

Estimating individual survival using territory occupancy data on unmarked animals

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Summary

1. Survival estimation forms the basis of much ecological research, and usually requires data on marked animals. In population studies of territorial animals, however, data are often collected on animal territory occupancy without identification of individuals. Previously, these data could not be used to estimate demographic parameters such as survival.

2. We developed a hierarchical site-occupancy model for estimating survival from territory occupancy data without individual identification. We defined survival as the probability that an individual occupying a territory survives until the next reproductive period and settles in the same territory again. To evaluate our model, we used simulated data as well as real data from a long-term study on nightingales *Luscinia megarhynchos*, from which mark-recapture data and territory occupancy data were available.

3. When applied to simulated data sets on territory occupancy, with parameter settings that are typical for different monitoring programmes (i.e. 10 years duration, three or eight visits per season, and 55 or 200 territories surveyed), our model yielded unbiased estimates of survival if the probability of detecting an occupied territory during a single visit was $p = 0.5$ or $p = 0.7$.

4. When applied to the data on nightingale territory occupancy, estimates of survival from our model were very similar to the estimates obtained from a traditional mark-recapture model (Cormack–Jolly–Seber model) applied to the ringing data from the same nightingale population.

5. *Synthesis and applications.* Data collection for mark-recapture analysis is usually invasive and labour intensive, and suitable data are rarely available from large-scale monitoring programmes covering entire regions or countries. Applying our model to territory occupancy data from such monitoring programmes could make large amounts of data available for research on animal demography.

Key-words: Bayesian analysis, capture recapture, common birds census, robust design, state-space models, territory colonization, territory fidelity, WinBUGS

Introduction

Research in conservation biology, ecology and evolution often requires estimates of survival in individual animals (Stearns 1992; Hoekstra *et al.* 2001; McCarthy, Citroen & McCall 2008; Ruiz-Gutierrez, Gavin & Dhondt 2008). In field studies, estimates of survival and other demographic parameters are usually obtained from data on individually marked animals (Lebreton *et al.* 1992; Sandercock 2006). A major drawback of these methods is that they usually are invasive because individuals need to be captured and marked. This can be stressful for the animals and time- and labour-intensive for researchers (Vögeli *et al.* 2008).

However, large data sets from non-invasive monitoring programmes or from population studies on single species are available, where animals are not captured and marked and, thus, cannot be individually recognized. For instance, the British Trust of Ornithology (BTO) stores detailed maps of almost a million bird territories, collected during the British common birds census programme over more than 40 years (Baillie *et al.* 2009), and long-term territory occupancy data are available for many individual species (Sergio & Newton 2003). At present, this huge body of data cannot be used to rigorously estimate demographic parameters such as survival, for lack of a framework to analyse territory occupancy data without individual recognition.

Demographic parameters could not be estimated from territory occupancy data because a territory that is occupied in two

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successive seasons may be occupied by the same surviving individual, or by two different individuals. In the latter case, the territory owner of the first year may have died or left for some other place, and a new individual may have occupied the territory in the following season. Conceptually, territory occupancy data are thus the result of two different probabilistic events. The first is local survival of a territory owner, which is the probability that a particular individual occupying a territory during one breeding season survives and settles in the same territory during the next breeding season. The second event is territory colonization, which is the colonization of territories by individuals new to the study site, or by individuals that occupied another territory at the same study site during the previous breeding season. Clearly, without individual recognition, local survival of a territory owner cannot be observed directly.

We developed a model for estimating local survival of territory owners and colonization of territories, using territory occupancy data of unmarked animals. By also estimating the probability of detecting an occupied territory, the model can handle situations where occupied territories are detected imperfectly, i.e. where the probability of detecting an occupied territory is $P < 1$. The parameters of our model can be estimated only if the territories are surveyed more than once each year, i.e. if data are collected under a robust sampling design (Kendall, Nichols & Hines 1997). Our model builds on the framework of site-occupancy models, which usually estimate the dynamics of the proportion of sites being occupied by a species as a function of local species extinction and species colonization probabilities (MacKenzie *et al.* 2003, 2006; Royle & Kéry 2007). In our present model on territory occupancy data, we treat territories as concepts that are analogous to the single sites in site-occupancy models. We re-parameterized the dynamic site-occupancy model of Royle & Kéry (2007), to contain parameters for individual survival and territory colonization probability. We evaluated the performance of our model by using simulated data as well as data from a long-term population study on nightingales *Luscinia megarhynchos*. We used data on nightingales to obtain survival estimates from territory occupancy data under our model, and then compared those estimates with conventional survival estimates under a Cormack–Jolly–Seber (i.e. mark-recapture) model applied to data from ringed nightingales of the same population. We show that territory occupancy data without individual recognition are useful for estimating demographic parameters such as local survival, which should open up new opportunities for large-scale demographic analyses of animal populations.

Model structure and notation

SAMPLING STRATEGY

Suppose that a population of a territorial species is repeatedly sampled for the presence of territory owners in $i = 1, \dots, n$ territories during $t = 1, \dots, T$ breeding seasons. During each breeding season, the territories are surveyed at $j = 1, \dots, J$ visits, yielding observed territory occupancy histories that are based

on detection/non-detection data of anonymous territory owners. It is required that $J > 1$; such a sampling design is usually referred to as a robust design (Kendall *et al.* 1997). Sampling designs with repeated visits per year are typical for many monitoring programmes that use territory-mapping techniques to obtain population estimates of birds and other animals. For instance, in the common birds census of Switzerland, study plots of 1 km² are selected across the entire country, and each plot is visited 2–3 times within the breeding season of a species and over many years (Kéry & Schmid 2006). During each visit, the position of a detected territory owner, such as a singing male bird, is recorded on a map, yielding observations of occupancy status of territories all over Switzerland. A similar method with about eight visits per breeding season is used in the British common birds census (Baillie *et al.* 2009).

Denote $y_j(i, t)$ as the observed territory occupancy state, i.e. if territory i is observed to be occupied at breeding season t , at visit j , then $y_j(i, t) = 1$, or if it is not observed to be occupied, then $y_j(i, t) = 0$. We assume that $y_j(i, t)$ are independent and identically distributed for each territory i and breeding season t . Denote $x(i, t)$ as the true territory occupancy state, i.e. if territory i is occupied at time t , then $x(i, t) = 1$, or if it is not occupied, then $x(i, t) = 0$. Unlike traditional site-occupancy models, we modelled the occupancy history conditional on the first observed occupancy: the occupancy history for territory i occupied for the first time at $t = f_i$ is the vector $[x(i, t)]_{t=f_i}^T$ with $x(i, f_i) = 1$. Thus, potential territories are considered only from the first time they are occupied by a territorial individual; potential territories that have never been occupied, and territories before first occupation are not considered in the model.

An important point is that the true occupancy state variable $x(i, t)$ is usually not directly observable, i.e. $y_j(i, t)$ is not necessarily the same as $x(i, t)$ because a territory owner is not always detected. Our model accounts for this by including a component for the observation process (see below) that links the true occupancy state $x(i, t)$ with the observations $y_j(i, t)$. Thus, observed territory occupancy data can be naturally described as a state-space model (Royle & Kéry 2007).

DEMOGRAPHIC TERRITORY OCCUPANCY MODEL: THE STATE PROCESS

We describe the state process by using two submodels. The first submodel expresses territory occupancy dynamics as a function of the probability of individual survival and continued tenancy of a territory by its owner. This is what we define as local survival, because it includes both actual survival and territory fidelity. The second submodel includes the probability that an empty territory is colonized. Note that local survival is not the same as what is usually described as apparent survival when analysing mark-recapture data with a Cormack–Jolly–Seber model (Lebreton *et al.* 1992). In the context of mark-recapture data, apparent survival is usually the probability that an individual survives and returns to the same study site, which is the larger area containing all the territories of different individuals. Therefore, if surviving individuals do not switch territories between years within the study site, local

survival from our present territory occupancy model and apparent survival from a Cormack–Jolly–Seber model will coincide. However, if many individuals switch territories between years within a study site, local survival and apparent survival will diverge.

For the first submodel, let the parameter ϕ_t be the local survival probability of a territory owner from year $t - 1$ to t . Denote the latent (i.e. not directly observable) territory fidelity state $z(i, t)$; if a territory i is occupied at time t by the same individual as at time $t - 1$ then $z(i, t) = 1$, otherwise $z(i, t) = 0$. The latent territory fidelity state $z(i, t)$ is assumed to be Bernoulli distributed with parameter ϕ_t , depending on the true territory occupancy state of the previous year $x(i, t - 1)$. The local survival process (first submodel of the state process) is given by the conditional model

$$z(i, t) | x(i, t - 1) \sim \text{Bernoulli}[x(i, t - 1)\phi_t] \quad \text{eqn 1}$$

for $t = f_i + 1, \dots, T$. In other words, if an individual has occupied a territory at time $t - 1$ [i.e. $x(i, t - 1) = 1$], then its latent territory fidelity state $z(i, t)$ is a Bernoulli random variable with parameter ϕ_t . If no individual was occupying a territory at $t - 1$ [i.e. $x(i, t - 1) = 0$], then $z(i, t)$ is Bernoulli distributed with success $P = 0$, that is $z(i, t) = 0$ with $P = 1$.

The second submodel of the state process concerns the probability a currently not occupied territory is colonized by a new individual. Let the parameter r be the territory colonization probability. Conditional on the latent territory fidelity state $z(i, t)$, the true territory occupancy state $x(i, t)$ is a Bernoulli random variable with

$$x(i, t) | z(i, t) \sim \text{Bernoulli}\{z(i, t) + r[1 - z(i, t)]\} \quad \text{eqn 2}$$

Thus, if the latent territory fidelity state $z(i, t) = 1$, then the true territory occupancy state is $x(i, t) = 1$ with $P = 1$, otherwise $x(i, t)$ is a Bernoulli random variable with parameter r . Taking the two submodels eqn 1 and eqn 2 of the state process together, a territory is occupied at time t if the male occupying the territory at time $t - 1$ survives and returns to the same territory with probability ϕ_t , or if a new male colonizes the territory with probability r . The model assumes the same colonization probability r for territories that were not occupied the previous breeding season [i.e. $x(i, t - 1) = 0$], and for territories that were occupied the previous breeding season [i.e. $x(i, t - 1) = 1$] before the territory owner left or died. Thus, in the present model, the territory occupancy state $x(i, t)$ is assumed to be independent of the previous year territory occupancy state $x(i, t - 1)$ given that $z(i, t) = 0$ (i.e. given the territory was previously not occupied, or the former territory owner died or did not return to the same territory).

An alternative way of specifying a territory occupancy model could have been to describe territory occupancy directly in terms of local survival and territory colonization, similarly to Royle & Kéry (2007), who formulated site occupancy of a species as a result of local survival and colonization. Their formulation of a dynamic site-occupancy model could also be adapted to territory occupancy data, by treating territories as

sites. Here, we preferred a slightly different strategy by using the latent territory fidelity state variable $z(i, t)$ that indicates whether a particular territory owner was occupying the same territory also in the previous breeding season. The inclusion of the latent territory fidelity state into the model is not mathematically necessary, but is biologically relevant: territory owners can acquire fitness benefits from returning to a previously occupied territory, e.g. because they are familiar with the territory (Hoover 2003; Middleton, Morrissey & Green 2006). Having the latent territory fidelity state variable $z(i, t)$ specified, the model directly estimates whether a male present in a territory was there also one year before, and inference on biological differences between returning and colonizing males is straightforward.

OBSERVATION PROCESS

Usually, not all occupied territories in a study site are detected in monitoring programmes (Kéry & Schmid 2006; Amrhein *et al.* 2007; Royle *et al.* 2007); our model accounts for this imperfect detection by including the observation process. Let the parameter p be the probability of observing a territory owner during visit j given that the territory is occupied. Similarly to the recently developed site occupancy models (MacKenzie *et al.* 2003, 2006; Dorazio *et al.* 2006), the detection probability p and the true territory occupancy $x(i, t)$ need to be estimated from repeated visits to the territories each year (i.e. employing a robust design), otherwise the parameters cannot be identified. Conditional on the true territory occupancy state $x(i, t)$, the observation $y_j(i, t)$ is given as a Bernoulli random variable

$$y_j(i, t) | x(i, t) \sim \text{Bernoulli}[x(i, t)p] \quad \text{eqn 3}$$

Thus, if a territory is occupied [i.e. $x(i, t) = 1$], then it is observed during visit j to be occupied with probability p ; if a territory is not occupied [$x(i, t) = 0$], it is not observed to be occupied with $P = 1$.

Bayesian analysis and assessment of model performance

We used a Bayesian analysis of our model based on Markov chain Monte Carlo methods (MCMC, Link *et al.* 2002). We assessed convergence using the Gelman–Rubin diagnostic (Brooks & Gelman 1998). MCMC simulations were conducted using WinBUGS 1.4 (Gilks, Thomas & Spiegelhalter 1994), executed in R using the R add-on library R2WinBUGS (Sturtz, Ligges & Gelman 2005). See Appendix S1 (Supporting information) for the WinBUGS implementation of our model.

To explore the performance of our model, we simulated data sets under the territory occupancy model described above (Table 1). Annual local survival was simulated as normally distributed over the years with an overall mean (ϕ_{mean}) and standard deviation (ϕ_{sd}). See Appendix S2 (Supporting information) for an R function to simulate data under our model. For the Bayesian analyses of the simulated data, we

assumed conventional diffuse [i.e. $U(0, 1)$] prior distributions for r and p ; the ϕ_t were assigned normal priors on the logit scale with equal, but unknown mean and variance, i.e. $\text{logit}(\phi_t) \sim N(\mu, \tau)$. The parameters μ and τ were then assigned further distributions; we used the conjugate distributions $\mu \sim N(0, 0.67)$ and $\tau \sim \text{Gamma}(100, 100)$. Such a specification leads to rather diffuse priors for ϕ_t ; if instead a conventional diffuse prior distribution was used for μ , the logit-transformation of μ would result in a U-shaped parameter distribution with much of the density near 0 or 1 (Calvert *et al.* 2009).

The simulations revealed that our model performed well when the sample size was reasonably large and when there were eight visits to the territories per year (i.e. $n = 200$ and $J = 8$, Fig. 1, Table 1a). Under such conditions, the model provided estimates for local survival, territory colonization and detection probability that were close to the true values and had relatively narrow credible intervals. None of the estimators of the parameters were biased. When sample size was sparse and detection probability was low (i.e. $n = 55$, $p = 0.3$, $J = 8$, Table 1a), the parameter estimators were slightly biased: the model on average slightly overestimated r and slightly underestimated ϕ_{mean} . Biases in parameter estimators were rather strong, however, when low detection probability was coupled with fewer yearly visits to the territories (i.e. $p = 0.3$, $J = 3$, Table 1b). This is probably because the reduced information in the data resulted in a posterior distribution of the parameters that to some extent was influenced by the prior. Thus, for these small sample situations, the posterior distribution was probably highly skewed, and the posterior median or mode would likely be more appropriate point estimators (Gelman *et al.* 2004).

Case study: nightingale data

To further explore our model, we used data collected in a long-term population study on nightingales in the Petite Camargue Alsacienne in the Upper Rhine Valley in France. From 2000 to 2009, we monitored the occupancies of 55 territories by means of daily rounds of inspection following a fixed route covering

all 55 territory sites that were occupied at least once during the study period (Amrhein, Korner & Naguib 2002; Amrhein *et al.* 2007; Roth *et al.* 2009). Territories occupied by a singing male nightingale were relatively stable across years irrespectively of the identity of the territory holder, because nightingales frequently use the edges of bushes, paths or rivers as territory borders.

Each year, the field season lasted from the day the first male had settled at the study site (mean \pm SD = 9 April \pm 4.7 days; $n = 10$) until the end of May. On average, the males arrived on 18 April (\pm 2.3 days); no trend in the mean arrival date over the years could be detected (linear regression: year = -0.12 , d.f. = 8, $t = -0.44$, $P = 0.67$). In order to remove males from the data set that were present in a territory for a few days only (transients), we defined a territory as being occupied only if a male was heard singing during at least five inspection rounds per year. During the 10 years of the study, the 55 nightingale territories were occupied during 5.2 ± 2.8 years; six of the territories were occupied only once, and four of the territories were occupied each year. Each year, $52.3 \pm 15.0\%$ of the 55 territories were occupied.

The identity of males was ascertained by regular capturing and ringing throughout the field season (Amrhein *et al.* 2002, 2007). In the 10 years of the study, the territorial males were captured and ringed in $62.5 \pm 22.3\%$ of the territories that were occupied in a given year. Between 2000 and 2008, we captured 99 different males; males that were caught in 2009 for the first time were excluded from the analyses, as those males could not provide information on survival.

We analysed the nightingale territory occupancy data with our model, including year effects on local survival (ϕ_t), and assuming a constant territory colonization (r) and detection probability (p). For the Bayesian analyses, we assumed conventional diffuse [i.e. $U(0, 1)$] prior distributions for the parameters. To test how the model would perform when analysing results from a conventional breeding bird monitoring scheme, in which usually no more than eight to ten visits are being made to a given territory (Baillie *et al.* 2009), we applied the model to a subset of the at least 40 daily visits

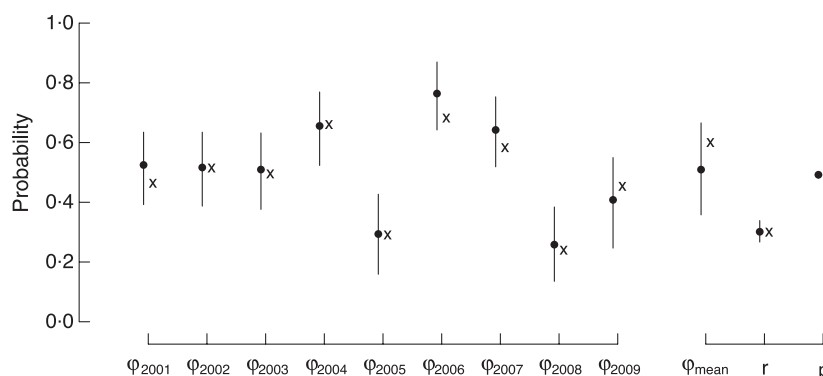


Fig. 1. Parameter estimates obtained from analysing a simulated data set with intermediate detection probability ($p = 0.5$) and with a relatively large sample size (number of territories $n = 200$; number of study years $T = 10$; number of visits per year $J = 8$). Shown are estimated means and 95% credible intervals of the posterior distribution of the local survival per year ($\phi_{2001} - \phi_{2009}$), the mean of the local survival per year (ϕ_{mean}), the colonization rate (r), and the detection probability (p). Crosses indicate the true parameter values used for the simulation.

Table 1. Summary of simulation results for the parameters φ_{mean} (mean of local survival per year), r (colonization rate) and p (detection probability). Given are credible interval (CRI) coverage (cover: proportion of 100 simulation replicates that the 95% CRI contained the true parameter value), bias (difference between mean estimate minus true value), and CRI length (length: mean length of CRI). True parameter values used for simulation were inspired by the analysis of our nightingale data, with $r = 0.30$, $\varphi_{\text{mean}} = 0.55$, and $\varphi_{\text{sd}} = 0.20$. The number of study years was set to $T = 10$. The number of territories was set to cover a relatively large sample size ($n = 200$) and, alternatively, the sample size from our nightingale data ($n = 55$)

Parameter	Cover	Bias	Length	Cover	Bias	Length	Cover	Bias	Length
(a) Eight visits per study year ($J = 8$), as in the British common birds census (Baillie <i>et al.</i> 2009)									
	$p = 0.7$ $n = 200$			$p = 0.5$ $n = 200$			$p = 0.3$ $n = 200$		
φ_{mean}	0.98	0.00	0.36	0.95	-0.02	0.38	0.94	-0.02	0.40
r	0.91	0.00	0.12	0.95	0.01	0.14	0.93	0.01	0.15
p	0.96	0.00	0.03	0.96	0.00	0.04	0.86	0.01	0.04
	$p = 0.7$ $n = 55$			$p = 0.5$ $n = 55$			$p = 0.3$ $n = 55$		
φ_{mean}	0.98	0.00	0.41	0.95	-0.04	0.46	0.95	-0.05	0.47
r	0.94	0.01	0.19	0.91	0.02	0.23	0.90	0.03	0.23
p	0.97	0.00	0.06	0.96	0.00	0.07	0.95	0.00	0.07
(b) Three visits per study year ($J = 3$), as in the Swiss common birds census (Kéry & Schmid 2006)									
	$p = 0.7$ $n = 200$			$p = 0.5$ $n = 200$			$p = 0.3$ $n = 200$		
φ_{mean}	0.91	-0.02	0.38	0.95	-0.04	0.42	0.80	-0.14	0.53
r	0.90	0.01	0.14	0.93	0.00	0.15	0.96	0.04	0.32
p	0.98	0.00	0.07	0.77	-0.06	0.09	0.50	0.06	0.17
	$p = 0.7$ $n = 55$			$p = 0.5$ $n = 55$			$p = 0.3$ $n = 55$		
φ_{mean}	0.95	-0.03	0.46	0.94	-0.07	0.56	0.58	-0.14	0.80
r	0.92	0.02	0.22	0.94	0.06	0.36	0.64	0.04	0.45
p	0.95	0.01	0.11	0.93	0.03	0.20	0.49	0.08	0.28

we made at the study site each year. This subset included observed nightingale territory occupancy data from eight arbitrarily chosen visits (observed territory occupancies from the visits made every fifth day from 15 April to 20 May). The results on local survival from our model were then compared with the yearly apparent survival (φ_t , which is the probability an individual survives between two years and returns to the same study site), obtained from analysing the data on captured individuals with a state-space formulation of the traditional Cormack–Jolly–Seber model (CJS, i.e. a mark-recapture model, Royle 2008). The CJS model also included a constant capturing probability (p). For the Bayesian analyses of the CJS model, we assumed conventional diffuse [i.e. $U(0, 1)$] prior distributions for all φ_t and p .

The results from analysing the nightingale data showed parallel fluctuations of the local survival calculated from territory occupancy data under our model, and of apparent survival estimated from mark-recapture data (Fig. 2); the posterior means of the yearly estimates were strongly correlated (Pearson’s correlation: $r = 0.82$, $t = 3.77$, d.f. = 7, $P = 0.007$).

Discussion

We developed and illustrated a new model for estimating local survival, using a demographic site-occupancy model applied to territory occupancy observations without individual recognition of animals. Similar to the recently developed site-occupancy models (MacKenzie *et al.* 2003, 2006; Dorazio

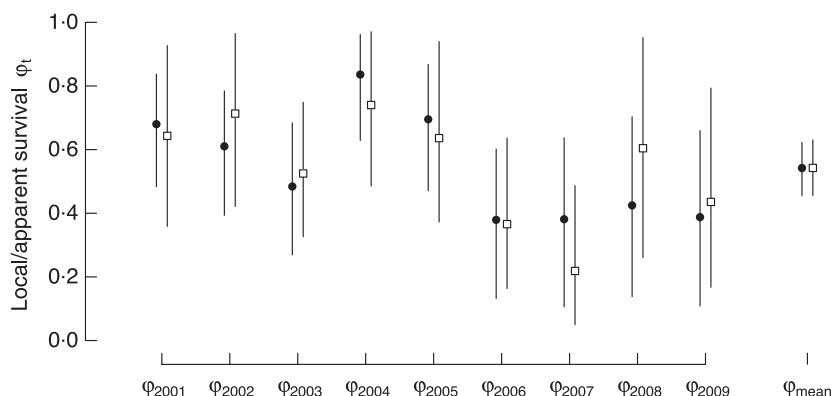


Fig. 2. Local survival estimates obtained from nightingale territory occupancy data under our model, compared to apparent survival estimates obtained from nightingale ringing data. Given are estimated values of local/apparent survival per year ($\varphi_{2001} - \varphi_{2009}$), and the mean local/apparent survival (φ_{mean}). Our present territory occupancy model was used to analyse eight visits per territory and year (●), and a traditional Cormack–Jolly–Seber model was applied to the mark-recapture data from ringed nightingales (□). Shown are means and 95% credible intervals of the posterior distributions.

et al. 2006), our model can cope with imperfect detection of the occupied territories. Unless data were very scarce, our simulation results revealed that parameter estimates were reliable even when some occupied territories are not detected due to a low detection probability or due to a small number of visits per territory. This is important, because territory occupancy data from monitoring schemes or from population studies of single species are usually obtained by visiting the potential territories only a few times per year, and because territory owners are not always detected (Kéry & Schmid 2006; Amrhein *et al.* 2007; Royle *et al.* 2007).

An important condition for applying our model is that territories can be monitored accurately in all years of a study. Arguably, the size and shape of territories may change between years depending on social and environmental variables (Pärt & Gustafsson 1989; Pons *et al.* 2008). However, in many species, the locations of territories remain relatively stable from year to year, because territory owners often defend areas that include rare but spatially stable resources such as isolated habitat patches, nest cavities, or food resources (Newton 1998). If the locations, but not the shape or size of the territories remain stable between years, accurate territory occupancy data may still be obtained. Indeed, high quality territory occupancy data are available for many species, e.g. from national monitoring schemes (Sergio & Newton 2003).

A benefit of the hierarchical model formulation that we used for our model is its great flexibility and ease with which the model can be adapted to different situations (Chapter 1, Royle & Dorazio 2008). The present model contained local survival probabilities that varied between years, but constant territory colonization and detection probabilities. If appropriate, however, dynamic effects could also be considered for temporally changing colonization and detection probabilities. Further, the hierarchical modelling approach also allows covariates to be included (Royle & Dorazio 2008). For example, our models could be used to investigate how the variation in local survival or territory colonization correlates with characteristics of the territories, or with characteristics of the territory owners such as measures of sexually selected traits or of pairing status. Such information could provide a deeper understanding of the populations and individuals under study (for the integration of covariates in hierarchical models in a Bayesian framework, see for instance Kéry & Royle 2008). Our model could also be used for large-scale investigations of demographic parameters, to compare local survival and colonization rates among regions in entire countries.

In most territorial species, only males are surveyed in monitoring programmes, because they often are more conspicuous than females and actively advertise their territories (Andersson 1994). When using data from monitoring programmes, our model thus is likely to estimate only local survival of males. However, the advantage of territory occupancy data is that they can easily be collected or, in the case of many national monitoring programmes (Kéry & Schmid 2006; Baillie *et al.* 2009), often already are available. Furthermore, in the case of certain endangered species or of species that are difficult to capture, researchers may prefer not to mark individuals.

Under such circumstances, observed territory occupancies might be the only data available.

In the case study on nightingales, the survival estimates obtained from our territory occupancy model corresponded very well with the survival estimates obtained from a mark-recapture model, suggesting that our territory occupancy model is generally reliable. Note, however, that local survival as estimated from our model and apparent survival as estimated from mark-recapture models are expected to coincide only if individuals do not switch territories between years within the study site. If such switches do occur, they are not usually detected in studies on territory occupancy of unmarked animals, leading to underestimation of true survival when applying our model. As in other bird species (Harvey, Greenwood & Perrins 1979; Beletsky & Orians 1987; Pärt & Gustafsson 1989), a moderate proportion of male nightingales at our study site do switch territories from one year to the next (unpublished data). Because the birds at our study site are part of a larger nightingale population in the Upper Rhine Valley, several males that switched territories may have selected new territories outside our study site. In cases where individuals emigrate from a study site, both the estimates of local survival of unmarked animals and the estimates of apparent survival of marked animals will be similarly biased due to territory switches, which may explain why in our nightingale study, both models yielded similar estimates.

Estimating demographic parameters from survey data without individual recognition seems to be a promising new tool, but its potential for general application needs to be further explored. More studies are needed that apply the model to other territorial species and compare the results with traditional estimates of demographic parameters using marked individuals. Additionally, further development of our model may contribute to the advancement of integrated population models that combine different sources of demographic data (Schaub *et al.* 2007). Thus, mark-recapture data and territory occupancy data may be combined to obtain more precise estimates of the parameters described in this study, or of estimates of additional parameters. In conclusion, we suggest that adopting hierarchical mark-recapture models to territory occupancy data can make large amounts of data available for research on animal demography.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. WinBUGS model specification for the model described in the paper.

Appendix S2. R code for the simulation function.

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