan, L., Pradel, R., 2011. Studying the reproductive skipping behavior in long-lived birds by adding nest inspection to individual-based data. *Ecol. Appl.* 21, 555–564.
- Team, R., 2013. R development core team. *RA Lang. Environ. Stat. Comput.* 55, 275–286.
- Valière, N., Fumagalli, L., Gielly, L., Miquel, C., Lequette, B., Pouille, M.-L., Weber, J.-M., et al., 2003. Long-distance wolf recolonization of France and Switzerland inferred from non-invasive genetic sampling over a period of 10 years. *Anim. Conserv.* 6, 83–92.
- Warton, D.I., Stoklosa, J., Guillera-arroita, G., Mackenzie, D.I., Welsh, A.H., 2017. Graphical diagnostics for occupancy models with imperfect detection. *Methods Ecol. Evol.* 8, 408–419.
- Zucchini, W., MacDonald, I.L., Langrock, R., 2016. *Hidden Markov Models for Time Series: An Introduction Using R*. CRC press.