

Improving abundance estimation by combining capture–recapture and occupancy data: example with a large carnivore

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Summary

1. Abundance is a key quantity for conservation and management strategies but remains challenging to assess in the field. Capture–recapture (CR) methods are often used to estimate abundance while correcting for imperfect detection, but these methods are costly. Occupancy, sometimes considered as a surrogate for abundance, is estimated through the collection of presence/absence data and is less costly while allowing gathering of information at a large spatial scale.

2. Building on the recent pieces of work on the combination of different data sources, we showed how abundance data can be complemented by presence/absence data and can be analysed conjointly to improve abundance estimates. Our approach relies on a hierarchical model that makes explicit the link between the abundance and occupancy state variables while formally accounting for imperfect detection.

3. We used a population of Eurasian lynx in France monitored via camera traps and a collection of presence signs as an illustration of our approach.

4. *Synthesis and applications.* We combined capture–recapture and occupancy data and demonstrated that we can efficiently improve abundance estimates. Our method can be used by managers when estimates of trends in abundance lack power due to sparse data collected during an intensive survey, by simply integrating data collected during non-systematic survey. Furthermore, combining these two sampling procedures makes full use of all available data and allows the development of conservation and management strategies based on precise abundance estimates. Overall, the combination of different data sources in an integrated statistical framework has great potential, especially for elusive species.

Key-words: abundance, Bayesian approach, camera-trapping, *Lynx lynx*, population size, presence signs, site-occupancy

Introduction

Management and conservation strategies require information on abundance, key quantity that is notoriously difficult to assess in the field. Due to the impossibility of carrying out an exhaustive census for free-ranging animal populations, sampling methods only yield a count of some portion of the population. As a consequence, researchers have to estimate in some ways the probability that an individual present and exposed to sampling is actually

detected and, therefore, that it appears in a count (Williams, Nichols & Conroy 2002).

Capture–recapture (CR) methods are often used to estimate abundance while correcting for imperfect detection (Otis *et al.* 1978; Williams, Nichols & Conroy 2002). However, CR methods with physical capture may be challenging when species are cryptic and individuals range over large distances. Non-invasive techniques have recently been developed to promote advancement in ecological research on such species (MacKay *et al.* 2008). However, gathering CR data requires individual identification that usually involves a great commitment of time and money.

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In parallel to the estimation of abundance, there has been increasing interest in alternative state variables such as occupancy, that is the proportion of area occupied by a species. Similar to CR models, site-occupancy models have been developed to infer occupancy while explicitly modelling detection probabilities (MacKenzie *et al.* 2002). This approach relies on replicate observations of ‘detection/non-detection’ (‘presence/absence’) from repeated surveys of a generic site, therefore allowing the separation of true absences from non-detections. Site-occupancy sampling is attractive to ecologists as it tends to be less costly than CR methods and enables the gathering of information at a relatively large spatial scale. As a consequence, such surveys are increasingly used in many areas of investigation in ecology (e.g. macroecology: Royle, Nichols & Kéry (2005)).

In general, abundance and occupancy are considered as two distinct variables answering different biological questions: abundance is often used to address questions dealing with population dynamics, while occupancy is used in biogeography and macroecology. Although apparently disconnected, occupancy and abundance are two linked state variables. By considering the sites at which a species is detected or not as individuals, the link between site-occupancy and CR models is straightforward. Occupancy data alone may inform estimates of abundance (Royle & Nichols 2003) since when a site is known to be occupied by a species, there is at least one individual of this species on this site (Mackenzie *et al.* 2005). This has led some authors to see occupancy as truncated abundance data (Mackenzie & Nichols 2004; Sólymos, Lele & Bayne 2012). Royle & Nichols (2003) exploited the relationship between occupancy and abundance to estimate population size from presence/absence data and occupancy techniques. Nevertheless, the relationship between the two variables is not explicit in their approach, in that they assumed the sources of variation in detection were mainly driven by the variation of abundance and used the detection probability to extract information on abundance.

Recognizing the interest in combining capture–recapture and occupancy protocols, Freeman & Besbeas (2012) developed an integrated approach in which they combined count survey and ring-recovery data to estimate abundance. Based on simulations and the analysis of a real case study, they demonstrated that combining different sources of data provided a better precision allowing the detection of change in abundance and other demographic parameters that would not be possible otherwise. Nevertheless, Freeman & Besbeas (2012) assumed that detectability was equal to 1 and did not explicitly consider the observation process.

Here, we developed an approach to combine site-occupancy models and CR models to estimate abundance while formally accounting for species and individual imperfect detection. We implemented our approach in a Bayesian framework and used a case study as an

illustration to estimate the local abundance of Eurasian lynx *Lynx lynx* in an area of the Jura Mountains, France. We used data collected through intensive monitoring protocols analysed with CR models and presence signs through volunteers monitoring programme analysed with site-occupancy models. Large carnivores are an ideal case study to demonstrate the improvement in estimating abundance by combining capture–recapture and occupancy data as they have low detection probability and large distribution areas leading to sparse data.

Materials and methods

In this section, we introduce the general procedure for implementing our hierarchical approach beginning with (i) the presentation of abundance and occupancy and the relationship between these two state variables that permits combining CR with presence/absence data then (ii) developing the observation processes leading to the measurement of these state variables using CR modelling for estimating abundance and site-occupancy modelling for estimating occupancy. We adopt a Bayesian approach (McCarthy 2007) to properly accommodate estimation uncertainty at every level of our hierarchical model. The Bayesian approach provides a convenient framework to combine information on important ecological parameters from multiple sources of data (Ellison 2004; Brooks *et al.* 2008). It uses powerful computer-intensive methods for handling complex models and combines the likelihood with prior probability distributions of the parameters to obtain the posterior distribution of the parameters of interest based on the Bayes’ theorem. We use Markov chain Monte Carlo (MCMC) methods to simulate observations from the posterior distributions.

STATE VARIABLES AND THE RELATIONSHIP BETWEEN ABUNDANCE AND OCCUPANCY

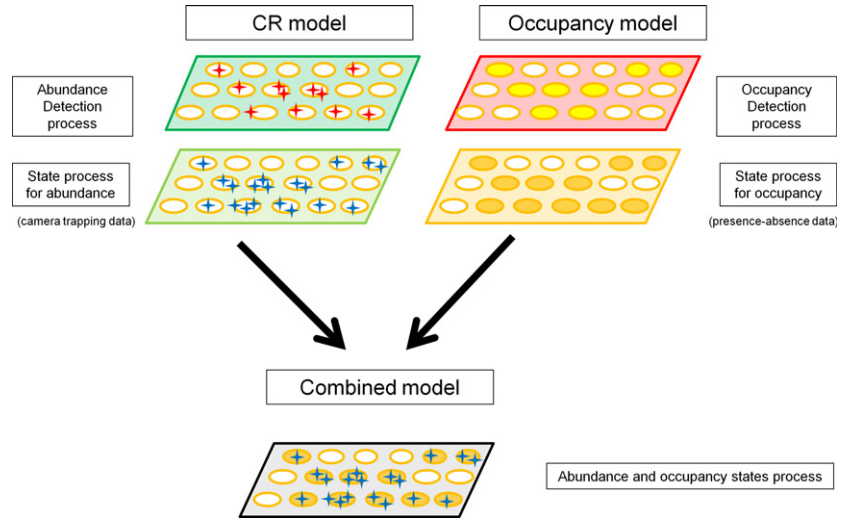
Our objective is to estimate the abundance state variable N . We assume that N is a realization of a Poisson random variable with rate λ . In parallel, we assume that we have access to another state variable, namely occupancy, defined as the proportion of occupied spatial units (e.g. patches or sites). We assume that occupancy Z is a realization of a Bernoulli process with index ψ .

Both state variables are inferred from monitoring protocols and modelling approaches that specifically deal with detectability less than one (see below) (Fig. 1). The link between abundance and occupancy is made by using the fact that when the probability of a site to be occupied is >0 , the abundance at this site is >0 (Fig. 1). More formally, the probability of having at least an individual is:

$$P(N > 0) = 1 - P(N = 0) = 1 - e^{-\lambda} \quad \text{eqn 1}$$

which is exactly the probability of having a true presence, that is the probability of occurrence ψ in patch occupancy models. Here, eqn 1 gives information on the probability that abundance is nonzero if one individual is detected on one site; we do not consider that two presence signs collected nearby necessarily come from two distinct individuals. For occupancy to bring information about abundance, the link between these two state variables needs to be made explicit. This is achieved by expressing the rate

Fig. 1. Diagram representing the capture–recapture and occupancy models used to estimate, respectively, abundance and occupancy. Both models deal with imperfect detection, that is not all the individuals are detected with camera traps and some sites were falsely considered as unoccupied while collecting presence/absence data. Red crosses represent individuals detected, and yellow circles represent sites detected as occupied. The link between abundance and occupancy is made by using the fact that when a site is occupied (orange circles), the abundance at this site is >0 (blue crosses).



of the Poisson distribution λ as a function of the probability of occurrence:

$$\lambda = -\log(1 - \psi) \quad \text{eqn 2}$$

OBSERVATION PROCESS FOR ABUNDANCE AND OCCUPANCY

Abundance and occupancy cannot be directly measured in the field. The observation process needs to be made explicit to reliably estimate these state variables. Regarding abundance, we resort to CR closed population model (Otis *et al.* 1978) to estimate population size. Because N is the key parameter that makes the link between occupancy and abundance (see above), the challenge was to find a flexible approach that would treat population size as an explicit parameter, in contrast with standard CR models in which it is often calculated as a derived parameter. We use the complete data likelihood approach proposed by Schofield & Barker (2014) to fit a CR model with individual heterogeneity on the detection process p_i for individual i . The originality of their approach lies in the fact that they consider N explicitly in the likelihood via the trans-dimensional approach (e.g. King & Brooks 2008). We denote X the complete $N \times k$ matrix of capture histories over k capture occasions where $x_{i,t}$ is 1 when individual i is captured at occasion t and 0 otherwise. Given N and the mean μ_p and variance τ_η governing the normal distribution that is used to deal with heterogeneity in the detection process, it can be shown that:

$$[X, p|N, \mu_p, \tau_\eta] = \frac{N!}{\sum_h z_h!} \prod_{i=1}^N \prod_{t=1}^k p_i^{x_{it}} (1 - p_i)^{1-x_{it}} \prod_{i=1}^N \text{Normal}(\mu_p, \tau_\eta) \quad \text{eqn 3}$$

where z_h is the number of individuals observed with capture history h . The unobserved p_i are dealt with a trans-dimensional algorithm (Carlin & Chib 1995). We refer to Schofield & Barker (2014) for the technical details of the implementation of eqn 3.

Now we define the occupancy as the probability that a randomly selected site or sampling unit in an area of interest is occupied by a species (at least one individual of the species). Obviously, we cannot have access to the genuine proportion of occupied sites since we do not see all the individuals, and species imperfect detection needs to be accounted for.

From the area of interest, R spatial units are selected to be surveyed for the species using appropriate methods (e.g. collection of presence signs). These sites are surveyed multiple times each season for T years. In each survey, detections are considered as true, meaning that we cannot falsely recognize the species, but the non-detections can arise from both (1) true absence and (2) false absence (i.e. presence but not detected). Within a season, we assume that sites were closed to changes in occupancy. So a unit must be either occupied or not for all visits in this season (MacKenzie *et al.* 2002). We denote $Y_{s,t}$ a binary random variable corresponding to the observation of an individual on site s at time t , which takes value 1 if the individual is observed and 0 otherwise. Given a realization $z_{s,t}$ of the state variable occupancy, $Y_{s,t}$ is distributed as:

$$[Y_{s,t}|z_{s,t}] \sim \text{Bernoulli}(z_{s,t} \times p_{Os}) \quad \text{eqn 4}$$

where p_{Os} is the probability of detecting the species at a site s .

APPLICATION

Material

For many elusive species such as large carnivores, it is easier to detect evidence of their presence than to actually see the animal. To overcome these issues, monitoring a carnivore population may be performed at various levels of resolution (Gese 2001). Biologists often resort to large-scale sign survey to provide information on species distribution or relative abundance at a lesser cost (mustelids: Ruiz-Olmo, Saavedra & Jiménez (2001); felids: Rolland, Basille & Marboutin (2011); canids: Llaneza *et al.* (2005)). If the financial support is substantial enough, intensive monitoring (camera trapping or DNA sampling) is conducted to provide absolute abundance estimates or density but is often restricted to small areas [mustelids: Graham (2002); felids: Karanth *et al.* (2004); canids: Cubaynes *et al.* (2010)].

In the French Jura Mountains (Fig. 2), this two-scale survey method is used for monitoring a population of Eurasian lynx. The monitoring is organized at two levels: an extensive sign survey carried out by a network of observers (state employees, hunters, naturalists, farmers and mountain guides; Duchamp *et al.* (2012)) who collect evidences of presence in the field (i.e. tracks, scat, hair, sightings, livestock and wildlife killed) and an intensive

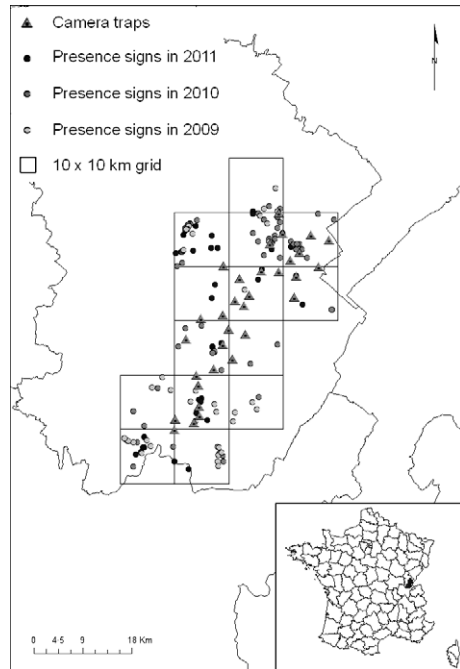


Fig. 2. Map of the area sampled in the French Jura department by camera traps (green triangles) during winter 2011. The yellow, orange and red dots represent location of the presence signs collected in 2009, 2010 and 2011, respectively.

survey using the non-invasive monitoring technique of camera trapping conducted since 2011 by the French National Wildlife Agency (Blanc *et al.* 2013). Each presence sign collected is associated with a 10×10 km grid cell (Marboutin *et al.* (2011); site EEA), which is the most convenient way to deal with a biological process occurring at the scale of species' distribution range. Only the cells within the camera-trapping zone are considered. We assume that the entire camera-trapping zone was surveyed by the observers' network that collected the presence signs, thus preventing false absence. Duchamp *et al.* 2012 estimated that 15 km was the mean distance at which signs were recorded relatively to the observers' living place. This information provides good support for our assumption that the camera-trapping area was covered by the network of lynx observers. To model the occurrence of lynx in the camera-trapping zone, we use a 3-year temporal window in the occupancy model (Stahl & Vandel 2001).

Due to the lack of an appropriate integrated framework, the data collected during extensive and intensive surveys have so far been separately analysed. Here, we illustrate how our new approach can be used to improve abundance estimates by combining these two sources of data.

Models

We fit three models, starting with the capture–recapture model to the camera-trapping data, then we model the presence/absence data with a single-season occupancy model, and finally, we implement the model to combine the two sources of data, that is CR data and presence/absence data, by combining the two state variables under interest, that is abundance and occupancy.

A previous analysis of the camera-trap data showed that individual attributes (e.g. age and sex classes) and home range features

(e.g. home range location relative to traps and composition) generated heterogeneity in the detection process (Blanc *et al.* 2013). Therefore, the detection probability in the CR model is considered as heterogeneous. More precisely, the logit of p_i , that is the detection probability for the individual i , is written as the sum of a mean detection probability μ_p and an individual random effect η_i . This latter variable is assumed to be normally distributed with mean 0 and variance σ_η^2 . As priors, we use a Gamma distribution with shape and scale, respectively, equal to 1.5 and 0.027 for σ_η^2 and a Logistic (0, 1) for μ_p (Schofield & Barker 2014). The rate λ is assigned a normal prior distribution with mean 0 and variance 1000 on the log scale.

We then fit a site-occupancy model (MacKenzie *et al.* 2002) with site-dependent ψ_s and site-specific detection probability p_{Os} as suggested by a previous analysis of the data (Rolland, Basille & Marboutin 2011). The site-dependent occupancy probability is defined by the mean occupancy μ_ψ and a site random effect β_s , normally distributed with mean 0 and variance σ_β^2 . Since we do not have any information on the occurrence of the species, we assign a Normal (0, 5) prior for μ_ψ on a log scale and a Uniform (0, 5) prior for σ_β^2 . Regarding the detection probability, the logit of p_{Os} is normally distributed with mean μ_p and a variance σ_ϵ^2 . We set a Normal (0, 10) prior for the logit of μ_p and a Uniform (0, 10) prior for σ_ϵ^2 .

Finally, we consider the model that combined the two state variables of interest, that is abundance and occupancy (see eqn 1). We use a site-dependent occupancy ψ_s and the mean occupancy μ_ψ in the function of the index λ for the Poisson distribution of N . Regarding the observation process, we consider a site-specific probability of detecting occupancy p_{Os} for the site-occupancy likelihood and a detection probability varying among individuals p_i in the capture–recapture likelihood. We keep similar priors that were used in the previous models.

STATISTICAL INFERENCE IN A BAYESIAN FRAMEWORK

We fitted the three models to the data by Bayesian statistical inference using MCMC sampling. Three chains were generated using 15 000 iterations each with a burn-in phase of length 2500. Convergence was diagnosed both visually (checking the traces and mixing of the chains) and numerically using the Gelman–Rubin statistic (Gelman & Rubin 1992). We implemented these analyses in JAGS (Plummer 2003) called from R using the rjags package. The code for the combined model is available in Appendix S1.

Results

A total of 172 presence signs were collected by the volunteers of the Réseau Loup-Lynx from 2009 to 2011 across the camera-trapping area. Regarding the camera-trapping protocol, lynx photographs were collected from February to April 2011 from 33 trap sites. We removed one trap site because of technical problems. The effective effort was reduced to 1816 effective trapping nights. We obtained 39 detections of lynx during the sampling period and identified nine individuals that were photographed on 14 of the 32 trap sites. Individuals were captured at up to six different trap sites. When the sole CR model with heterogeneous detection probability was fitted to these data,

we found that the mean estimated detection probability μ_p was 0.11 ± 0.07 and that the estimated abundance was 14.46 ± 7.50 individuals [95% CI: 9.0; 35.0] (Fig. 3). Using the single-season occupancy model, the mean occupancy was estimated at 0.96 ± 0.04 [95% CI: 0.83; 0.99] and the mean detection probability was quite high: 0.71 ± 0.16 [95% CI: 0.30; 0; 0.97]. Using our new approach to combine CR and presence/absence data, abundance was estimated at 9.96 ± 1.18 individuals [95% CI: 9.0; 13.0] (Fig. 3) while detection probability was on average estimated at 0.16 ± 0.06 in the CR model likelihood. The probability of detecting occupancy was estimated on average at 0.71 ± 0.15 , while the occurrence probability was estimated at 0.99 ± 0.01 . All the parameters estimated in the three models converged towards their stationary distribution.

Discussion

The choice of the state variable to monitor is challenging when dealing with rare and elusive species. Abundance data have commonly been assumed to be more informative on a per site basis, but presence/absence data allow for more sites to be visited and allow carrying out inference across a much larger study area. Moreover, estimating animal abundance requires consistent and standardized application of a technique to be able to detect changes or differences with some degree of accuracy (Macdonald, Mace & Rushton 1998). These techniques are often costly and time-consuming, to a point that systematic surveys are in some situations unaffordable.

Indeed, while studying wild populations, practitioners frequently encounter difficulties in collecting good quality data in sufficient quantity to estimate abundance. Most practitioners have to cope with limited financial resources

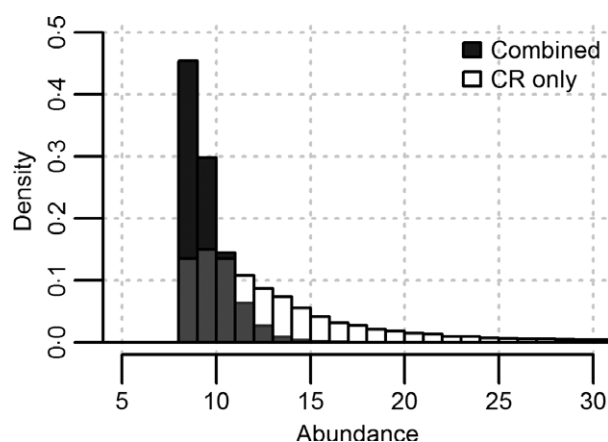


Fig. 3. Posterior distribution of the abundance of Eurasian lynx in the camera-trapping area in the Jura Mountains while using only capture–recapture data (salmon) or combining the presence/absence data and the capture–recapture data (blue). The overlap between the two distributions is displayed in purple.

and data sampling jeopardy. In the case study we developed, we raised the issue of scarce data due to the ecology of the species. Large carnivores have secretive and nocturnal behaviour, are distributed over large areas and live at low density, which means that even standardized and consistent protocols do not guarantee precise estimates. In this context, there is clear need to develop optimal methods to analyse data resulting from such population monitoring schemes, in particular in regions where resources for monitoring programmes are limited (Balmford, Green & Jenkins 2003; Roberts, Donald & Green 2007), or for species with low detectability. Additional presence/absence data, coming from citizen science programmes for instance, may profoundly increase our confidence in abundance estimates, enabling to develop more sound management and conservation strategies. Our approach is a first step in that direction.

Indeed, we showed how abundance data can be complemented by presence/absence data and be analysed jointly to improve abundance estimates. Our approach is similar to the Freeman and Besbeas approach in that we combine different sources of data but differs from it in the way that we extended their model by adding the detection process to account for imperfect detection. By combining camera-trapping data and presence signs through an explicit link between the state variables of abundance and occupancy, we significantly reduced the width of the credible interval on lynx abundance estimates. The reduced effort associated with the collection of presence/absence data means that occupancy surveys have already proved to be very useful in large-scale surveys for various species. They now are shown to be very useful in small-scale surveys to estimate population size. There is an increasing number of participative programmes on birds (Greenwood 2007, *Christmas Bird Count*, *eBird*) and amphibians (*FrogwatchUSA*, *Global Amphibian BioBlitz*) that could be used to complement individual-level data, collected occasionally, when financial resources are sufficient. Our model is easily applicable to such taxa since the spatial unit to which occupancy is estimated is well defined: closed units, such as nests or ponds, fulfil the closure assumption underlying single-season occupancy models, although application to mammals is more complicated.

Precautions must be taken when using our new approach regarding the assumptions underlying the model and the sampling design. First, we used presence signs that were collected during 3 years prior to the camera-trapping session and so, we assumed that the population of interest was geographically closed during the sampling period. Thus, the presence/absence data collected were assumed to be presence signs of individuals that were part of the population monitored via the camera-trapping protocol. The geographical assumption is valid for the Eurasian lynx, but it would not be the case for a non-territorial species. Secondly, false positives in presence data may lead to abundance overestimation, and care

must be taken to ensure the quality of the presence signs which are collected, possibly with a validation step (Molinari-Jobin *et al.* 2011) or using models that explicitly account for identification errors (Miller *et al.* 2011). In our case study, objective and standardized identification and reliability assessment criteria have been defined for each category of field signs (Vandel & Stahl 1998), which guarantees a negligible false-positive rate. Thirdly, we assumed that abundance N was a realization of a homogeneous Poisson random variable. The violation of this assumption might lead to underestimating the variance of N . To relax this assumption, we would need to resort to spatially explicit capture–recapture (SECR) surveys that were formulated by Borchers and Efford (2008) using a general non-homogeneous Poisson process to model animal home range locations. However, to combine the SECR model likelihood with the occupancy model likelihood, N has to appear explicitly as a parameter in the former likelihood, which is not the case since N is obtained as a by-product. Further work is needed to extend the (Schofield & Barker 2014) approach to SECR surveys.

Presence/absence surveys in studies with small budgets or targeting elusive species remain useful in an attempt to successfully assign IUCN Red List categories of threat (Joseph *et al.* 2006) and can accurately represent trends in population size. For these reasons, Royle & Nichols (2003) suggested the idea of using presence/absence data to infer abundance in a proper way. Assuming that the most important source of heterogeneity in detection was in animal abundance, they defined the probability of detecting occupancy as a function of N and used heterogeneity in detection to extract information about abundance in the occupancy surveys. As for our study, we focused on the direct relationship between abundance and occupancy and directly connected abundance and occupancy in the model. It results in more flexibility when combining various sources of information as our approach can accommodate several sources of data. For example, recent studies made use of replicated counts on spatial units that do not rely on individual identification. As an alternative to CR models, these so-called N -mixture models (Royle 2004) are used to estimate population size while adjusting for detectability <1 (Kéry, Royle & Schmid 2005; Royle, Nichols & Kéry 2005). These models are widely used to estimate bird abundance (Royle 2004; Kéry, Royle & Schmid 2005). Various bird surveys have two levels of resolution as it is the case for carnivores: a standardized survey with repeated visits on a sampling area provides count data used to estimate abundance, while some observers distributed over the area all year long collect presence of the bird species of interest. The first kind of data can be analysed in the N -mixture framework, while the presence/absence data collected by can be analysed in a site-occupancy framework. Our approach can also be used with data arising from distance sampling protocols (Buckland *et al.* 2001)

pending some modifications of the abundance component of the model. We assumed the lynx population was closed during the CR survey since the sampling period was out of the breeding (Breitenmoser-Würsten *et al.* 2007) and the dispersal period (Zimmermann, Breitenmoser-Würsten & Breitenmoser 2005), and the species being territorial, migration in or out of the study area that would have biased the abundance estimates was avoided. We used the same closure assumption for the occupancy survey. We assumed that one site that was occupied once has been occupied during all survey and any non-detection at this site is considered as a ‘false negative’ (Rota *et al.* 2009). Moreover, here, we clearly deal with what Efford and Dawson (2012) referred to as ‘asymptotic occupancy’. The authors made the distinction between instantaneous occupancy referring to the probability of a cell being occupied at a particular time, whereas the overall occupancy of a given cell refers to the probability that at least one individual will enter the cell during the study period. Since large carnivores are territorial, we can safely assume that if a cell is detected as occupied once, it will remain occupied during all the survey (provided that the size of their home range does not go through major fluctuations). For large carnivores and other organisms, the generalization of our approach to geographically open population system involving local extinction and colonization processes deserves further exploration. Since our case study involved a real data set and the true abundance was unknown, simulations will be used in future to test the robustness and accuracy of our estimates.

Acknowledgements

L. Blanc was supported by Labex Centre Méditerranéen de l'Environnement et de la Biodiversité (CeMEB) and University of Montpellier 2. We especially thank the staff from the French National Game and Wildlife Agency, the Forest National Agency and the Departmental Federation of Hunters of Jura department, who collected the photographs during the camera-trapping session. We also thank Matthew Schofield for his technical support for modelling explicitly capture–recapture data. We finally thank all the volunteers that are members of the Réseau Loup-Lynx that collect every year precious presence signs of lynx all over its distribution area.

References

- Balmford, A., Green, R.E. & Jenkins, M. (2003) Measuring the changing state in Nature. *Trends in Ecology and Evolution*, **18**, 326–330.
- Blanc, L., Marboutin, E., Gatti, S. & Gimenez, O. (2013) Abundance of rare and elusive species: empirical investigation of closed versus spatially explicit capture – recapture models with lynx as a case study. *Journal of Wildlife Management*, **77**, 372–378.
- Borchers, D.L. & Efford, M.G. (2008) Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, **64**, 377–385.
- Breitenmoser-Würsten, C., Vandel, J.-M., Zimmermann, F. & Breitenmoser, U. (2007) Demography of lynx *Lynx lynx* in the Jura Mountains. *Wildlife Biology*, **13**, 381–392.
- Brooks, S.P., Freeman, S.N., Greenwood, J.J.D., King, R. & Mazzetta, C. (2008) Quantifying conservation concern – Bayesian statistics, birds and the red lists. *Biological Conservation*, **141**, 1436–1441.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling: Estimating*

- Abundance of Biological Population*. Oxford University Press, Oxford, USA.
- Carlin, B.P. & Chib, S. (1995) Bayesian model choice via MCMC methods. *Journal of the Royal Statistical Society*, **57**, 473–484.
- Cubaynes, S., Pradel, R., Choquet, R., Duchamp, C., Gaillard, J.-M., Lebreton, J.-D. *et al.* (2010) Importance of accounting for detection heterogeneity when estimating abundance: the case of French wolves. *Conservation Biology*, **24**, 621–626.
- Duchamp, C., Boyer, J., Briaudet, P.-E., Leonard, Y., Moris, P., Bataille, A. *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.
- Efford, M.G. & Dawson, D.K. (2012) Occupancy in continuous habitat. *Ecosphere*, **3**, 32.
- Ellison, A.M. (2004) Bayesian inference in ecology. *Ecology Letters*, **7**, 509–520.
- Freeman, S.N. & Besbeas, P. (2012) Quantifying changes in abundance without counting animals: extensions to a method of fitting integrated population models. *Journal of Ornithology*, **152**, 409–418.
- Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457–511.
- Gese, E.M. (2001) *Monitoring of Terrestrial Carnivore Populations*, pp. 690–690. Cambridge University Press, Cambridge, UK.
- Graham, I.M. (2002) Estimating weasel *Mustela nivalis* abundance from tunnel tracking indices at fluctuating field vole *Microtus agrestis* density. *Wildlife Biology*, **8**, 279–287.
- Greenwood, J.D. (2007) Citizens, science and bird conservation. *Journal of Ornithology*, **148**(Suppl 1), 77–124.
- Joseph, L.N., Field, S.A., Wilcox, C. & Possingham, H.P. (2006) Presence – absence versus abundance data for monitoring threatened species. *Conservation Biology*, **20**, 1679–1687.
- Karanth, K.U., Chundawat, R.S., Nichols, J.D. & Kumar, S.N. (2004) Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Animal Conservation*, **7**, 285–290.
- Kéry, M., Royle, J.A. & Schmid, H. (2005) Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications*, **15**, 1450–1461.
- King, R. & Brooks, S.P. (2008) On the Bayesian estimation of a closed population size in the presence of heterogeneity and model uncertainty. *Biometrics*, **64**, 816–824.
- Llaneza, L., Ordiz, A., Palacios, V. & Uzal, A. (2005) Monitoring wolf populations using howling points combined with sign survey transects. *Wildlife Biology in Practice*, **1**, 108–117.
- Macdonald, D.W., Mace, G. & Rushton, S. (1998) *Proposals for Future Monitoring of British Mammals*. Department of the Environment, Transport and the Regions, London, UK.
- MacKay, P., Zielinski, W.J., Long, R.A. & Ray, J.C. (2008) Noninvasive research and carnivore conservation. *Noninvasive Survey Methods for Carnivores* (eds R.A. Long, P. MacKay, W.J. Zielinski & J.C. Ray), pp. 1–7. Island Press, Washington, District of Columbia, USA.
- Mackenzie, D.I. & Nichols, J.D. (2004) Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation*, **27.1**, 461–467.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- Mackenzie, D.I., Nichols, J.D., Sutton, N., Kawanishi, K. & Bailey, L.L. (2005) Improving inferences in population studies of rare species that are detected imperfectly. *Ecology*, **86**, 1101–1113.
- Marboutin, E., Pruszek, M., Calenge, C. & Duchamp, C. (2011) On the effects of grid size and shape when mapping the distribution range of a recolonising wolf (*Canis lupus*) population. *European Journal of Wildlife Research*, **57**, 457–465.
- McCarthy, M.A. (2007) *Bayesian Methods for Ecology*. Cambridge University Press, Cambridge, UK.
- Miller, D.A., Nichols, J.D., McClintock, B.T., Campbell Grant, E.H., 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.
- Molinari-Jobin, A., Kéry, M., Marboutin, E., Molinari, P., Koren, I., Fuxjäger, C. *et al.* (2011) Monitoring in the presence of species misidentification: the case of the Eurasian lynx in the Alps. *Animal Conservation*, **15**, 266–273.
- Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, **62**, 1–135.
- Plummer, M. (2003) *JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, Vienna, Austria.
- Roberts, R.L., Donald, P.F. & Green, R.E. (2007) Using single species list to monitor trends in animal populations: new methods and a comparison with independent data. *Animal Conservation*, **10**, 332–339.
- Rolland, J., Basille, M. & Marboutin, É. (2011) Comparing profile methods and site-occupancy modelling for the study of occurrence of an elusive species. *European Journal of Wildlife Research*, **57**, 1115–1118.
- Rota, C.T., Fletcher, R.J., Dorazio, R.M. & Betts, M.G. (2009) Occupancy estimation and the closure assumption. *Journal of Applied Ecology*, **46**, 1173–1181.
- Royle, J.A. (2004) N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, **60**, 108–115.
- Royle, J.A. & Nichols, J.D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**, 777–790.
- Royle, J.A., Nichols, J.D. & Kéry, M. (2005) Modelling occurrence and abundance of species when detection is imperfect. *Oikos*, **2**, 353–359.
- Ruiz-Olmo, J., Saavedra, D. & Jiménez, J. (2001) Testing the surveys and visual and track censuses of Eurasian otters (*Lutra lutra*). *Journal of Zoology*, **253**, 359–369.
- Schofield, M.R. & Barker, R.J. (2014) Hierarchical modelling of abundance in closed population capture–recapture models under heterogeneity. *Environmental and Ecological Statistics*, **21**, 435–451.
- Sólymos, P., Lele, S. & Bayne, E. (2012) Conditional likelihood approach for analyzing single visit abundance survey data in the presence of zero inflation and detection error. *Environmetrics*, **23**, 197–205.
- Stahl, P. & Vandell, J.-M. (2001) Lynx distribution in the French Alps (1995–1999). *Hystrix*, **12**, 11–15.
- Vandell, J.M. & Stahl, P. (1998) Lynx (*Lynx lynx*) population monitoring in France: comments on a method of data collection applied over a 6-year period. *Environmental Encounters*, **38**, 97–104.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making*. Academic Press, San Diego, California, USA.
- Zimmermann, F., Breitenmoser-Würsten, C. & Breitenmoser, U. (2005) Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. *Journal of Zoology*, **267**, 381.

Received 12 February 2014; accepted 10 July 2014

Handling Editor: Hamish McCallum

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. R code for the combined model.