OPEN MODELS FOR REMOVAL DATA

By Eleni Matechou, Rachel S. McCrea, Byron J.T. Morgan, Darryn J. Nash and Richard A. Griffiths

University of Kent

Individuals of protected species, such as amphibians and reptiles, often need to be removed from sites before development commences. Usually, the population is considered to be closed. All individuals are assumed to i) be present and available for detection at the start of the study period and ii) remain at the site until the end of the study, unless they are detected. However, the assumption of population closure is not always valid. We present new removal models which allow for population renewal through birth and/or immigration, and population depletion through sampling as well as through death/emigration. When appropriate, productivity may be estimated and a Bayesian approach allows the estimation of the probability of total population depletion. We demonstrate the performance of the models using data on common lizards, *Zootoca vivipara*, and great crested newts, *Triturus cristatus*.

1. Introduction. When protected species occur on a site scheduled for development, there may be a legal requirement for them to be relocated to an alternative site before the development can proceed (Germano et al., 2015). In the UK, such relocations are often required for amphibians and reptiles. These relocations are typically achieved by conducting regular surveys during which detected animals are relocated to a suitable alternative habitat. We refer to collection and removal as translocation. The duration of the translocation is determined by the predicted size of the community and/or constituent species present. Current guidelines (developed 18 years ago) state that translocations should last between 60 and 120 'suitable' days (HGBI, 1998). After the prescribed period has elapsed, a minimum of five trap-free days is required before the translocation is considered to be complete. Although it is acknowledged that some individuals may be left behind, this is considered to be 'reasonable effort' in line with current UK legislation. More recent guidance is less prescriptive, but suggests survey effort may need to last for 1-3 years (Natural England/ Defra 2015) .

Our proposed methods were motivated by removal sampling data of the kind illustrated in Tables 1 and 2. The species surveyed are respectively common lizards, *Zootoca vivipara*, and great crested newts, *Triturus cristatus*. Both of these are protected species, which are frequently removed from the path of development, giving rise to data of the form illustrated.

The original model for removal sampling dates back to Moran (1951) and Zippin (1956). The model is the same as model M_b in the Otis notation for closed population models, (McCrea and Morgan, 2014, Chapter 3), which allows for behavioural response to trapping, with recapture probability constrained to zero. Under this model, expected numbers of individuals decrease geometrically over time, as a consequence of the assumptions of closure and constant capture probability. We refer to this as the geometric model. Recent work on removal sampling includes Bohrmann and Christman (2013), who discuss sampling design, and Dorazio, Jelks and Jordan (2005), who present a hierarchical model for when the sample site can be considered to be made up of several distinct sub-sites distributed spatially, with independent counts taken at each site. In addition, Dorazio, Jelks and Jordan (2005) allow for heterogeneity in capture using a beta-binomial distribution. We note in passing that such an extension to the basic removal model corresponds to models for digit preference in fecundability studies, when the total number of individuals in the study is unknown; see Morgan and Ridout (1991). Dorazio et al. (2008) propose a Bayesian non-parametric model for dealing with unobserved sources of heterogeneity and Ruiz and Laplanche (2010) account for the effect of individual variability on population size estimation from removal data.

Existing removal models assume population closure for the duration of the study. However, it is often the case when sampling amphibians and reptiles that the study period encompasses the reproduction period, and hence the population is renewed by the emergence of newborn individuals, violating the assumption of closure. This population renewal is suggested by the data set of common lizards (TABLE 1) where it can be seen that the number of individuals detected peaks in August, three months after the study commenced. The ecology of the species suggests that this is the result of a renewal of the population due to birth (Avery, 1975). Motivated by this and similar data sets, we develop a model that allows for a group or groups, of unknown size, of individuals to emerge/arrive at an unknown time while accounting for individuals that may die or permanently emigrate during the study period. In addition, the model estimates the number of undetected individuals, that is the number of individuals remaining at the site at the end of the study. We note that the number of undetected individuals is the demographic parameter of interest in removal studies. We fit the model using a Bayesian approach to obtain the posterior distribution of the population size. An attractive feature of the Bayesian approach is that it is straightforward to estimate the probability that no animals remain (i.e. that the population is totally depleted). This is analogous to the use of Bayesian methods to estimate the probabilities of bird species being endangered (see Brooks et al., 2008).

Additionally, when the study takes place at an unfenced breeding site and commences before the start of the breeding season, individuals can migrate into or out of the breeding site, thus violating the assumption of population closure. Populations of great crested newts are a typical example, because they are known to migrate to breeding ponds in a staggered manner and then depart at the end of the breeding season. In this case, the number of renewal groups is unknown. We therefore further extend the model to allow for

an unknown number of renewal groups and we use a reversible jump (Green, 1995, RJ) MCMC algorithm to fit the model and estimate the renewal pattern and the number of renewal groups.

The model we present responds to a practical ecological need, as data of the type we analyse are often encountered. It provides a completely general modelling framework which extends existing simple models to include features such as survival and recruitment. Conclusions resulting from using rules of thumb or inappropriate model fitting, with no allowance for features such as renewal or variable detection, may be used to conform to current legislative guidelines, therefore it is critical that new statistical approaches are developed so that deleterious effects on protected species can be prevented.

We introduce the model and the parameters in section 2. We present each motivating example and the results of model fitting in sections 3 and 4 respectively. Further extensions to the model are discussed in section 5. Convergence diagnostics, RJMCMC details and simulation results are provided in the Appendix.

2. Model. We assume that there are T sampling occasions taking place at times τ_t, $\in$ **R**, $t = 1, \ldots, T$ and individuals detected at an occasion are permanently removed from the study site. The data set of a single species, **n**, is a vector of length T with entry n_t, $t = 1, \ldots, T$ denoting the number of individuals of that species removed at occasion t. The total number of individuals of a species detected and removed from the site is denoted by $D = \sum_{t=1}^{T} n_t$, and the unknown number of individuals that will remain at the site when the study ends by N with $N \geq 0$. The primary aim of sampling is population depletion, and hence the main objective of modelling is to estimate N or its posterior distribution.

Each individual in the population belongs to one of $T + 2$ categories. If an individual belongs to category t, $t = 1, \ldots, T$, then it was removed at sampling occasion t. The N individuals that were never detected and not removed belong to category $T + 1$. The remainder of the individuals, M, left the study site either through death or emigration before being detected and before the study ended.

The probability, γ_t, of an individual belonging to category t is a function of the following parameters:

- $\beta_{t-1}, t = 1, \ldots, T$: entry parameters. The proportion of individuals that became available for detection for the first time at sampling occasion t.
  The proportion of individuals that became available for detection at least once during the study is $\Omega = \sum_{t=1}^{T} \beta_{t-1}$, while the complement of Ω, $1 - \Omega$, is equal to the proportion of individuals that arrived after the end of the study and therefore never became available for detection. It is anticipated that Ω will be close to 1 by study design.
- ϕ_t: survival probability. The probability an individual present at sampling occasion t remains until occasion $t + 1$. The parameter ϕ is used to account for natural mortality and emigration, in addition to the removal process for detected individuals,

and therefore denotes apparent survival, as it is referred to in the capture-recapture
literature.

- p_{t-b}: detection probability. The probability of detecting an individual that is present
  at sampling occasion t and first became available for detection at occasion b, hence
  having avoided detection $t - b$ times, at occasions $b, \ldots, (t-1)$. The parameter p_0
  denotes the probability of being detected upon arrival.

Therefore, the probability γ_t can be expressed as

$$
\gamma_t = \begin{cases}
\sum_{b=1}^{t} \left[\beta_{b-1} \left\{ \prod_{k=b}^{t-1} \phi_k \right\} p_{t-b} \right], & t = 1, \ldots, T \\[3mm]
\sum_{b=1}^{T} \left[\beta_{b-1} \left\{ \prod_{k=b}^{T-1} \phi_k \right\} \left(1 - \sum_{k=b}^{T} p_{k-b} \right) \right] + (1 - \Omega), & t = T + 1 \\[3mm]
1 - \sum_{t=1}^{T+1} \gamma_t, & t = T + 2
\end{cases}
$$

where the empty product $\prod_{k=t}^{t-1} \phi_k$ is taken to be unity.

If we denote the vector of model parameters by $\boldsymbol{\theta}$, the data are described by the multi-
nomial distribution,

$$
(2.1) \qquad \mathcal{P}(\mathbf{n}|\boldsymbol{\theta}) = \frac{(N + M + D)!}{\left(\prod_{t=1}^{T} n_t! \right) N! M!} \left\{ \prod_{t=1}^{T} \gamma_t^{n_t} \right\} (\gamma_{T+1})^N \left(1 - \sum_{t=1}^{T+1} \gamma_t \right)^M .
$$

Alternatively, conditioning on the event of surviving until detection (or until the end of the
study for undetected individuals), we can work in terms of the conditional probabilities,

$$
(2.2) \qquad \mathcal{P}_c(\mathbf{n}|\boldsymbol{\theta}) = \frac{(N + D)!}{\left(\prod_{t=1}^{T} n_t! \right) N!} \left\{ \prod_{t=1}^{T} \left(\frac{\gamma_t}{\sum_{t=1}^{T+1} \gamma_t} \right)^{n_t} \right\} \left(\frac{\gamma_{T+1}}{\sum_{t=1}^{T+1} \gamma_t} \right)^N .
$$

Instead of using Eq. (2.1), we shall follow the conditional approach and use Eq. (2.2),
which is not a function of M, for two reasons: 1) M is of no ecological interest in this case
as the aim of sampling is to estimate N and the probability that it is zero, and 2) using
the unconditional approach of Eq. (2.1) results in poor mixing in the MCMC algorithm
to be used, especially for parameter M. If M is of interest then the mixing of the chain
can be improved by using more sophisticated proposal distributions that account for the
correlations between M and $\{\phi_t\}$ and running the algorithm for longer.

We assume that individuals arriving or emerging into the population do so in groups,
called renewal groups, and we model the arrival pattern of these groups using the probabil-
ity density function (pdf) of a normal distribution. Mixtures of normal distributions have
also been used by Matechou et al. (2014) to model emergence of butterfly broods and by
Matechou et al. (2015) to model arrival of flocks of birds at stopover sites.

For the data set of common lizards we allow for one renewal group of unknown size, which corresponds to newborn individuals. We assume that the proportion of individuals in this renewal group is equal to π_2, with $\pi_1 = 1 - \pi_2$ denoting the proportion of individuals already present at the start of the study. We further assume that the arrival times of members of the renewal group can be described by a normal pdf with mean μ and variance σ^2, so that the proportion of individuals with arrival time in the interval $(\tau_{b-1}, \tau_b]$ is equal to

$$\beta_{b-1} = \pi_2 P(\tau_{b-1} < X \le \tau_b)$$

for $b \in \{2, \ldots, T\}$ while $\beta_0 = \pi_1 + \pi_2 P(X \le \tau_1)$, where $X \sim N(\mu, \sigma^2)$.

For the data set of great crested newts, we allow for an unknown number, G, of renewal groups, each of unknown size and unknown arrival/emergence pattern, and each modelled by a normal pdf as explained in the previous paragraph. In this case, π_g, μ_g, and σ_g^2, $g = 1, \ldots, G$, are respectively, population fractions, mean arrival times, and variance of arrival times of the G renewal groups, with $\sum_{g=1}^{G} \pi_g = 1$. The proportion of individuals with arrival time in the interval $(\tau_{b-1}, \tau_b]$ is now given as

$$\beta_{b-1} = \begin{cases} \sum_{g=1}^{G} \pi_g P(\tau_{b-1} < X_g \le \tau_b), & b = 2, \ldots, T \\[2mm] \sum_{g=1}^{G} \pi_g P(X_g \le \tau_1), & b = 1 \end{cases}$$

where $X_g \sim N(\mu_g, \sigma_g^2)$.

We adopt a Bayesian approach for inference and fit the model by using an MCMC algorithm. In the case of an unknown number of renewal groups, we use an RJMCMC algorithm, that moves between models with different numbers of groups. The two detailed applications that follow are designed to take into account known features of the studied animals.

3. Common lizards. To facilitate the redevelopment of a large area of brownfield land in Cumbria, a region in the north of England, a programme of reptile collection and removal was undertaken in 2007. Three areas of land that supported reptiles were enclosed by purpose-built reptile exclusion fencing. Within each of the resulting compartments, artificial refuges ($0.5m^2$ sheets of felt and metal) were placed at a density of approximately $50ha^{-1}$ within suitable habitat. These refuges were checked once per day in the mornings only during suitable weather conditions. Common lizards were captured by hand and moved to an ex situ receptor site. The resulting removal data and daily records of temperature (maximum temperature in $^\circ C$) are presented in TABLE 1.

Profile likelihood plots for N obtained from fitting the geometric model (which corresponds to the case of $\beta_0 = 1$, $\beta_{t-1} = 0, \forall t > 1$, and $\phi_t = 1, \forall t$ for the data show (FIG. A6(a)) that the maximum-likelihood estimate obtained for N is equal to 903 individuals. This estimate for N is over four times the sample size and the likelihood surface is practically flat over a large range of values for N. The curvature around the maximum likelihood

estimate for N is low, resulting in profile likelihood intervals that extend beyond values of N greater than 10000, 50 times the sample size. The wide profile likelihood intervals are due to the fact that the assumption of population closure is violated, because it is evident that a large proportion of the common lizard population actually arrived/emerged long after the start of the study. The result suggests that when there is renewal of the population during a removal study then a different model from the geometric is needed. For comparison, we also show the profile log-likelihood plot for N obtained from fitting the model presented in section 2, which allows for one renewal group to demonstrate that the likelihood surface is no longer flat in this case (FIG. A6(b)). Note that we constrain $\phi = 1$ for this illustration.

Based on the literature concerned with the effect of temperature on the detection probability of reptiles (Sewell et al., 2012), we logistically regress detection probability on maximum temperature and its square, and hence set

$$\log\left(\frac{\eta_t}{1 - \eta_t}\right) = \alpha_0 + \alpha_1 x_t + \alpha_2 x_t^2,$$

with x_t the maximum recorded temperature on sampling occasion t and $\alpha_0, \alpha_1, \alpha_2$ the regression coefficients, which gives the following expression for p_{t-b}

$$(3.1) \qquad p_{t-b} = \eta_t \left\{ \prod_{k=b}^{t-1} (1 - \eta_k) \right\}^{\mathbb{I}(t>b)},$$

where the indicator variable $\mathbb{I}(t > b)$ is equal to 1 if $t > b$ and 0 otherwise.

We chose a Unif$[0, 1000]$ prior for the population size and a Dirichlet$(1, 1)$ for the proportion of N in each group, π_1, π_2. We set the prior for the mean arrival time of the renewal group to be Normal with mean which corresponds to the end of July - beginning of August, based on the ecology of the species (Avery, 1975) and a standard deviation of roughly one month (30 days). Finally, we chose a half-normal prior for the standard deviation of arrival times of the renewal group with parameter 0.1, a N$(0, 1)$ prior for the coefficients of the covariates in the logistic regression model for detection probability, p, and a Unif$(0, 1)$ prior for ϕ.

We provide the results of convergence diagnostics in Section A8.1. The posterior distribution and cumulative posterior distribution for N are shown in FIG. 1. Although the probability that the population has actually been depleted, which corresponds to the probability that $N = 0$, is lower than 10%, most of the posterior distribution mass is concentrated on values that are close to 0. In fact, the model estimates that with a 95% probability, there were at most eight common lizards at the site after the end of the study. From the observed data, one might have expected that it would be likely that the population was totally depleted at the end of the sampling due to the observed trailing zeros, however as noted above, the probability of total depletion is actually less than 0.1.

Because in this application the renewal group is thought to consist of juvenile common lizards which are born in the current breeding season, by comparing the estimated proportion of individuals in each emergence group to the estimated total population we can also extract information on the number of juveniles per adult (i.e. the rate of productivity). The posterior mean for π_2/π_1 is equal to 3.16 with a 95% posterior credible interval (CI) of (2.20, 4.43). Avery (1975) reports that female common lizards each produce between 3 and 11 juveniles per breeding season, with an average of 7.74. Therefore assuming an equal sex-ratio of individuals in our study, our estimate of productivity is in close agreement with this previous finding.

The mean arrival time of the juvenile renewal group has a posterior mean of 77.89 (95% posterior CI = (76.34, 80.47)), which corresponds to the beginning of August, as would be expected given the northern location of this study site in England (Van Damme, Bauwens and Verheyen, 1990).

The posterior mean of apparent survival probability is 0.997 (95% posterior CI = (0.989, 0.999)), suggesting that the reduction in the size of the population by the end of the study is mostly due to sampling instead of emigration or death.

The fit of the model is assessed by generating data from randomly chosen parts of the chain and comparing them to the true data set in FIG. 2, where it can be seen that the model provides a good description of the increase in the number of individuals detected due to population renewal, and the actual numbers of common lizards detected are mostly encompassed by the 95% quantile intervals of the simulated values. The model achieves a good fit to the data despite the sparseness of the data and the fact that no samples were collected during the days when emergence of juveniles peaked.

Finally, the posterior distribution of detection probability as a quadratic function of maximum temperature is summarised in FIG. 3. We find that detection probability is at its maximum in mild weather when maximum temperature is roughly equal to 14°C, while it decreases considerably as maximum temperature decreases or increases. Our conclusion regarding the relationship between detection probability and temperature is in agreement with literature on the subject (Reading, 1997; Gent and Gibson, 1998; Joppa et al., 2009). The large width of the posterior CI at low temperatures is due to the fact that there were very few surveys conducted under these conditions compared to higher temperatures.

4. Male great crested newts. An extensive removal study was conducted at a site in the east of England in 2010 prior to a substantial commercial development project. The areas where great crested newts were most likely to be found were fenced off to intercept the animals coming in from their hibernation areas to the ponds which were in the middle of the site. The trapping consisted mainly of collecting animals from pitfall traps and this was supplemented by two evenings of sampling using torchlight. The data we consider here consist of removals of adult male individuals. Minimum air temperature was also recorded for most sampling occasions.

An RJMCMC algorithm was used to fit a model with an unknown number of arrival

groups assuming constant survival probability, ϕ, and detection probability varying with minimum air temperature at sampling occasion t, x_t, such that

$$\log\left(\frac{\eta_t}{1 - \eta_t}\right) = \alpha_0 + \alpha_1 x_t.$$

Missing values for the covariate were imputed using the average of minimum temperatures recorded on the two adjacent sampling occasions.

We used a vague Unif$\{1, \ldots, 20\}$ for the number of renewal groups, G, a Unif$[0, 1000]$ prior for N, a Dirichlet with all concentration parameters equal to 1 for π_g, $\forall g$, a Unif$(1, T)$ prior for μ_g to reflect our expectation that individuals are arriving during the study and not before or after, a half-normal with parameter 0.1 for σ_g $\forall g$, a $N(0, 1)$ for the coefficients of the logistic regression model for p and a Unif$(0, 1)$ prior for ϕ.

We present details on the RJMCMC algorithm and the convergence diagnostics used in Section A8.2.

The posterior distribution for G, the number of arrival groups, is mostly (87%) concentrated on the values 7 and 8 (Fig. A10(a)). The posterior distribution for N is mostly (80%) concentrated on 0 (Fig. A10(b)) and we estimate that there is a probability of 5% that 2 or more individuals were at the site after the study ended. The low estimated number of undetected individuals is unsurprising as not only do the data have a large number of trailing zeros at the end of the study, but the estimated mean arrival times of the renewal groups are primarily in the first half of the study (see Fig 4).

Posterior summaries of the probability of detection as a function of minimum air temperature are presented in Fig. 5 where it can be seen that, as expected (Sewell, Beebee and Griffiths, 2010), newts are more likely to fall into the traps as the temperature increases. Although the slope of the logistic curve is steep, the 95% posterior CIs are fairly wide. The large width of the posterior CIs is possibly due to a moderate effect of minimum air temperature on detection probability but it could also be an artefact of the increased uncertainty due to the use of RJMCMC.

The posterior mode for survival probability is around 0.1, with the posterior mean equal to 0.19 (95% posterior CI: 0, 0.6 and 95% HPD interval : 0, 0.5) because the posterior density has a long right tail. This low apparent survival probability in comparison to the common lizard apparent survival probability is likely due to study design. Within the newt study, the traps are outside of the ponds and so newts are able to more easily leave the study area without falling into the traps.

The fit of the model is assessed graphically in Fig. 4(b) where it is seen that all of the observed counts lie within the boundaries of the 95% quantile intervals of the counts simulated by the model using randomly chosen iterations of the algorithm.

5. Possible extensions. The effect of unmodelled individual heterogeneity in either detection or survival probability on the estimation of population size has been well documented in the literature (McCrea and Morgan, 2014, Chapter 3, and references therein).

Our simulations presented in Section A8.3 suggest that in the case of removal data, such as those considered in this paper, if there exists heterogeneity in p which the model does not account for, then the posterior for N tends to be concentrated to the left of the true value for N. If N is small, as in the case studies considered in sections 3 and 4, then the resulting bias is also small. However, when N is large and the population is far from being depleted, then the bias in N can be substantial.

If individuals are expected to exhibit variation in their detectability, then the probability of detection can be modelled as a random variable with a beta-geometric distribution with respective mean and shape parameters η and θ (see Morgan, 2008, section 2.3) which gives

$$(5.1) \qquad p_{t-b} = \eta \frac{\prod_{k=b}^{t-1} \{1 - \eta + (k-b)\theta\}}{\prod_{k=b}^{t} \{1 + (k-b)\theta\}}.$$

Note that in the case of common detection probabilities between individuals (i.e. when $\theta = 0$) p_{t-b} simplifies to a standard geometric model with probability of success η, and

$$p_{t-b} = \eta \prod_{k=b}^{t-1} (1 - \eta) = \eta(1 - \eta)^{t-b}.$$

Similarly, if it is anticipated that detection probability depends on covariates, such as environmental factors, as was the case for the applications in sections 3 and 4, then η can be modelled as a function of these, using a logistic regression model. If $\mathbf{x}_1, \ldots, \mathbf{x}_q$ are q environmental covariates and $\boldsymbol{\alpha}$ is a set of coefficients of length $q + 1$

$$\log\left(\frac{\eta_t}{1 - \eta_t}\right) = \alpha_0 + \alpha_1 x_{1t} + \ldots + \alpha_q x_{qt},$$

which for example in the case $\theta = 0$ gives

$$p_{t-b} = \eta_t \prod_{k=b}^{t-1} (1 - \eta_k).$$

It is easy to show that when appropriate the model can naturally accommodate both heterogeneity and environmental covariates, as long as the covariate(s) are discrete or discretised so that the values for all years are not all different. In this discrete case, the recapture probabilities are suitable products of terms of the form illustrated in expression (5.1).

An alternative approach for modelling heterogeneity, both in detection and survival probabilities, is provided by Pledger (2000) via the use of finite mixture models. Finite mixture models have been used extensively in the capture-recapture literature for both open and closed populations and they provide an effective way to model heterogeneity.

Our presented model assumes that there is no temporary emigration and hence once an individual has been removed or has departed from the study it does not return. However,

amphibians and reptiles have activity patterns that vary according to weather conditions and may become unavailable for detection for a period of time. This issue of temporary unavailability for capture is the equivalent of temporary emigration in the capture-recapture literature - see for example Barker (1997), Kendall, Pollock and Brownie (1997) and Kendall and Nichols (2002). Although for the data sets considered in this paper we estimated that the population was practically depleted before the expected start of the hibernation period (i.e end of October (Beebee and Griffiths, 2000)), it is possible that some individuals evaded detection by becoming less active as winter approached. We are currently working on extensions of the models presented in this paper that use a multi-state approach to allow for temporary emigration of individuals, developing methodology from standard capture-recapture literature (Pradel, 2005).

Removal data alone may be insufficient to estimate all parameters of interest, however models for removal data have survival and detection parameters in common with capture-recapture models. Therefore it may be possible to perform an integrated analysis - simultaneously modelling removal data and independent capture-recapture data (see Besbeas et al., 2002). This integrated analysis would result in generally improved precision of parameter estimates and may overcome challenges such as near-singularity and parameter redundancy of models (Cole and McCrea, 2015).

6. Discussion. Translocations of protected species from the path of development are widespread in the UK and globally. However, such actions are expensive, often poorly designed and monitored, and undetected animals may comprise a significant proportion of the population left behind at the development site (Lewis et al., 2014; Germano et al., 2015). The models we propose here provide a basis for determining the effectiveness of such translocations and thereby improving policy and guidance for such actions.

We have proposed a new model for the case of removal data when the assumption of population closure is violated because of: a) individuals emerging/arriving sometime after the start of the study, either through birth and/or immigration, and renewing the population and b) individuals departing from the study site before being detected through death and/or emigration.

The model allows for either a fixed number of known renewal groups or an unknown number, and estimates their sizes as well as the means and variances of arrival times of the individuals in these groups. The model of this paper responds to a practical need, as the data described are commonly encountered.

We provided two applications:

i) a data set of common lizards collected during a period that encompassed the reproduction period and hence there was one renewal group which consisted of juveniles that emerged in late summer. We estimated the probability of population depletion as less than 10%. The ratio of juveniles to adults in the population was also derived as a by-product of the analysis.

ii) a data set of male great crested newts collected during the time when individuals are migrating to ponds to breed, where we used an RJMCMC algorithm to account for and estimate the number of renewal groups. In this case, the probability of population depletion was estimated at around 80%.

We have also incorporated environmental covariates in the estimation of detection probabilities and although we have not undertaken a detailed model-selection exercise for our choice of covariates, we have shown using simulation that the model provides a good description of the data. The functional form of the covariate regression used for each application was guided by ecological knowledge. Our results suggest that detection probability of common lizards is lower when the maximum daily temperature is too low or too high, with the optimum being roughly at $14°$C. We found that the detection probability of great crested newts varied with minimum air temperature, and as minimum air temperature increased, so did detection probability which is in-line with previous findings relating weather conditions to detectability of these animals (see Sewell, Beebee and Griffiths, 2010).

It is important to note that while the new model incorporating both arrivals and departures provides good descriptions of the two data sets that we analyse in the paper, if capture probability is high then there could be difficulties in estimating ϕ: if individuals are removed soon after arrival then retention due to survival cannot be observed. The model has performed well in both case studies considered but care should be taken when fitting complex models to sparse data. The diagnosis of possible parameter redundancy of the new model, along with how it might be overcome by combining additional information is an area of current research.

A great advantage of adopting a Bayesian approach for model fitting is that we can evaluate the probability that more than n individuals remain at the study site for any n. In further work, we plan to investigate the posterior predictive distribution after each sample is collected to use this as a guide for calculating the number of samples still required before total population depletion is achieved.

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TABLE 1
Removal sampling: counts of common lizards removed in 2007. A dash indicates that no sampling took place on that day. Temp denotes the maximum daily temperature (°C) recorded on each visit to the study site. Here, the number of removed individuals, $D = 213$.

Date	Count	Temp	Date	Count	Temp	Date	Count	Temp	Date	Count	Temp
24-May	0	20	02-Jul	2	15	10-Aug	7	19	18-Sep	6	16
25-May	-	-	03-Jul	7	17	11-Aug	-	-	19-Sep	6	16
26-May	-	-	04-Jul	3	16	12-Aug	-	-	20-Sep	6	14
27-May	-	-	05-Jul	1	15	13-Aug	12	18	21-Sep	4	14
28-May	-	-	06-Jul	1	15	14-Aug	8	20	22-Sep	-	-
29-May	-	-	07-Jul	-	-	15-Aug	1	18	23-Sep	4	14
30-May	-	-	08-Jul	-	-	16-Aug	10	14	24-Sep	1	14
31-May	-	-	09-Jul	1	16	17-Aug	9	16	25-Sep	5	11
01-Jun	0	22	10-Jul	-	-	18-Aug	-	-	26-Sep	5	12
02-Jun	-	-	11-Jul	-	-	19-Aug	-	-	27-Sep	0	12
03-Jun	-	-	12-Jul	2	17	20-Aug	6	17	28-Sep	2	12
04-Jun	-	-	13-Jul	-	-	21-Aug	-	-	29-Sep	-	-
05-Jun	1	21	14-Jul	-	-	22-Aug	-	-	30-Sep	1	14
06-Jun	0	21	15-Jul	-	-	23-Aug	-	-	01-Oct	3	16
07-Jun	2	21	16-Jul	0	18	24-Aug	-	-	02-Oct	0	16
08-Jun	0	23	17-Jul	0	16	25-Aug	-	-	03-Oct	1	16
09-Jun	-	-	18-Jul	3	18	26-Aug	-	-	04-Oct	0	16
10-Jun	-	-	19-Jul	-	-	27-Aug	-	-	05-Oct	0	16
11-Jun	1	26	20-Jul	0	13	28-Aug	-	-	06-Oct	0	16
12-Jun	1	20	21-Jul	-	-	29-Aug	-	-	07-Oct	-	-
13-Jun	-	-	22-Jul	-	-	30-Aug	-	-	08-Oct	0	16
14-Jun	-	-	23-Jul	1	18	31-Aug	-	-	09-Oct	1	14
15-Jun	0	13	24-Jul	-	-	01-Sep	-	-	10-Oct	1	15
16-Jun	-	-	25-Jul	0	16	02-Sep	9	18	11-Oct	1	15
17-Jun	-	-	26-Jul	-	-	03-Sep	-	-	12-Oct	0	16
18-Jun	-	-	27-Jul	-	-	04-Sep	-	-	13-Oct	1	16
19-Jun	-	-	28-Jul	-	-	05-Sep	1	18	14-Oct	-	-
20-Jun	1	18	29-Jul	-	-	06-Sep	8	17	15-Oct	0	16
21-Jun	2	19	30-Jul	-	-	07-Sep	2	18	16-Oct	0	12
22-Jun	3	16	31-Jul	-	-	08-Sep	-	-	17-Oct	0	15
23-Jun	-	-	01-Aug	1	18	09-Sep	11	18	18-Oct	0	15
24-Jun	-	-	02-Aug	0	15	10-Sep	7	18	19-Oct	0	13
25-Jun	2	15	03-Aug	1	15	11-Sep	9	18	20-Oct	-	-
26-Jun	-	-	04-Aug	-	-	12-Sep	1	18	21-Oct	-	-
27-Jun	2	15	05-Aug	-	-	13-Sep	1	17	22-Oct	0	12
28-Jun	2	17	06-Aug	1	16	14-Sep	5	18	23-Oct	0	13
29-Jun	5	18	07-Aug	1	18	15-Sep	-	-	24-Oct	0	9
30-Jun	-	-	08-Aug	4	20	16-Sep	-	-	25-Oct	0	19
01-Jul	-	-	09-Aug	3	20	17-Sep	4	12			

TABLE 2

Removal sampling: counts of male great crested newts removed in 2010. A dash indicates that no sampling took place on that day. Temp denotes the minimum daily air temperature (°C) recorded on each visit to the study site. Here, the number of removed individuals, $D = 741$. The nine missing covariate values were imputed using the average of the previous and next observed values.

Date	Count	Temp	Date	Count	Temp	Date	Count	Temp
18-Mar	65	7	13-Apr	0	2.8	09-May	1	7.1
19-Mar	115	5.2	14-Apr	0	6.5	10-May	0	9
20-Mar	185	12.4	15-Apr	0	1.1	11-May	0	-0.7
21-Mar	49	6.5	16-Apr	0	-	12-May	0	2.2
22-Mar	64	3.6	17-Apr	0	3.5	13-May	0	13.2
23-Mar	9	2.3	18-Apr	-	-	14-May	1	0.6
24-Mar	38	5.2	19-Apr	-	-	15-May	1	6.9
25-Mar	102	12.4	20-Apr	-	-	16-May	0	1.4
26-Mar	16	5.2	21-Apr	0	-1	17-May	4	1.4
27-Mar	7	2.7	22-Apr	0	-3.2	18-May	0	-
28-Mar	5	3.1	23-Apr	0	-4.2	19-May	1	2.2
29-Mar	8	10.8	24-Apr	0	-4	20-May	1	10.8
30-Mar	22	-	25-Apr	0	6	21-May	0	9.3
31-Mar	0	3.1	26-Apr	16	4.2	22-May	-	-
01-Apr	2	-	27-Apr	2	4	23-May	-	-
02-Apr	-	-	28-Apr	1	7	24-May	1	-
03-Apr	-	-	29-Apr	3	4.3	25-May	0	-
04-Apr	-	-	30-Apr	3	7.7	26-May	0	18
05-Apr	-	-	01-May	4	5.1	27-May	0	10.3
06-Apr	3	-	02-May	1	8.2	28-May	0	-
07-Apr	3	3.7	03-May	0	4.2	29-May	0	15
08-Apr	2	2.1	04-May	0	2.5	30-May	0	11.5
09-Apr	0	1.3	05-May	1	2	31-May	0	-
10-Apr	4	1.8	06-May	1	4.9	01-Jun	0	5.1
11-Apr	0	3.2	07-May	0	3	02-Jun	0	3.9
12-Apr	0	6.1	08-May	0	3	03-Jun	0	3.9
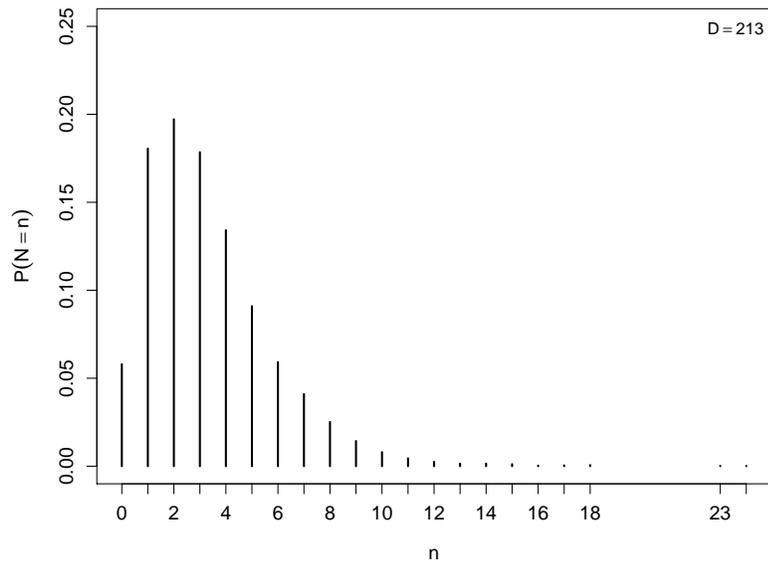
(a)
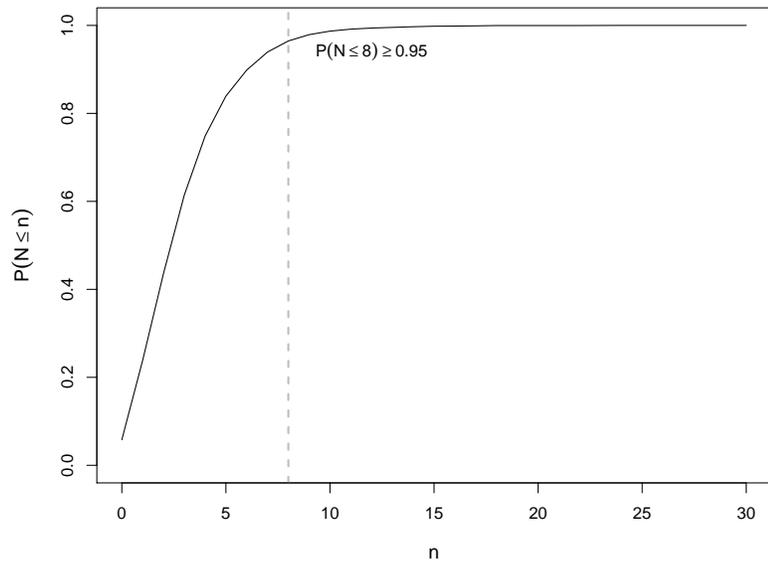
(b)

FIG. 1: Common lizard data. (a) Posterior distribution, and (b) cumulative posterior distribution of N. Also shown in (b) is the value of N which corresponds to the 95% quantile of the posterior distribution.
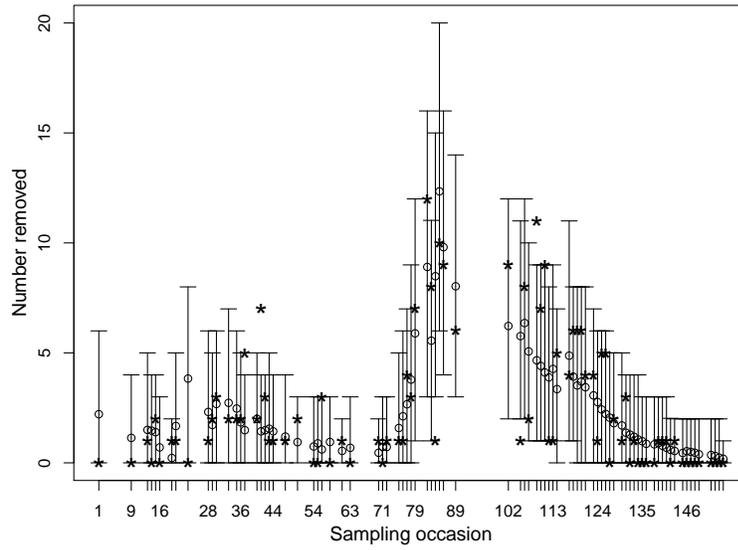
FIG. 2: Common lizard data: assessment of model fit. The vertical bars show the width of the 95% quantile interval of values generated from 1000 randomly sampled parts of the chain, the circles show the mean simulated values and the stars the observed values. The gaps in the data correspond to days when sampling was not conducted.
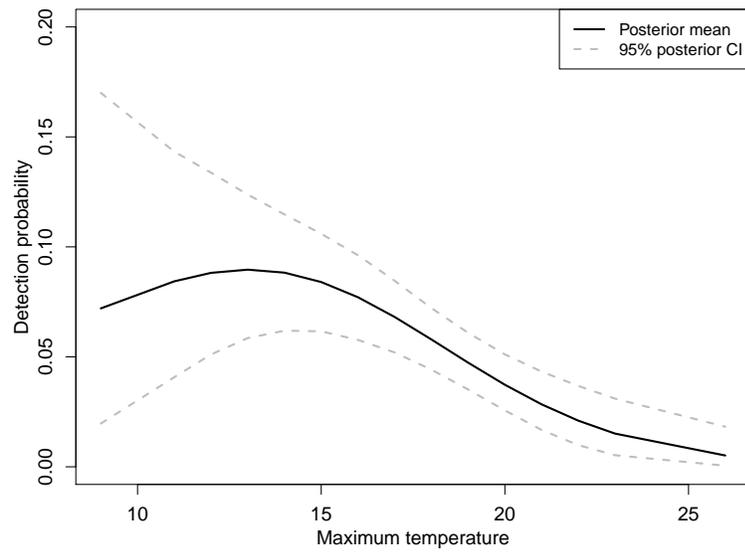
FIG. 3: Common lizard data. Summaries of the posterior distribution of detection probability as a function of maximum daily recorded temperature. A logistic-quadratic function has been fitted.
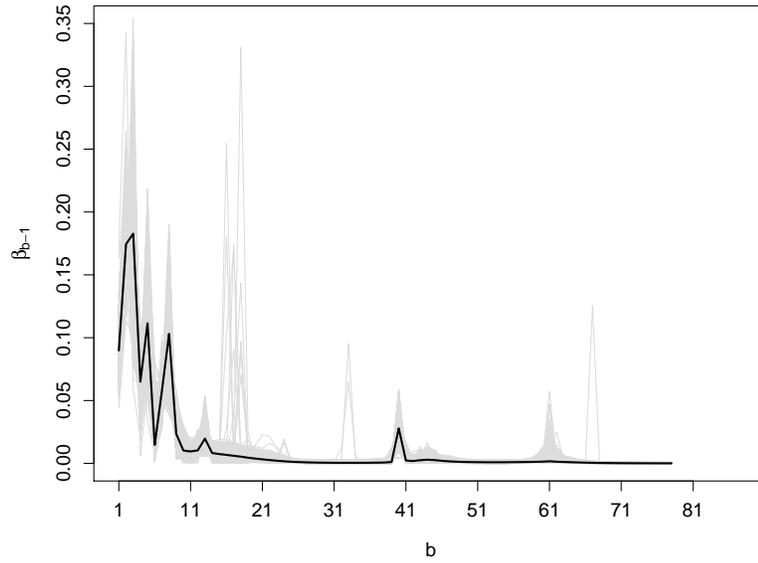
(a)
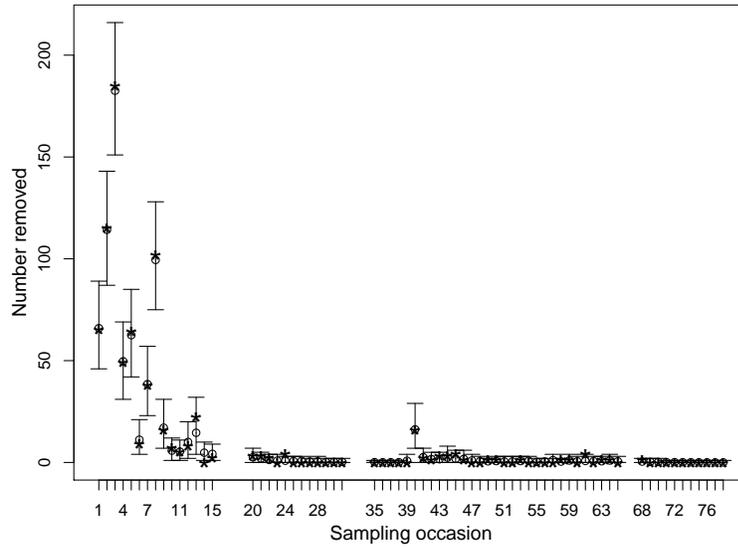
(b)

Fig. 4: Male great crested newt data. (a): Estimated entry parameters obtained at each iteration of the RJMCMC algorithm, gray lines, together with the mean of all iterations, shown by the black line. The values on the x-axis correspond to sampling occasions. (b): Assessment of model fit. The observed counts, stars, lie within the 95% quantile intervals of counts simulated from the model, bars, using randomly selected iterations of the algorithm.
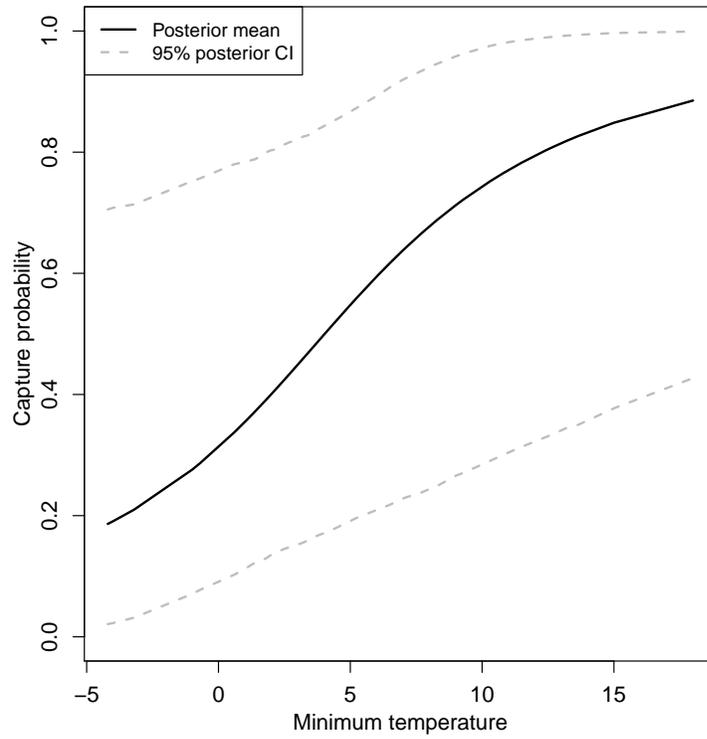
FIG. 5: Male great crested newt data. Summaries of the posterior distribution of detection probability as a function of minimum daily recorded temperature. A logistic function has been fitted.

8. Appendix.

8.1. *Common lizards.*

8.1.1. *Profile likelihood plots.* Profile likelihood plots shown in Fig. A6.

(a) (b)
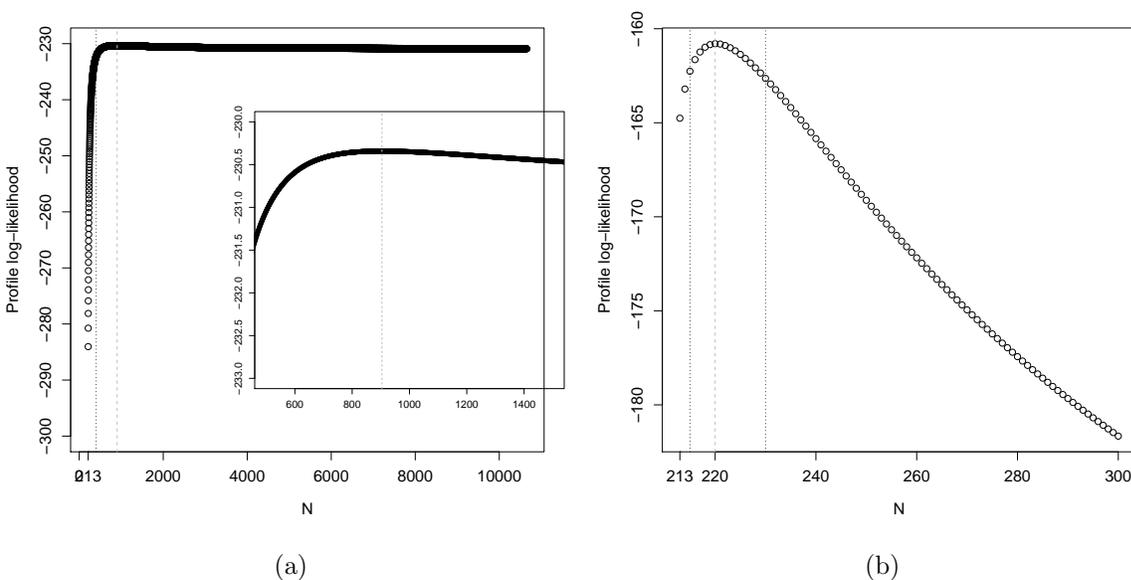
Fig. A6: Common lizard data. Profile log-likelihood plots for N obtained by the geometric model, (a), and the proposed model, (b). The gray vertical lines indicate the maximum likelihood estimates for N in each case. The values of N included in the corresponding 95% profile likelihood intervals are those that lie between the two black dotted lines in (b) while in (a) the log-likelihood value decreases so slowly that the upper bound has not been found even after allowing N to be equal to 10000 individuals. The smaller plot in the bottom right corner of (a) shows the log-likelihood surface around the maximum. Note that (b) is constructed by assuming a constant detection probability and apparent survival probability equal to 1, in contrast to the results presented in section 3 where detection probability is a function of maximum daily temperature and ϕ is estimated.

8.1.2. *Convergence diagnostics.*   We run three chains with starting values for the parameters chosen at random from the corresponding parameter space in each case and we compared the chains using the Gelman-Rubin diagnostic plot produced using the R-package coda and by visual inspection of trace plots (FIG. A7).
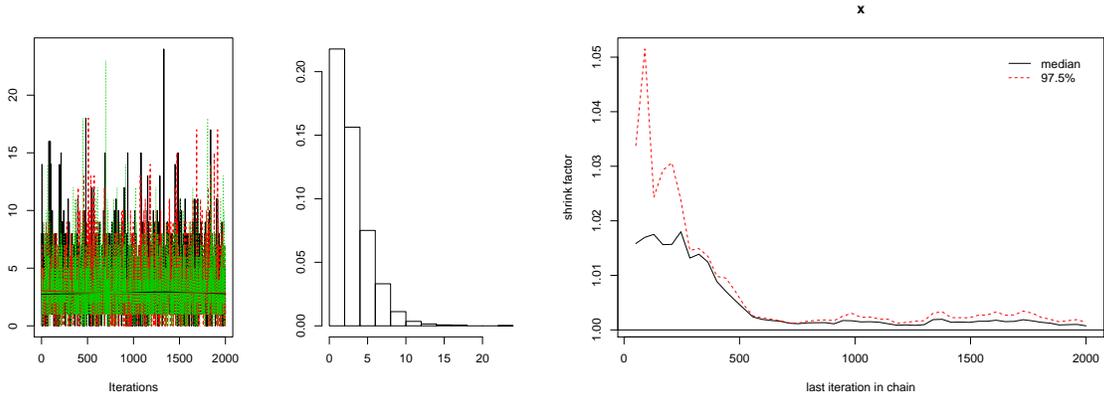
(a)
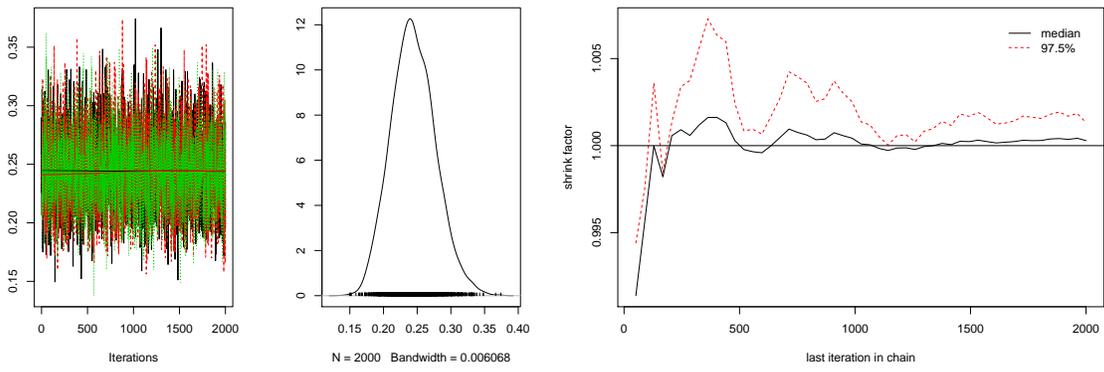
(b)
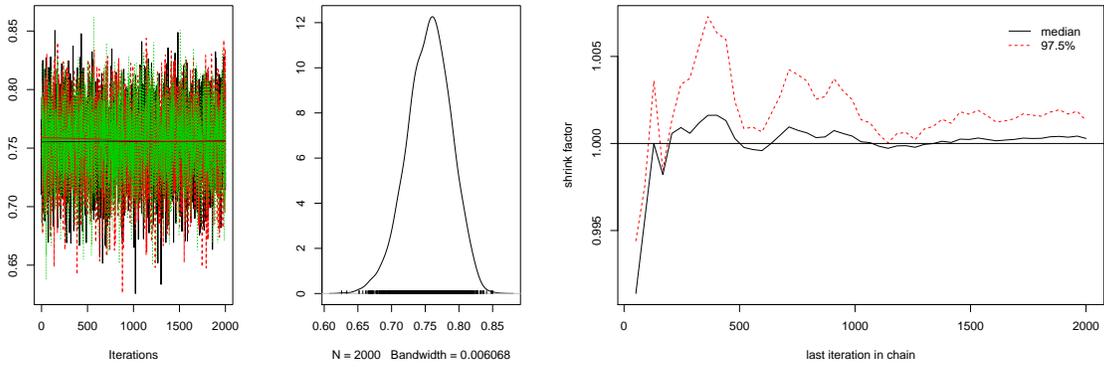
(c)
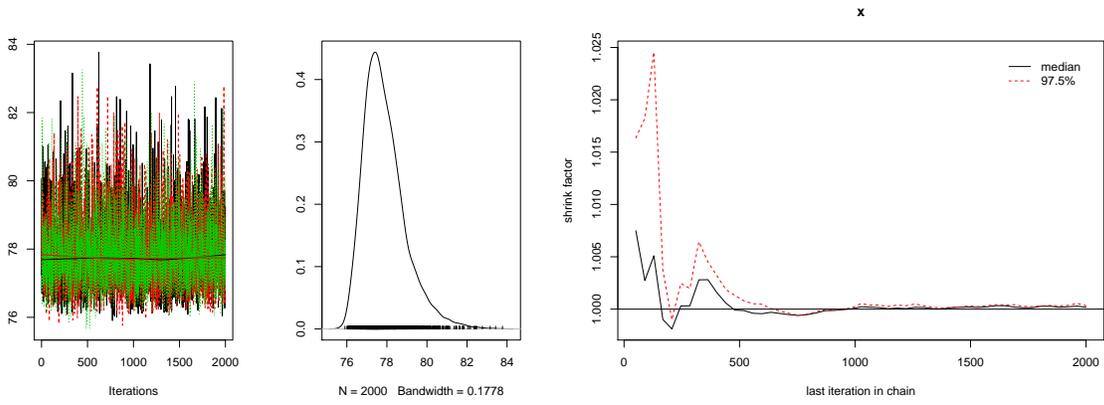
(d)
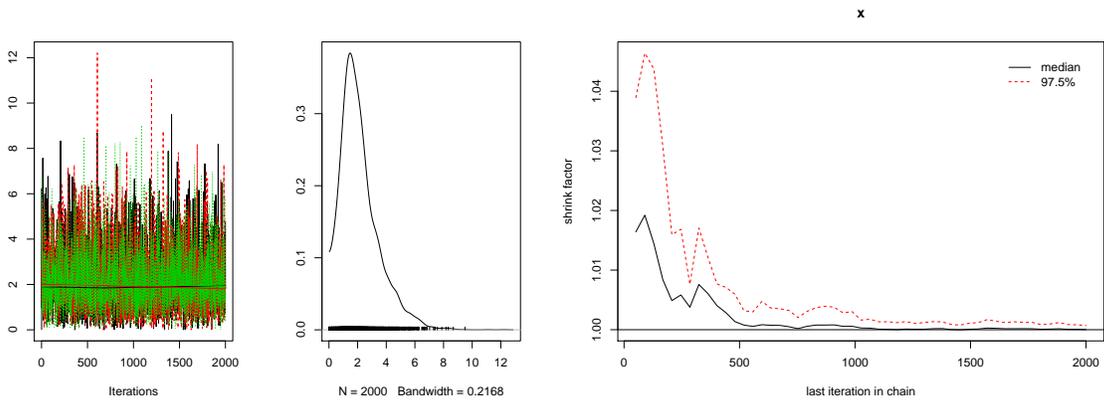
(e)
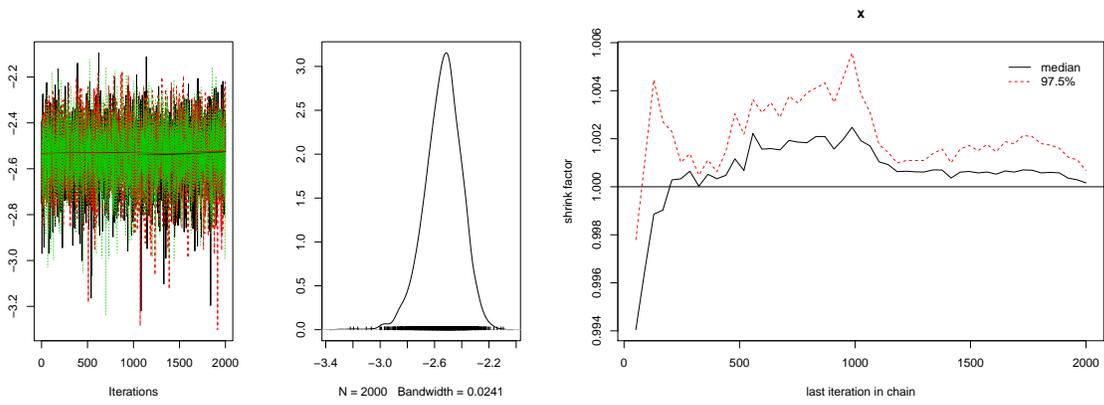
(f)
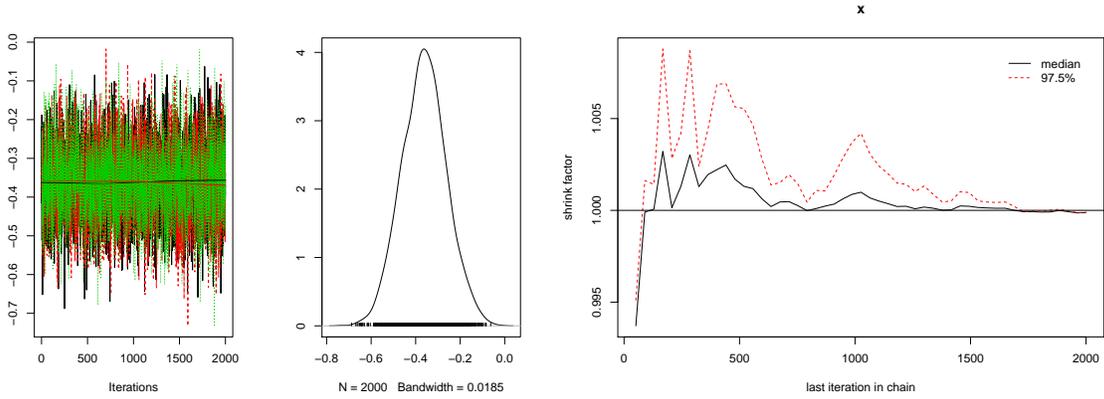
(g)
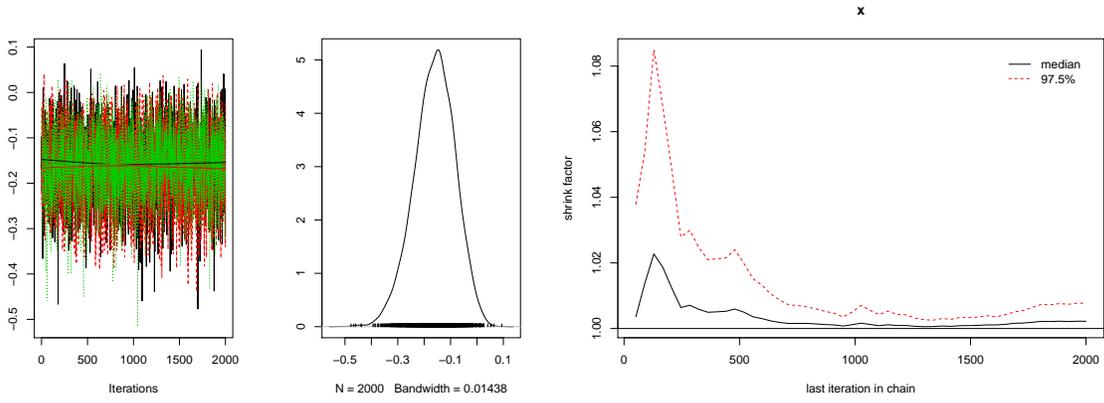
(h)
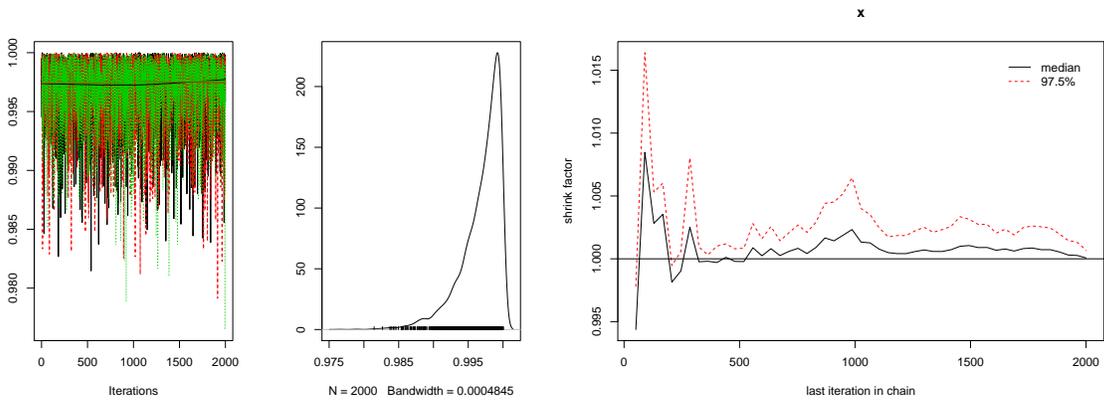
(i)

FIG. A7: Common lizard data. Convergence diagnostics for (a) N, (b) π_1, (c) π_2, (d) μ, (e) σ, (f) α_0, (g) α_1, (h) α_2 and (i) ϕ.

8.2. *Male great crested newts.*

8.2.1. *RJMCMC algorithm.* We based our algorithm on the work of **?**. Here, $\boldsymbol{\theta} = (G, N, \boldsymbol{\pi}, \boldsymbol{\mu}, \boldsymbol{\sigma}, p)$. We seek an expression for the posterior distribution,

$$\mathcal{P}(\boldsymbol{\theta}|\mathbf{n}) \propto \mathcal{P}(\mathbf{n}|\boldsymbol{\theta})\mathcal{P}(\boldsymbol{\theta}),$$

where $\mathcal{P}(\boldsymbol{\theta})$ is the joint prior of the parameters.

We summarise $\mathcal{P}(\boldsymbol{\theta}|\mathbf{n})$ using a RJMCMC algorithm. This has two update types: one for updating parameters within models and one for updating the number of mixture components, G.

We update within-model parameters using a standard single update Metropolis Hastings random walk, described for example in King et al. (2009, section 5.3.2). Mixing proportions, $\boldsymbol{\pi}$, are updated as follows: two groups are chosen at random, say a and b, ϵ is defined as $\epsilon = \gamma(\pi_a + \pi_b)$, where $\gamma \in (0, 1)$ is fixed and chosen during tuning, x is drawn from Unif($-\epsilon$, ϵ) and π'_a and π'_b are calculated by $\pi'_a = \pi_a + x$ and $\pi'_b = \pi_b - x$. If $\pi'_a, \pi'_b \geq 0$ and $\pi'_a \leq (\pi_a + \pi_b)$ the standard Metropolis-Hastings acceptance probability is calculated.

The value of G is updated using a RJMCMC move. The proposal transition probability to a model with G' mixture components and $\boldsymbol{\theta}'$ parameters from a model with G components and $\boldsymbol{\theta}$ parameters is denoted by $P_G(G'|G)$.

Suppose that the proposed move is to a model with $G' = G + 1$ groups. We allocate mass to this newly formed group by removing some mass from an existing group. Specifically, the proposed proportion of individuals in this new group, π'_{G+1}, is generated by choosing one of the existing G groups at random, say group a, with probability $1/G$, drawing x from Unif(0, π_a), setting π'_{G+1} equal to x and π'_a equal to $\pi_a - x$.

Suppose that the proposed move is to a model with $G' = G - 1$ groups. We choose a from Unif$\{1, \ldots, G\}$ and b from Unif$\{1, \ldots, a - 1, a + 1, \ldots, G\}$. We remove group a and allocate its mass to group b.

We set $P_G(G + 1|G) = P_G(G - 1|G) = 0.5$, $G = 2, \ldots, 20$ and $P_G(2|1) = P_G(19|20) = 1$.

If the proposed move is to a model with $G' = G + 1$ renewal groups then values for the mean, μ', and standard deviation, σ', of the arrival times of the additional group are generated from the corresponding priors.

The priors for the parameters not involved in the normal mixture components are common between models with different numbers of renewal groups, and therefore cancel from the acceptance ratio as they appear in both the numerator and denominator of the acceptance probability. The same holds for the prior for G, which is symmetric. The prior for $(\pi_g, \mu_g, \sigma_g)_{g=1,\ldots,G}$ is equal to $G!(G-1)! \{\mathcal{P}_\mu(\mu)\mathcal{P}_\sigma(\sigma)\}^G$. Therefore, the acceptance probability for a model with $G + 1$ arrival groups is given by:

$$
\begin{aligned}
\alpha(\boldsymbol{\theta}, \boldsymbol{\theta}') &= \min\left(1, \frac{\mathcal{P}(\mathbf{n}|\boldsymbol{\theta}')G!(G+1)! \{\mathcal{P}_\mu(\mu)\mathcal{P}_\sigma(\sigma)\}^{G+1} P_G(G|G+1)\frac{1}{G+1}\frac{1}{G}}{\mathcal{P}(\mathbf{n}|\boldsymbol{\theta})(G-1)!G! \{\mathcal{P}_\mu(\mu)\mathcal{P}_\sigma(\sigma)\}^{G} P_G(G+1|G)\frac{1}{G}\frac{1}{\pi_a}\mathcal{P}_\mu(\mu)\mathcal{P}_\sigma(\sigma)}\right) \\
&= \min\left(1, \frac{\mathcal{P}(\mathbf{n}|\boldsymbol{\theta}')GP_G(G|G+1)}{\mathcal{P}(\mathbf{n}|\boldsymbol{\theta})P_G(G+1|G)\frac{1}{\pi_a}}\right).
\end{aligned}
$$

Similarly, the acceptance probability for a model with $G - 1$ arrival groups has the form:

$$\alpha(\boldsymbol{\theta}, \boldsymbol{\theta}') = \min\left(1, \frac{\mathcal{P}(\mathbf{n}|\boldsymbol{\theta}')P_G(G|G-1)\frac{1}{\pi_a + \pi_b}}{\mathcal{P}(\mathbf{n}|\boldsymbol{\theta})(G-1)P_G(G-1|G)}\right).$$

The Jacobian term (see King et al., 2009, p. 165) required in forming these acceptance probabilities is equal to 1 because G' and π_a', π_{G+1}' are, respectively, linear functions of G and π_a and $\boldsymbol{\mu}_{G+1}'$, $\boldsymbol{\sigma}_{G+1}'$ are generated from their priors.

8.2.2. *Convergence diagnostics.* We run three chains using the model of Eq. (**??**) with starting values for the parameters chosen at random from the corresponding parameter space in each case and we compared the chains for the parameters not involved in the RJ step, i.e. N, α_0, α_1 and ϕ using the Gelman-Rubin diagnostic plot available in the R package *coda* and by visual inspection of the traceplots (FIG. A8). The results obtained using the unconditional multinomial model of Eq. (2.1) are shown in FIG. A9 for comparison.
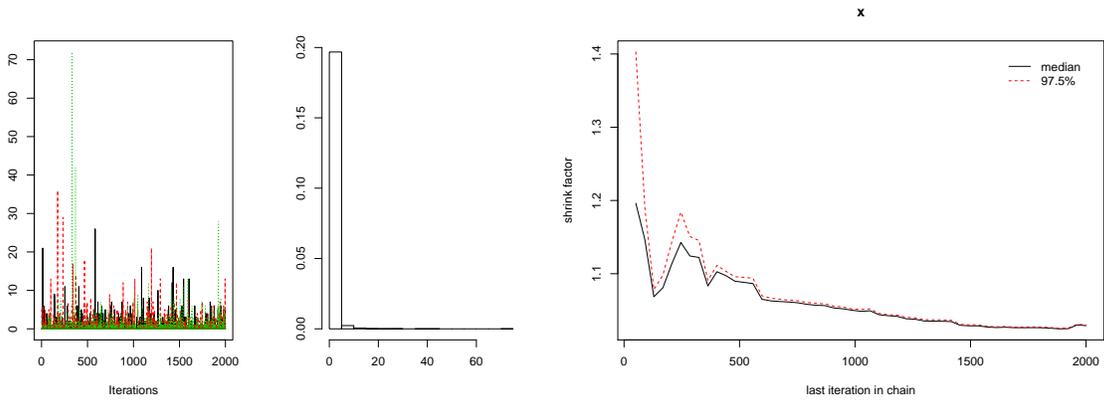
(a)
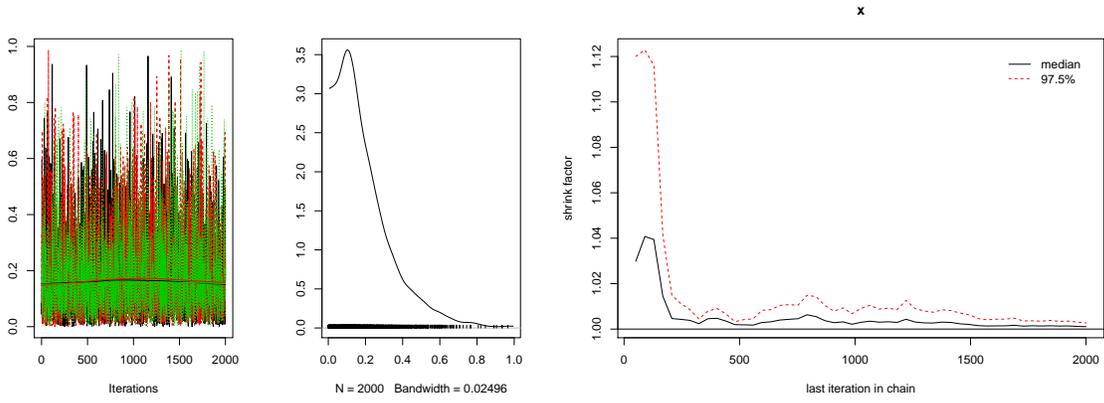
(b)
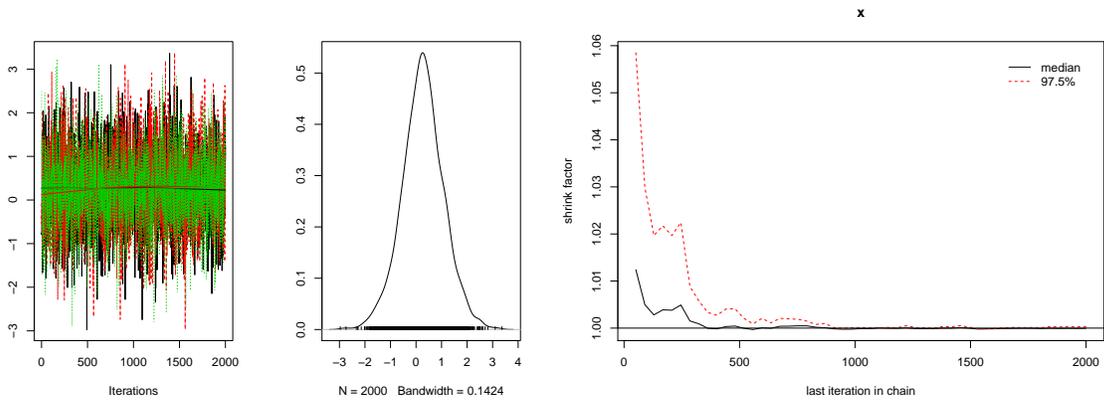
(c)

We repeated the above diagnostic checks for each of the $T = 78$ entry parameters over the 3 chains
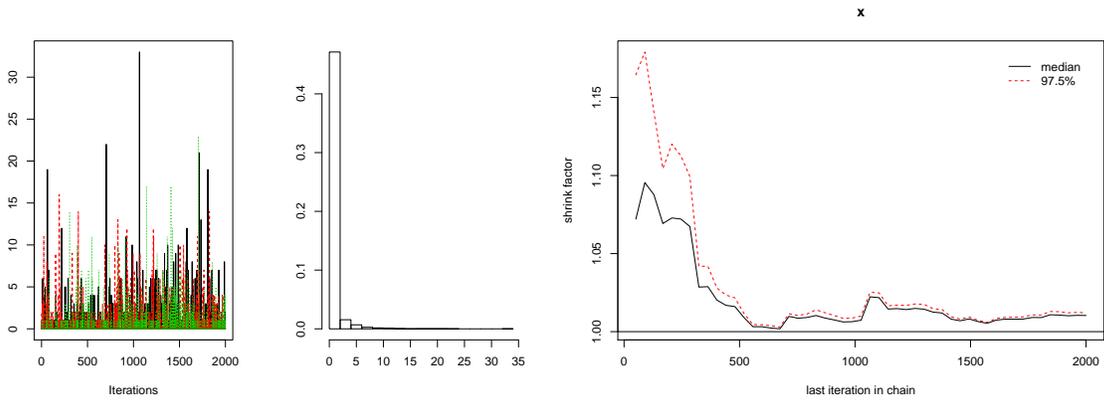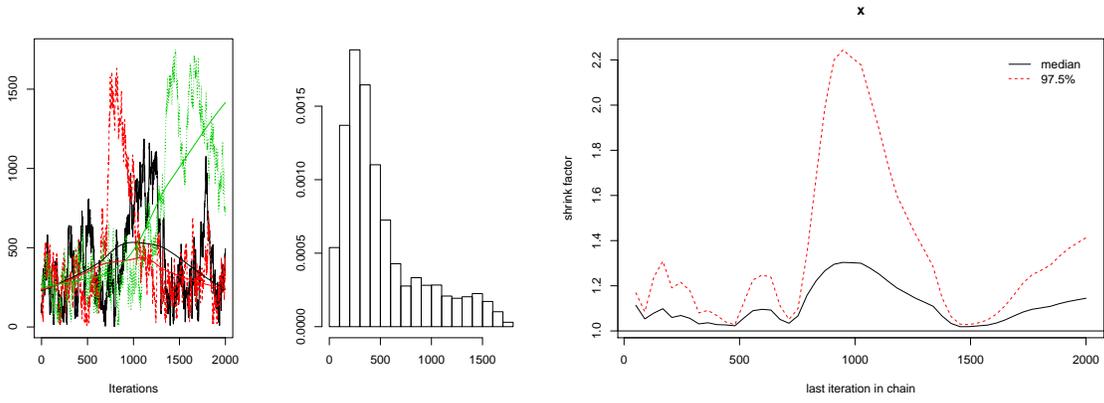
(d)
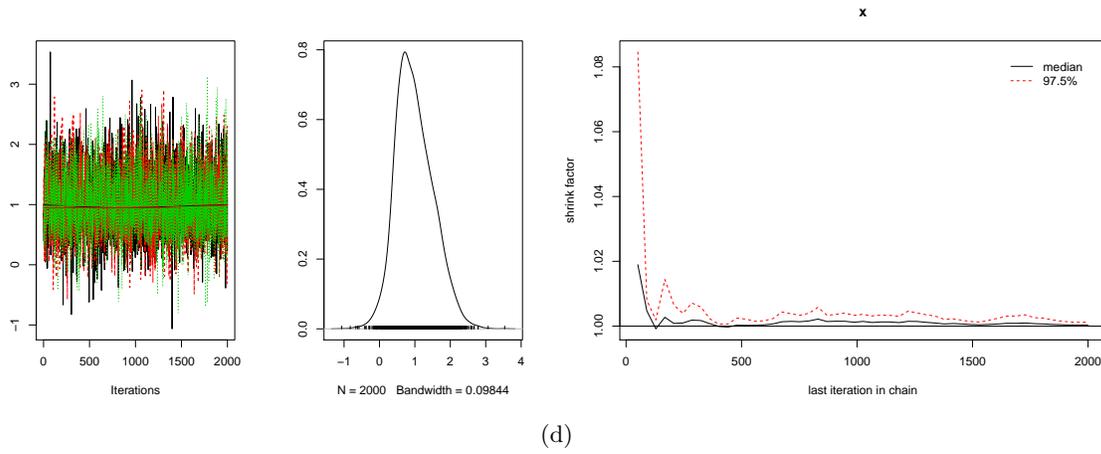
FIG. A8: Male great crested newt data. Convergence diagnostics for (a) N, (b) ϕ, (c) α_0 and (d) α_1.
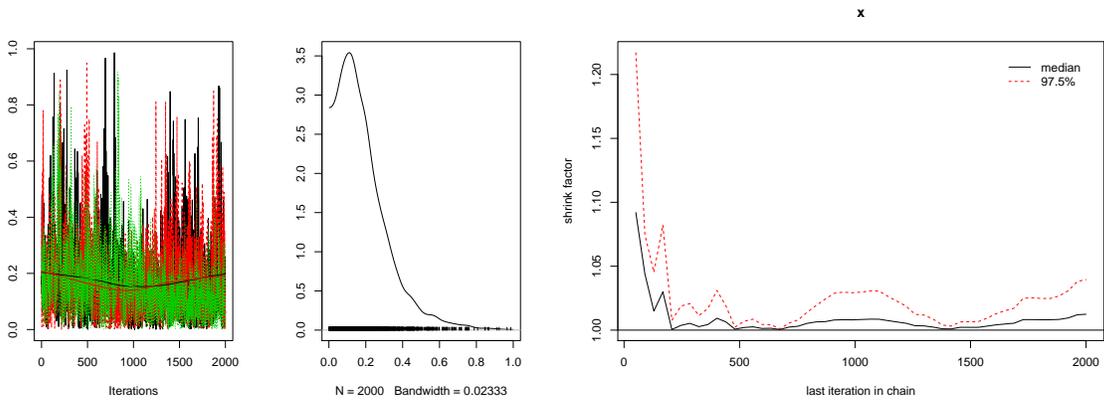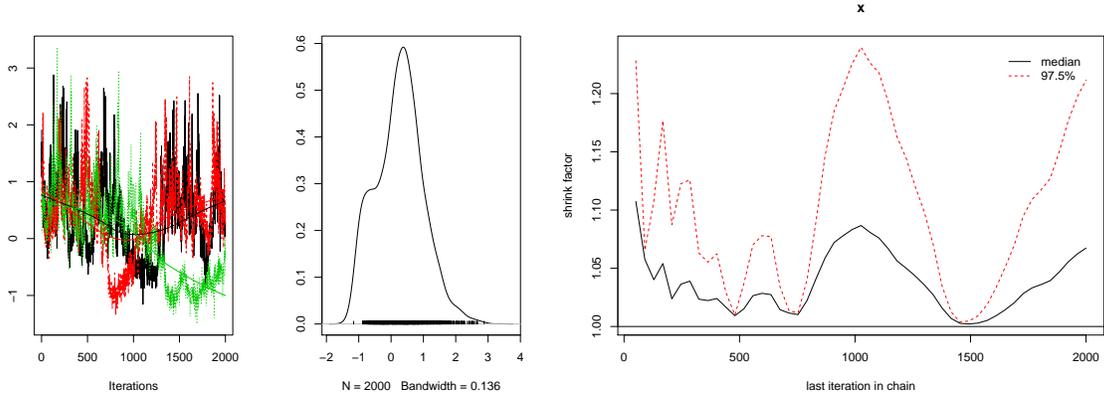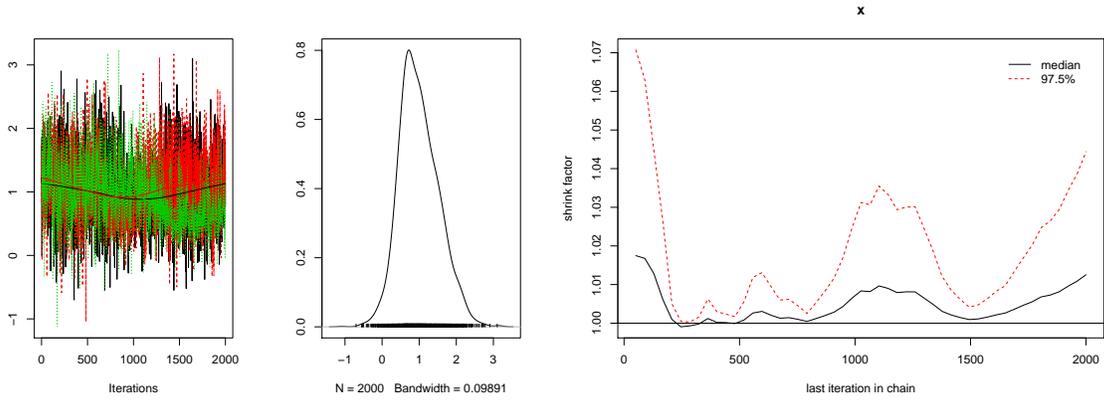
but we have not included the figures here.

(a)

(b)

(c)

FIG. A9: Male great crested newt data. Convergence diagnostics for (a) N, (b) M, (c) ϕ, (d) α_0 and (e) α_1 when the unconditional multinomial is used (Eq. (2.1)) instead of the model of Eq. (2.2).
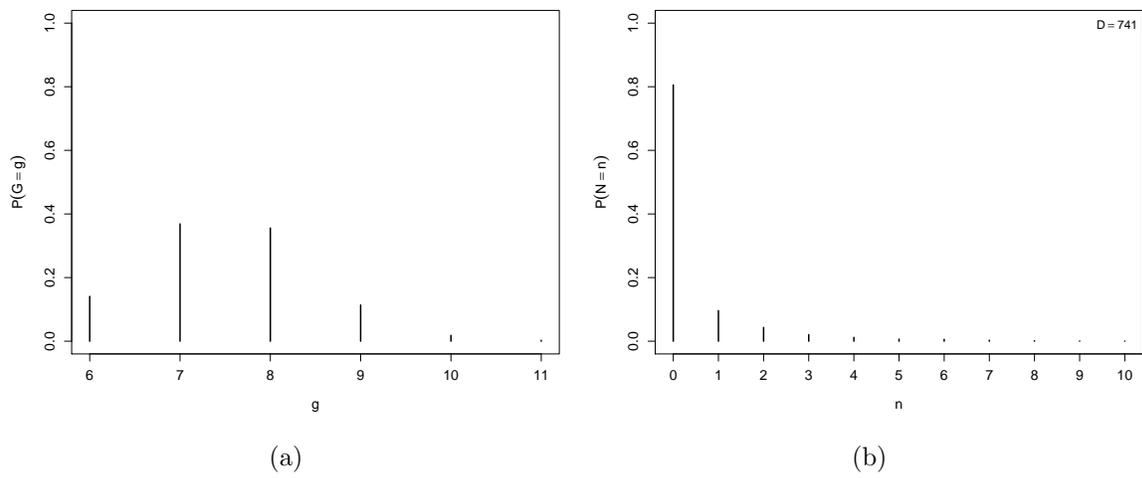
Fig. A10: Male great crested newt data. Posterior distributions for the number of arrival groups, G (a), and the number of individuals remaining at the site after the end of the study, N (b).

8.3. *Unmodelled heterogeneity in detection probabilities.*   We simulated data using a beta-geometric model for detection probabilities with parameters $\mu = 1$ and $\theta = 1$. This results in a probability of 0.5 of detecting an individual as soon as it enters the population. This probability then decreases as the number of occasions an individual has been present for increases.

We performed two simulations, assuming an unknown number of renewal groups and hence using an RJMCMC algorithm: in the first the population was essentially depleted (true $N = 9$, similarly to the two case studies considered in the paper, while in the second it was not with a large number of individuals remaining at the end of the study (true $N = 150$). We present the resulting posterior distributions obtained for N in Fig. A11, where it can be seen that, as expected, the posterior mass in both cases is concentrated to the left of the true value for N used to simulate the data. This effect is particularly prominent in the case where N is large, where the posterior median obtained for N is 77 individuals, which is about half of the true value. When N is low, the median is 30% lower than the true value but of course in absolute terms this corresponds to just 3 individuals.

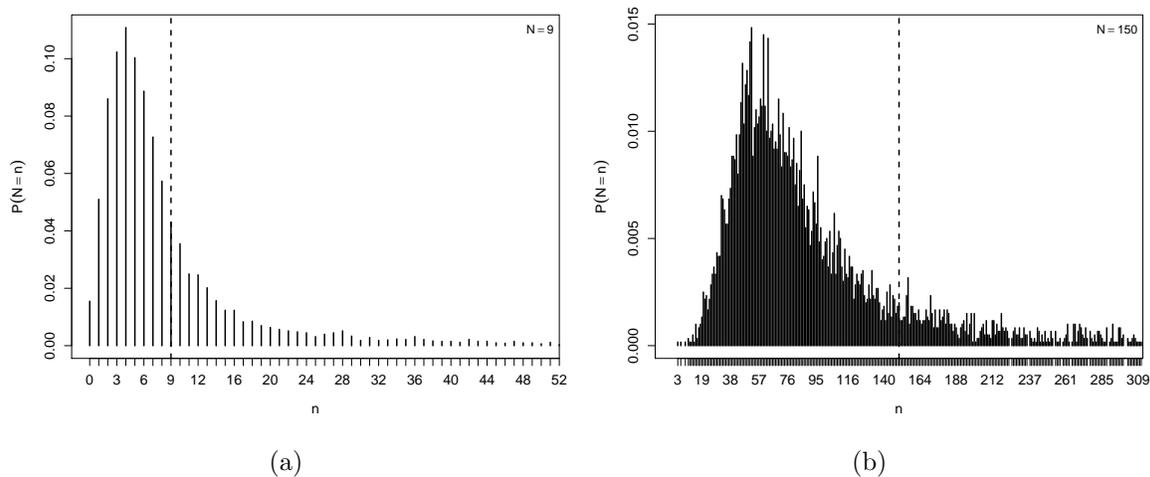(a)   (b)

Fig. A11: Simulation. Posterior distributions for N obtained when detection probabilities are generated from a Beta-Geometric distribution but the model assumes a constant detection probability. In (a), renewal of the population was concluded before the end of the study and hence the population was essentially depleted. In (b), the number of individuals remaining is large because renewal took place until the end of the study. In both cases, the posterior for N is concentrated to the left of the true value for N used to simulate the data. In (b) this is particularly evident as the true value for N is far from 0, which is the lower boundary for N.

8.4. *Population far from being depleted.*   In this simulation there are two renewal groups, with the second arriving towards the end of the study. As a result, N is large -in this particular simulation it is 259 individuals while 530 individuals were removed.

We run our RJMCMC algorithm using the same set up as that for the analysis of the male great crested newt data set in section 4, i.e. assuming an unknown number of arrival groups. In Fig. A12 we present the obtained posterior densities for N, ϕ and the coefficients of the logistic regression model for p, α_0 and α_1 and an assessment of the fit of the model. The simulated data set shown in Fig. A12 (e) shows how the number of detected individuals is not decreasing towards the end of the study, in contrast to the two data sets considered in the main body of the paper, and the model provides a good description of the data.
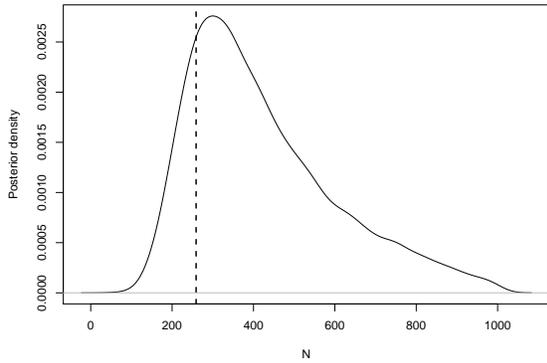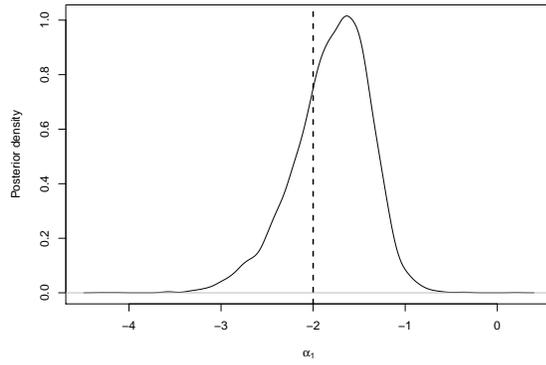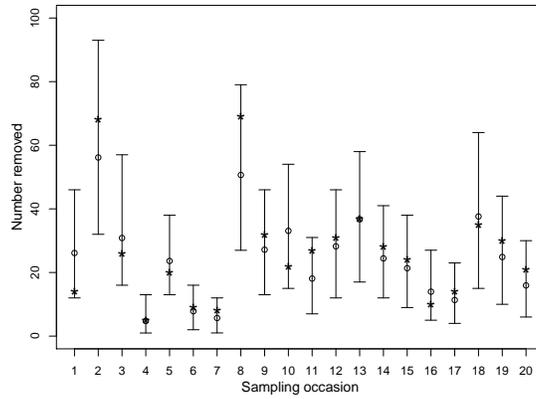
(a)
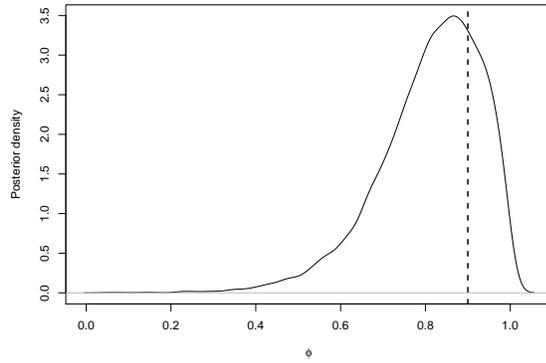
(b)
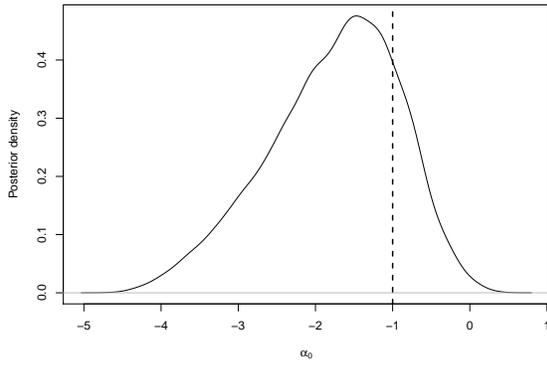
(c)

(d)

(e)

FIG. A12: Simulation. Posterior distribution for (a) N, (b) ϕ, (c) α_0 and (d) α_1. (e) compares summaries of data simulated using parameter values at randomly chosen iterations of the algorithm (bars) with the original simulated data (stars). In (a)-(d) the values of the parameters used to simulate the data are shown by the black dashed lines.

E-mail: E.Matechou@kent.ac.uk   E-mail: R.S.McCrea@kent.ac.uk

E-mail: B.J.T.Morgan@kent.ac.uk   E-mail: djn8@kent.ac.uk

                                   E-mail: R.A.Griffiths@kent.ac.uk