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Accounting for false positive detection error induced by transient individuals

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Abstract

Context. In metapopulations, colonisation is the result of dispersal from neighbouring occupied patches, typically juveniles dispersing from natal to breeding sites. When occupancy dynamics are dispersal driven, occupancy should refer to the presence of established, breeding populations. The detection of transient individuals at sites that are, by definition, unoccupied (i.e. false positive detections), may result in misleading conclusions about metapopulation dynamics. Until recently, the issue of false positives has been considered negligible and current efforts to account for such error have been restricted to the context of species misidentification. However, the detection of transient individuals visiting multiple sites while dispersing is a distinct source of false positives that can bias estimates of occupancy because visited sites do not contribute to metapopulation dynamics in the same way as do sites occupied by established, reproducing populations. Although transient-induced false positive error presents a challenge to occupancy studies aiming to account for all sources of detection error and estimate occupancy without bias, accounting for it has received little attention.

Aims. Using a novel application of an existing occupancy model, we sought to account for false positives that result from transient individuals being observed at truly unoccupied sites (i.e. where no establishment has occurred).

Methods. We applied a Bayesian multi-season occupancy model correcting for false negative and false positive errors, to 3 years of detection or non-detection data from a metapopulation of water voles, *Arvicola amphibious*, in which both types of patch-state misclassification are suspected.

Key results. We provide evidence that transient individuals can cause false positive detection errors. We then demonstrate the flexibility of the occupancy model to account for both false negative and false positive detection errors beyond the typical application to species misidentification. Accounting for both types of observation error reduces the bias in estimates of occupancy and avoids misleading conclusions about the status of (meta) populations by allowing for the distinction to be made between resident and transient occupancy.

Conclusion. In many species, transience may result in patch-state misclassification which needs to be accounted for so as to draw correct inference about metapopulation status. Making the distinction between occupancy by established populations and visitation by transients will influence how we interpret patch occupancy dynamics, with important implications for the management of wildlife.

Implications. The ability to estimate occupancy free of bias induced by false positive detections can help ensure that downward trends in occupancy are detected despite such declines being accompanied by increasing frequency of transients associated with, for example, reductions in mate availability or failure to establish. Our approach can be applied to any occupancy study in which false positive detections are suspected because of the behaviour of the focal species.

Additional keywords: Bayesian, colonisation, conservation, extinction, metapopulation, site-occupancy model, utilisation, water vole.

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Introduction

The successful monitoring and management of threatened species relies heavily on the ability to correctly assess the true status of a species and hence make predictions about likely persistence. 'Site occupancy' is one measure of a species' status that is widely used in ecological studies and conservation programs (MacKenzie *et al*. 2006; Royle and Dorazio 2008). Using data collected from multiple site visits, site occupancy models formally account for imperfect detection (MacKenzie *et al*. 2002, 2006; Royle *et al*. 2005; Royle and Kéry 2007) and have contributed greatly to our ability to understand and reduce bias in species assessments, including the study of patch-occupancy dynamics in classic metapopulations (Moilanen 2004; Harrison *et al*. 2011; Risk *et al*. 2011). One key mechanism underpinning patch-occupancy dynamics in metapopulations is the colonisation of empty patches, typically by dispersing juveniles produced by established breeding populations. Therefore, consistent with the classical view of metapopulations, occupancy should refer to sites with established, breeding populations because only such sites are likely to contribute to patch-occupancy dynamics. The establishment of a breeding population requires that, during a transient phase in which potentially many sites may be sampled, individuals of the opposite sex meet and settle. This presents an interesting challenge in occupancy studies because signs left by dispersing individuals during dispersal before settlement may result in observers correctly recording positive detections but erroneously classifying the sites as occupied under our interpretation of 'resident' occupancy above (i.e. false positives).

Standard (false negative only) occupancy models typically assume that a species cannot be observed at a site that is, in truth, unoccupied (MacKenzie and Royle 2005). However, it is evident that, in reality, false positive observations are common and non-trivial (Royle and Link 2006; McClintock *et al*. 2010*a*; Miller *et al*. 2011). Until now, studies addressing the issue of false positives have done so exclusively in the context of species misidentification, a result of either animals being difficult to distinguish from closely related co-occurring species (McClintock *et al*. 2010*a*, 2010*b*; Miller *et al*. 2011), or high variability in observer identification skills (Royle and Link 2006; Fitzpatrick *et al*. 2009). Arguably, however, an equally common source of false-positive observation error is the detection of evidence that an individual is only temporarily present at, or had at some earlier point temporarily visited, a site that is, in truth, unoccupied because the presence of that individual is transient rather than permanent. A consequence of transient-induced false positives is that sites can be mistakenly classified as occupied when in truth no breeding population is present. This is particularly relevant when assessing the occupancy status of species of conservation concern that occur at relatively low densities because such individuals are subject to a range of additional pressures associated with behavioural changes. Specifically, the difficulty associated with locating a suitable mate at low densities may result in extended transient or dispersive stages (Courchamp *et al*. 1999; Clobert *et al*. 2004) or, in extreme cases, in the complete failure of dispersing individuals to settle (Stephens and Sutherland 1999; Fisher *et al*. 2009). MacKenzie *et al*. (2004) suggested that if movement into and out of sites occurs at random, the interpretation of occupancy must be altered to instead mean utilisation, which, in the presence of false positive observations, relates to sites that are both occupied by established populations and those that have been visited only by transients. When studying colonisation–extinction dynamics in a metapopulation context, i.e. when colonisation is modelled as a function of surrounding sites, with established populations producing potentially colonising offspring (Moilanen and Nieminen 2002), utilisation may not be fit for purpose because treating sites without established populations as occupied will influence estimates of colonisation rates and bias estimates of dispersal. This will affect our ability to evaluate the true status and extinction risk of a (meta) population and, therefore, the choice of whether to focus on utilisation or resident occupancy is an important one (see also McClintock *et al*. 2010*a*).

In an attempt to account for both types of detection error, Royle and Link (2006) generalised the site occupancy model to allow for both false-negative and false-positive observation errors. Through simulations, they demonstrated that even very low rates of false positive error (0.1) can result in substantially biased estimates of occupancy (36%; see table 3 in Royle and Link 2006). A growing number of empirical examples are in general agreement regarding the importance of accounting for the misclassification of site-occupancy states resulting from species misidentification (McClintock *et al*. 2010*a*; Miller *et al*. 2011; Molinari-Jobin and Kéry 2012; but see Fitzpatrick *et al*. 2009). However, the model can also be used to account for site misclassification as a result of transient-induced false-positive error rates, whereby a positive detection of sign left by a transient individual at an 'empty' site is deemed a false positive observation or misclassification. We propose that where species identification is unambiguous, i.e. the probability of species misidentification can be assumed to be 0, such as with camera trapping or characteristic signs, and where movements that result in deposition of signs at unoccupied sites approaches a random process, the parameter for quantifying false positives (*sensu* Royle and Link 2006) allows for positive detections that are false only in the sense that the site it is not occupied by breeding individuals. Allowing for both types of observation error, when they are suspected, can reduce the bias in estimates of important ecological processes such as occupancy, and rates of colonisation and extinction and, moreover, avoid ill-informed recommendations for the conservation and management of the focal species or population.

We apply the generalised occupancy model of Royle and Link (2006), which allows for both false-negative and false-positive observation errors, to detection or non-detection data from a metapopulation of water voles, *Arvicola amphibius* (Linnaeus, 1758), resulting from several repeated site visits in each of 3 years. We demonstrate that estimates of occupancy and detection probabilities differ substantially depending on whether or not false positives are accounted for and that models that allow for false positives are a substantially better fit to the data than models ignoring false positives.

Methods

State–space occupancy model allowing for false positives

Here, we describe a dynamic site-occupancy model that allows for false-positive and false-negative errors. This model is a multi-year extension of the misclassification (false positive) model of Royle and Link (2006) implemented in a Bayesian setting (alternatively, it can be viewed as an extension of the model of Royle and Kéry (2007) relaxing the restriction that the probability of false positive observations equals zero). The model has five key parameters, $\theta = p, fp, \psi_1, \gamma$ or φ, that, with the exception of ψ_1, can either vary with time (subscript t) or else be time invariant (subscript **.**). The parameter ψ_1 is the expected proportion of patches occupied in the initial year. Patch-state transitions are governed by γ, the colonisation probability, and φ, the probability of population or patch persistence (also termed survival). Site-occupancy studies often focus on estimating patch extinction probability, ε, which is simply the complement of φ, as follows: $\varepsilon = 1 - \varphi$. The classification parameters relating to the observation errors are p, the probability of detecting a species at a truly occupied site, and fp, the probability of a positive detection when, in truth, the site is empty. As demonstrated by Royle and Kéry (2007), this model can be naturally formulated as a state–space model where the latent occupancy states $z_{i,t}$ ($z_{i,t} = 1$ if Site i is occupied in Year t, and 0 otherwise) in the initial period is described as

$$z_{i,1} \sim \text{Bernoulli } (\psi_1). \tag{1}$$

In all subsequent periods, the occupancy state is conditional on the occupancy state in the previous period, $z_{i,t-1}$, and is a function of the transition probability φ_{t-1} when occupied, and γ_{t-1} when empty, as follows:

$$z_{i,t}|z_{i,t-1} \sim \text{Bernoulli } (z_{i,t-1}\varphi_{t-1} + [1 - z_{i,t-1}]\gamma_{t-1}). \tag{2}$$

The observation process relates the truth to the data such that

$$y_{i,t}|z_{i,t} \sim \text{Binomial } (J_{i,t},\ z_{i,t}p_t + (1 - z_{i,t})fp_t), \tag{3}$$

which requires only the site- and year-specific detection data, $y_{i,t}$, which summarise the total number of positive visits to the ith site in the tth year across a total of $J_{i,t}$ visits. Notably, the false-positive error rate applies only to sites that are in truth unoccupied ($z_{i,t} = 0$) and our formulation includes the reasonable restriction that $p > fp$ (see Royle and Link 2006 for discussion).

Given a finite sample of sites, say S, the proportion of occupied sites in each year is derived from the latent state variables (Royle and Kéry 2007), as follows:

$$\psi_t^{fs} = \frac{1}{S}\sum_i z_{i,t}.$$

This model can then be compared with the standard occupancy model, which is identical in all respects except that the false positive is fixed to take the value 0 (see MacKenzie *et al*. 2003; Royle and Kéry 2007). Under this model, the proportion of occupied sites π_t^{fs} can be calculated in the same way, but in the presence of potential random movements into and out of sites, is interpreted as proportional utilisation (the proportion of sites used by the species).

An important caveat of this method is that the false-positive model is in fact indistinguishable from some models that account for among-site variability in detection probability (detection heterogeneity from here; MacKenzie *et al*. 2006) and, just as ignoring false positives leads to overestimates of occupancy, so ignoring the existence of detection heterogeneity will lead to the underestimation of occupancy. Therefore, the use and successful interpretation of results from this method requires detailed knowledge about the data generating process *a priori*. Specifically, we assume that there is no or negligible detection heterogeneity, an assumption which we consider valid in our situation with detection or non-detection data that are binary for each visit, but which may not always be so defensible.

Case study: the Assynt water vole metapopulation

Water voles are large rodents (up to 300 g) that, in Assynt, north-western Scotland (58°8′N, 5°1′W), occupy discrete narrow vegetated stretches of riparian habitat with slow-flowing water which is surrounded by unsuitable heather moorland. In 1999, the ~140-km^2 study area was mapped and all suitable habitat patches (sites hereafter) were identified. Sites are widely distributed across the study area and are, on average, 0.92 km long (range: 0.16–3.00 km), with the mean distance to the nearest occupied sites between 2009 and 2011 being 0.526 km (range: 0.088–1.856 km). Although sites have been surveyed every summer for the presence of water vole signs since 1999, multiple visits to sites began only in 2009.

Water voles are elusive, live at low densities (median total colony size: 4, range: 1–37) and are rarely observed directly. The presence or absence of water voles is therefore determined by the detection or non-detection, during each of multiple site visits, of highly distinctive latrines that are composed of pellets deposited repeatedly and prominently on emergent rocks or ‘beaches’. Latrines are used to mark territories at sites occupied by established colonies, although, given that they are a highly dispersive species (Lambin *et al*. 2012; Sutherland *et al*. 2012), are sometimes observed at very low frequencies at unoccupied sites (Woodroffe and Lawton 1990). In Appendix S1 (available in the Supplementary Material for this paper), we provide evidence that fewer latrines are found at sites that are more likely to be false positives. Moreover, in Assynt, there are no co-occurring species that leave similar signs or markings and, therefore, when detected, water vole signs are identified with considerable confidence. The focus in the present study was to account for sites that were visited by transients and, therefore, not occupied according to our definition of occupancy, i.e. they are false positives. Occupancy states are therefore not regarded as certain, although sites with just a single positive visit are regarded as more likely to be false positive detections of transient individuals than are sites that have two or three positive visits (see also Appendix S1).

Surveys were carried out during the water vole breeding season, over 6 weeks in July and August, when voles establish and defend territories and, therefore, when latrines are used for marking and are most frequent. Repeated visits were separated by no more than 2 weeks (see Sutherland *et al*. (2012) for a full description of the water vole metapopulation and data collection). Like for many site-occupancy studies, our data are binary detection or non-detection data, with no auxiliary information, and so, retrospective classification of observations into multiple states is not possible as is required by the multi-state modelling approach that could otherwise be used to characterise two (or more) types of occupancy, i.e. true occupancy and transient occupancy (Nichols *et al*. 2007; MacKenzie *et al*. 2009; see Discussion), is not possible. However, we note that in 2011 the number of latrines observed at each site was recorded which has the potential to provide a means of making patch-state categorisations (Appendix S1).

We fitted the false-positive dynamic site-occupancy model to detection histories from multiple visits (J = between 2 and 4 within-season visits) to 102 sites known to have been occupied at least once since 1999 (I = 102 sites) in each summer from 2009 to 2011 ($T = 3$ years). We considered 16 candidate models, containing all combinations of time invariant and time-varying parameters (Table 1). So as to compare estimates of occupancy (ψ_t as estimated under the false positive model) with estimates of utilisation (π_t as estimated under the false negative-only model in which $fp = 0$), we fitted a further eight models containing all combinations of time-invariant and time-varying parameters, but with the restriction that $fp = 0$ (*sensu* MacKenzie *et al*. 2003; Table 1). All models were fitted in OpenBUGS (Lunn *et al*. 2009) called from R (R Core Team 2012), using the package R2OpenBUGS (Sturtz *et al*. 2005). BUGS model code is available in the Supplementary Material for this paper. For each model, we calculated the deviance information criterion (DIC), and the corresponding DIC differences (ΔDIC) and model weights (ω) (Spiegelhalter *et al*. 2002). We note that there are issues associated with the use of DIC for models with latent variables (Celeux and Forbes 2006) and so, for comparison, we fitted three single-season occupancy models using the R code provided in Royle and Link (2006). This approach uses maximum likelihood and provides AIC values which confirmed support for a model that accounts for false positives over one that constrains the false positive rate to be 0 (Appendix S1). Model weights (based on DIC) were then used to discriminate between models and also in the model averaging process. We used flat priors (uniform on the interval [0, 1]) for all parameters except for the classification parameters p and fp for which we used a uniform prior for $1 \geq p \geq 0.5$ in combination, with a uniform prior for $0.5 > fp \geq 0$. The choice of 0.5 as a separating barrier between p and fp was made after preliminary analysis indicated this would not unduly restrict the posterior distribution of either parameter.

Table 1. Candidate model list showing model parameterisation, the number of parameters (*K*), values of deviance information criterion (DIC) and their differences from the model with most support (ΔDIC) used for model selection and ω, model weights used for model averaging

$DIC_{fp} = 0$ shows the DIC values for equivalent models, including the restriction $fp = 0$, i.e. not accounting for false positives. When fp is restricted to 0, models that differ only in the parameterisation of fp become identical and are denoted by '–'. Models in bold received most support in both $fp \neq 0$ and $fp = 0$ parameterisations of the model and were used for model averaging using the inclusion cut-off $\omega > 0.01$

Model	Description	*K*	DIC	ΔDIC	ω	$DIC_{fp} = 0$
M1	ψ_1 φ(.) γ(.) *p*(.) *fp*(.)	5	667.63	17.29	0	771.51
M2	ψ_1 φ(.) γ(.) *p*(.) *fp*(t)	7	665.37	15.04	0	–
M3	ψ_1 φ(.) γ(.) *p*(t) *fp*(.)	7	690.61	40.28	0	783.23
M4	ψ_1 φ(.) γ(.) *p*(t) *fp*(t)	9	670.10	19.77	0	–
M5	ψ_1 φ(.) γ(t) *p*(.) *fp*(.)	6	671.29	20.96	0	754.56
M6	ψ_1 φ(.) γ(t) *p*(.) *fp*(t)	8	661.37	11.04	0	–
M7	ψ_1 φ(.) γ(t) *p*(t) *fp*(.)	8	669.84	19.51	0	747.13
M8	ψ_1 φ(.) γ(t) *p*(t) *fp*(t)	10	675.58	25.25	0	–
M9	**ψ_1 φ(t) γ(.) *p*(.) *fp*(.)**	**6**	**653.37**	**3.04**	**0.18**	**702.79**
M10	ψ_1 φ(t) γ(.) *p*(.) *fp*(t)	8	664.01	13.68	0	–
M11	ψ_1 φ(t) γ(.) *p*(t) *fp*(.)	8	664.84	14.51	0	715.50
M12	ψ_1 φ(t) γ(.) *p*(t) *fp*(t)	10	666.93	16.60	0	–
M13	**ψ_1 φ(t) γ(t) *p*(.) *fp*(.)**	**7**	**650.33**	**0**	**0.80**	**695.11**
M14	ψ_1 φ(t) γ(t) *p*(.) *fp*(t)	9	660.86	10.53	0	–
M15	ψ_1 φ(t) γ(t) *p*(t) *fp*(.)	9	658.70	8.37	0.01	703.98
M16	ψ_1 φ(t) γ(t) *p*(t) *fp*(t)	11	667.33	17.00	0	–

Results

Accounting for both types of observation error (false positive and false negative observations) systematically provided better fitting models than those that force the condition $fp = 0$ (Table 1). When accounting for false positives, two models received substantial support and, therefore, using the cut-off of $\omega > 0.01$, we used model averaging to account for model uncertainty (Table 1). The model-averaged marginal posterior distribution of each parameter was computed as the weighted average of the model-specific posterior using the DIC model weights (ω, Table 1). All parameter estimates reported below are model-averaged posterior means accompanied by, in parentheses, Bayesian 95% credible intervals. We found most support for models in which γ, the colonisation probability, and φ, the probability that an occupied patch persists, were year specific, whereas the detection probability, p, and the false positive misclassification rate, fp, were constant over time (Table 2). Patch occupancy, ψ_t^{fs}, as estimated by the false positive model, increased between years from 0.26 (0.17–0.37) in 2009 to 0.46 (0.35–0.57) in 2010 and was highest in 2011 at 0.68 (0.56–0.79). Moreover, the estimated underlying probability of occupancy in the first year, ψ_1, was 0.27 (0.17–0.37). The detection probability and the false-positive classification rate were $p_{\bullet} = 0.87$ (0.82–0.92) and $fp_{\bullet} = 0.12$ (0.08–0.16), respectively, i.e. they were constant across time. Colonisation probability, γ, was 0.37 (0.23–0.49) for the transition 2009→2010 and 0.46 (0.33–0.67) for the transition 2010→2011, whereas extinction probabilities (1 – φ) were 0.28 (0.11–0.48) for the transition 2009→2010 and 0.08 (0.01–0.21) for the transition 2010→2011.

The posterior mean of the detection probability parameter was lower under the false negative only ($fp = 0$) model than under the model where $fp > 0$, this being another contributing factor to the difference in posterior mean values for occupancy between the two models (ψ_t^{fs} vs π_t^{fs} in Table 2). In fact, estimates of occupancy under the standard model ($fp = 0$) were higher in all years than those estimated under the false positive model (ψ_t^{fs} vs π_t^{fs} in 2009: 0.26 vs 0.51; in 2010: 0.46 vs 0.65; and in 2011: 0.68 vs 0.86; Table 2, Fig. 1). The posterior distributions of the patch persistence and colonisation rates were less affected by whether or not false positive errors are allowed for, although there is a tendency for them to take larger values when false positives were ignored (Table 2).

Discussion

The issue of false positive detection in occupancy studies has until recently been considered a negligible or non-existent problem. It is now becoming apparent that even at low levels, failure to account for false positives can introduce substantial bias into estimates of both detection and occupancy (Royle and Link 2006). However, until now false positives have been investigated solely in the context of correcting for species misidentification (Royle and Link 2006; McClintock *et al*. 2010*a*, 2010*b*). Here, we have provided evidence of an alternative and arguably equally common source of false positive observations; the detection of transient, highly mobile or dispersive individuals at sites in which they do not settle or establish, and which can thus be considered to be in truth unoccupied. Moreover, using a novel application of an occupancy model that accounts for both false

Table 2. Summary table of posterior mean parameter estimates with, in parenthesis, 95% Bayesian credible intervals

For the model that allows both false positive and false negative errors ($fp \neq 0$), we provide the model averaged parameter summaries ('averaged') and estimates from the models used for model averaging (see Table 1). For comparison, we also provide model-averaged parameter estimates from the false negative-only model $M_{fp=0}$. The direction of bias in parameter estimates from model $M_{fp=0}$ is illustrated using arrows, where ↑denotes an upward bias, ↓ denotes a downward bias and ↔ denotes negligible difference. § parameter is π for model $M_{fp=0}$

Parameter	$M_{fp} \neq 0$			$M_{fP}=0$	Bias
	Averaged	*M9* ω = *0.18*	*M13* ω = *0.80*	*M13*	
ψ_1 §	0.27 (0.17–0.37)	0.26 (0.17–0.36)	0.27 (0.18–0.37)	0.51 (0.41–0.61)	↑
ψ^{fs}_{2009} §	0.26 (0.17–0.37)	0.26 (0.17–0.36)	0.27 (0.18–0.37)	0.51 (0.41–0.61)	↑
ψ^{fs}_{2010} §	0.46 (0.35–0.57)	0.49 (0.4–0.58)	0.44 (0.33–0.54)	0.65 (0.54–0.75)	↑
ψ^{fs}_{2011} §	0.68 (0.56–0.79)	0.65 (0.54–0.76)	0.7 (0.58–0.81)	0.86 (0.78–0.93)	↑
$p.$	0.87 (0.82–0.92)	0.87 (0.82–0.92)	0.87 (0.81–0.92)	0.69 (0.65–0.73)	↓
$fp.$	0.13 (0.09–0.17)	0.13 (0.09–0.17)	0.12 (0.09–0.17)	0	–
γ_{09-10}	0.37 (0.23–0.49)	0.41 (0.31–0.51)	0.33 (0.22–0.45)	0.55 (0.39–0.69)	↑
γ_{10-11}	0.46 (0.33–0.67)	0.41 (0.31–0.51)	0.53 (0.37–0.69)	0.67 (0.51–0.85)	↔
φ_{09-10}	0.72 (0.52–0.89)	0.71 (0.51–0.88)	0.72 (0.53–0.89)	0.75 (0.62–0.87)	↔
φ_{10-11}	0.92 (0.79–0.99)	0.92 (0.79–0.99)	0.91 (0.8–0.99)	0.97 (0.9–1.0)	↔

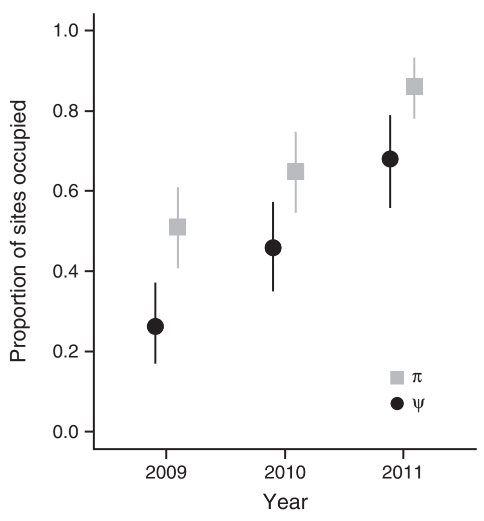

Fig. 1. Model predictions, with 95% Bayesian credible intervals, of occupancy estimates in the 3 years of 2009–11. Grey squares are estimates of utilisation from the model with the condition $fp=0$ (π). Black circles are estimates of occupancy from the model that accounts for false positive errors: $fp \neq 0$ (ψ).

positives and false negatives, we have demonstrated that, under certain circumstances, it is possible to use this model to account for transient-induced false-positive detection error.

Animal movements that may act to increase the chance of false positive observations is a common feature of many natural systems and has been well documented in many species, e.g. 'floating' tigers (Karanth and Sunquist 2000; Karanth *et al*. 2009), nomadic brown hyaenas (Mills 1984; Hulsman *et al*. 2010), highly dispersive butterflies (Hovestadt *et al*. 2011) and stepping-stone dispersal by water voles (Fisher *et al*. 2009; Lambin *et al*. 2012). However, perhaps of greater concern is that such misclassification of unoccupied sites as being occupied may be more prevalent in species occurring at relatively low density (which species of conservation concern generally are) and whose likelihood of survival and establishment are lowered (Courchamp *et al*. 1999; Fisher *et al*. 2009; Stephens and Sutherland 1999). It is interesting that, despite having the potential to influence how we characterise and understand patch-occupancy dynamics, transient-induced false positive detection error has received very scant interest. The water vole metapopulation we study here provides an ideal model system to investigate this issue for two main reasons. First, the colonisation process is driven almost exclusively by juvenile dispersal from the year of birth to the following (breeding) year; water voles very rarely survive beyond their first breeding season (Sutherland *et al*. 2012), hence, the requirement for a strict definition of occupancy, i.e. sites with established, breeding water vole colonies. Second, latrine counts in 2011 showed far fewer latrines at sites with a single positive visit than at sites with more than one positive visit, suggesting that such 'single positive visit' sites are more likely to be transient-induced false positive observation (Appendix S1). In fact, this is consistent with observations by Woodroffe and Lawton (1990), who readily found latrines in 'core' water vole sites in which breeding colonies were found, whereas in peripheral and vacant sites with no evidence of breeding, latrines were observed, but only very infrequently. Accounting for the observation error that we attribute to transient-induced false positive detections led to lower posterior mean values for occupancy and higher posterior mean values for detection probabilities. Given the differential support from the data for these models, we regard these differences as being a correction for model mis-specification bias induced by ignoring the potential for false positives. Thus, using our approach we were able to infer effective occupancy, i.e. the number of sites likely to be occupied by established and reproductively viable water vole colonies.

The distinction between resident and transient occupancy should be of great interest to ecologists and conservationists because it has long been recognised that if both false positive and false negative prediction errors are not placed within an ecological context, results may be misleading (Fielding and Bell 1997). One of the greatest causes for concern is that overestimates of occupancy will reduce our ability to detect, diagnose and act on species reaching critical thresholds, such as extinction thresholds (Lande 1987) or the minimum viable metapopulation (MVP, Hanski Moilanen and Gyllenberg 1996). We suggest, therefore, that the ability to identify and correct for transient occupancy has profound implications for how species are managed and predictions made about species persistence or extinction risk.

How important the distinction is between resident and transient occupancy depends on how these two states are defined and the focus of the study. Although standard, false negative-only estimates of occupancy are considered to be robust to random movements into and out of sites (MacKenzie *et al.* 2004), occupancy must then be interpreted as utilisation, i.e. site use. Here, as is common in studies of classical metapopulations, we adopt a functional definition of occupancy (sites with breeding colonies that are likely to produce dispersing and potentially colonising offspring) because this is likely to be the best measure of occupancy for connectivity or dispersal-driven metapopulation dynamics. Estimating instead the broader measure of utilisation in this case is less helpful, because not distinguishing between resident and transient occupancy means that we can be less certain about the status of the metapopulation and, hence, less confident of how the metapopulation might persist through time.

Accounting for false positive errors, we were able to compare year-specific estimates of occupancy from both formulations of the occupancy model. In agreement with Royle and Link (2006), we found that ignoring positives produces higher estimates of occupancy than when false positives are allowed for ($\psi^{fs}_{2009:2011} = 0.26$, 0.46, 0.68, versus $\pi^{fs}_{2009:2011} = 0.51$, 0.65, 0.86; Fig. 1). However, in many cases utilisation may well be a sufficient (or even better) measure a species' spatial distribution, although we believe that the ability to distinguish between occupancy and utilisation when appropriate and/or required is an important one. The distinction becomes particularly important when considering multi-year site-occupancy dynamics (MacKenzie *et al.* 2003; Royle and Kéry 2007), particularly when these are driven by dispersal (Hanski 1994; Moilanen 1999). For example, when only sites occupied by established populations are the source of potentially colonising individuals, overestimation of occupancy will overstate the colonisation potential, accentuate rates of local extinction and, as a consequence, incorrectly predict occupancy dynamics (Moilanen 2002; Dorazio 2007).

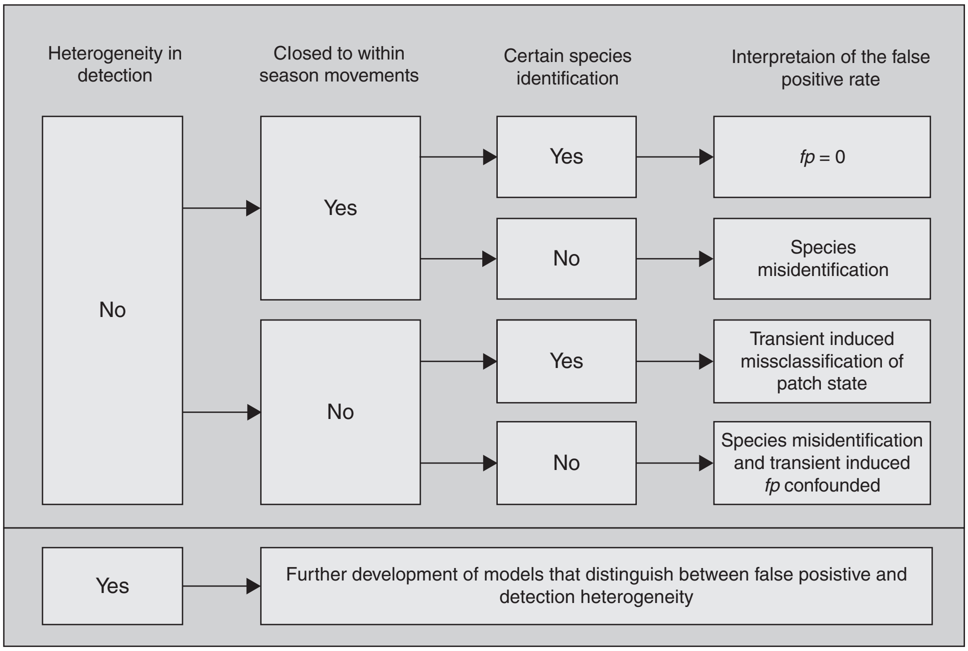

Fig. 2. An inferential framework for the interpretation of the false positive error rate *fp* under what we consider to be the most common situations in which false positive detections can occur, including when there is and is not heterogeneity in detection.

Our study has added to the growing evidence that the issue of false-positive detection error is an important one in occupancy-based studies. However, it is also necessary to make clear that our approach requires careful consideration and that there are potential pitfalls that could yield misleading results otherwise. Specifically, the method we applied is mathematically identical to some models that account for heterogeneity in the detection process owing to, for example, variation in colony or population size (MacKenzie *et al*. 2006; Royle and Link 2006). The existence of detection heterogeneity will result in underestimation of occupancy, whereas false positives will result in occupancy being overestimated; the two are confounded and indistinguishable using the current model. Here, on the basis of our knowledge of the water vole system and to demonstrate how transience might result in false positive detections, we assumed negligible levels of detection heterogeneity.

We note also that recent developments have increased the flexibility of occupancy models to allow for multiple states and state uncertainty to be formally incorporated into the modelling framework, which goes some way towards addressing the issue of erroneous occupancy-state allocation (Nichols *et al*. 2007; MacKenzie *et al*. 2009; Miller *et al*. 2011). However, these approaches rely on the ability to categorise positive detections into states such as, but not exclusively, breeding or non-breeding determined by additional information such as the observation of chicks (Nichols *et al*. 2007) or the behaviour of adults (MacKenzie *et al*. 2009). The multi-state occupancy model is a recent development, meaning that many (mostly historical) occupancy studies of metapopulations (Hanski 1997), or those that have carried out repeated-measures sampling in line with suggestions in Moilanen (2002) or MacKenzie and Royle (2005), lack auxiliary information that allows for retrospective classification of observations. When studies can meet the data requirements for multi-state approaches, additional data should be collected and used in the subsequent analysis, but this might not always be a viable option. The rationale behind our work was partly motivated by this very fact; rather than either ignoring the issue of false positives or rendering historic data redundant, the misclassification model of Royle and Link (2006) offers a useful alternative to the multi-state model in the absence of classification data.

Although the recent interest in quantifying false-positive detection errors has focussed on species misidentification, we suspect that it is not uncommon for studies to assume that positive detections can be made with certainty (e.g. camera traps, Karanth and Nichols 1998; professional trackers, Stander 1998; unmistakeable sign, Sutherland *et al*. 2012). Our aim here was to demonstrate an alternative source of false-positive detection errors, namely, the detection of transient individuals, resulting in sites being categorised as occupied when in truth they may not be. In the absence of detection heterogeneity (see above), the false positive rate can therefore be interpreted as the probability of observing a transient individual at an unoccupied site, and, in the presence of such false positives, allows a reduction in bias of occupancy resulting from model mis-specification to be achieved. However, there may also be occasions when there is potential for heterogeneity in detection, misidentification of species and of observing transient individuals, resulting in a confounding of the false positive-rate parameter. It is important, therefore, to consider how the false positive rate is interpreted when using the false positive model. In Fig. 2, we attempt to provide a framework to guide the interpretation of the false positive-rate parameter, fp, in what we consider to be the most common situations where false positives may occur in the absence of detection heterogeneity. We also highlight the need for continued development of models that attempt to formally disentangle false positive detections and detection heterogeneity, which are likely to be fruitful areas of research, particularly in situations where auxiliary data that allow this distinction to be made, do not exist. That said, however, it is important to recognise that, although model-based solutions to address the issue of false positive detections and detection heterogeneity are necessary in cases of retrospective analyses, well-conceived field protocols designed with these specific issues in mind will allow for a more natural treatment of these confounding effects, e.g. resident vs transient occupancy, detection heterogeneity vs false positives (MacKenzie and Royle 2005; Miller *et al*. 2011; Pacifici *et al*. 2012).

Regardless of how they occur, it is clear that the influence of false positive observations, even at low rates, can be substantial, and a failure to account for species misidentification or site misclassification when suspected may be costly. The model for misclassification allows the user to model as empty those sites that are in truth unoccupied but at which positive signs are observed. Doing so leads to improved estimates of occupancy and detection and allows the user to estimate and distinguish between true and apparent occupancy, which is important in the context of on-going policy and management but also for long-term predictions and decisions regarding species conservation and persistence. The present study has highlighted the value of modelling both types of observation error in occupancy studies to (1) improve our understanding of site-occupancy dynamics, (2) enhance our ability to make predictions and (3) increase the potential of occupancy studies as effective wildlife-management tools. The challenge remains to continue the formal development of occupancy models that can account for all potential sources of detection error.

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