A BAYESIAN CHANGE-POINT MODEL FOR DESCRIBING PARTIAL SEMELPARITY OF A NEOTROPICAL DIDELPHID MARSUPIAL

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- *ABSTRACT: Post-reproductive survival defines the position of any given species in the continuum from semelparity, a condition in which males die after one breeding season and females can survive for a second year, to iteroparity, a condition in which males have multiple mating opportunities over the length of their adult lives. Based on a capture-recapture study for open populations, it was previously described that a neotropic didelphid marsupial, the Brazilian gracile mouse opossum (Gracilinanus microtarsus) is partially semelparous, a condition in which mortality after the first mating is high but graded over time, with a fraction of males surviving for a second breeding season. Here we explore Bayesian change-point models for detecting a shift on the availability over time of the males in the field due to partial semelparity. Such methodology allows for more precise specification of the time when postmating begins.*

- *KEYWORDS: Bayesian methods;· change-point models; · MCMC; · semelparity · small mammals.*

1 Introduction

Change-point identification is important in many data analysis problems, such as genetics, industrial quality control, signal processing and medical diagnosis. The main issue is to make inference about the location of one or more points of the data sequence at which there is a regime shift. A change-point model allows different parts of a dataset to obey different probability laws. For example, in DNA sequence data the observations along the sequence are expressed by the alphabet A, C, G or T. Suppose that there are regions or segments which follow the same or nearly the same statistical distribution, so that the entire DNA sequence data can be organized into homogeneous segments.

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According to Braun and Muller (1998), the DNA segmentation problem can be put into the framework of the multiple change-point problem for categorical data. In quality control, Hawkins et al. (2003) used change-point models for detecting changes over time in the production process pattern. Jacqmin-Gadda et al. (2006) working with cognitive decline associated with the aging process proposed a change-point model to describe the time when the cognitive evolution of subjects in the pre-dementia phase becomes distinguishable from normal evolution.

In this article we apply a Bayesian change-point model to describe partial semelparity of a neotropical didelphid marsupial, the Brazilian gracile mouse opossum (*Gracilinanus microtarsus*). Post-reproductive survival defines the position of any given species in the continuum from semelparity, a condition in which males die after one breeding season and females can survive for a second year, to iteroparity, a condition in which males have multiple mating opportunities over the length of their adult lives (Boonstra 2005). Martins et al. (2006a) estimated survival rates for *G. microtarsus* using Cormack-Jolly-Seber type models. Their results indicated that survival decreased sharply after the beginning of the breeding season although mortality is not complete and a small percentage of males may survive to a second breeding season, the reason why the *G. microtarsus* can be described as partially semelparous. The decrease in the male survival is reflected on their number of recaptures over time. During the premating period the number of recaptures is large, decreasing during the post-mating period. Such shift in the recapture process can be better understood when approached with the use of a change-point model with a single change, since it makes possible to estimate more precisely the time when postmating begins. In the next section we introduce some Bayesian concepts to be used in the change-point model formulation.

2 Bayesian background

According to the Bayesian paradigm, the uncertainty about the true value of a given parameter, θ, is dealt with by considering θ as a random variable, so the rules of probability are used directly to make inferences about such parameter. Those inferences are based upon the posterior distribution of θ, P(θ | D), which is a function of a prior distribution, P(θ), which summarizes the prior probabilistic knowledge about θ, and the likelihood, L(D | θ), of the data D under some assumed model. Given the data D and the prior model, the Bayesian updating process of the information about θ involves the Bayes theorem as follows

$$P(\theta|D) = \frac{L(D|\theta)P(\theta)}{\int L(D|h)P(h)dh}. \quad (1)$$

The denominator of Eq. (1) is not a function of θ, since such parameter is summed up or integrated out over all its possible values. Therefore, the term in the denominator has no impact on the inferences about θ. Thus, the posterior distribution is usually described as being proportional to the likelihood times the prior distribution, i.e.,

$$P(\theta|D) \propto L(D|\theta)P(\theta).$$

For some problems and some choices of priors, when the denominator of (1) can be evaluated, it may be possible to prove that the distribution of $(\theta \mid D)$ follows a standard or known form, and the simulation process of it is, in most cases, straightforward. However, in general, the right hand side of Eq. (1) cannot be solved analytically, especially for high-dimensional problems. Instead, computational techniques based on Markov Chain Monte Carlo (MCMC) algorithms make possible to draw samples from the posterior distribution in order to estimate θ. Based on those samples one can compute summary statistics like mean, median and quantiles, which help to characterize the posterior distribution of θ. More details about Bayesian estimation can be found in Gelman *et al.* (2003).

The central idea behind the MCMC method is to build up a Markov chain that is easy to simulate and has target or equilibrium distribution given by the distribution of interest. For θ univariate the target distribution may be the posterior distribution itself. However, for multiparameter problems for which the sampling process from the joint posterior is generally very complex, a good strategy consists of obtaining approximations to some joint posterior components, as it is the case of the so called full conditional posteriors of the parameters in the model. The Metropolis-Hastings algorithm (Metropolis et al. 1953; Hastings 1970) is widely used for that purpose since it helps to create such a Markov chain with special properties that assure, in most cases, convergence to the target distribution.

A special case of the Metropolis-Hastings algorithm is the Gibbs sampler. Each iteration of the Gibbs sampler cycles through the vector of parameters θ, which is divided into some subvector components. Each subvector is drawn conditionally on the value of all the others (through the mentioned full conditional posteriors). For a large number of Gibbs sampling cycles, the sampled values obtained are from the joint posterior distribution.

Let $\theta=(\theta 1, \ldots,\theta k)$ be a k dimensional vector, D a vector of observed data and $P(\theta|D)$ be the corresponding joint posterior distribution. Let $P(\theta j|D,\theta j\text{-}1)$ be the full conditional distribution of θj with $\theta j\text{-}1$ denoting the vector θ with θj removed. The following scheme illustrates the method.

1. Choose starting values $\theta 1(o), \ldots,\theta k\ (o)$;
2. Sample $\theta 1(j+1)$ from $P(\theta 1 \mid \theta 2(j),...,\theta 2(j),D)$;
3. Sample $\theta 2(j+1)$ from $P(\theta 2 \mid \theta 1(j+1),\theta 3(j),...,\theta k(j),D)$;

...

4. Sample $\theta k(j+1)$ from $P(\theta k \mid \theta 1(j+1), \theta 2(j+1),\ldots,\theta k\text{-}1(j+1),D)$;
5. Repeat steps (ii) to (iv) thousands of times.

An extensive discussion about the Gibbs sampler can be found in Casella and George (1992).

The MCMC is started from an arbitrary initial state. The amount of time it takes to converge to its stationary or target distribution is called the mixing time or burn-in time. Once the chain has converged, it is "safe" to start collecting samples. Since the samples are correlated, it is common to pick a subset of them (say every 10th), a practice known as thinning. The sequence of simulations can be monitored using the software CODA (Best

et al. 1995), using both graphical and statistical methods to check mixing and convergence. The advantage of using a Bayesian approach is to obtain reliable and accurate credible intervals for the model parameters, especially for small sample problems since for the Bayesian methods there is no need of making any asymptotic assumption, as it is the case in most for non-Bayesian approaches.

3 Poisson process with change-point

A Bayesian model introduced by Carlin et al. (1992) for dealing with change-point problems considering a Poisson process is now described. Such methodology has been applied to the G. microtarsus data.

Let y1,…,yn be a sample from a Poisson distribution in which one suspects there was a change point k along the observation process, k=1,…,n. When k=n that is interpreted as "no change". Given k, the basic distributions involved in the model formulation are described as yi|θ ~ Poisson(θ), i=1,...,k and yi|λ ~ Poisson(λ), i=k+1,...,n . Therefore, the likelihood is given by Eq. (2)

$$\begin{aligned} L(\mathbf{Y} \mid \theta, \lambda, k) &= \left[\prod_{i=1}^{k} \frac{e^{-\theta}\theta^{y_i}}{y_i!}\right]\left[\prod_{i=k+1}^{n} \frac{e^{-\lambda}\lambda^{y_i}}{y_i!}\right] \propto e^{-k\theta}\theta^{\sum_{i=1}^{k} y_i} \cdot e^{-(n-k-1)\lambda}\lambda^{\sum_{i=k+1}^{n} y_i} \\ &\propto e^{(\lambda-\theta)k}\left(\frac{\theta}{\lambda}\right)^{\sum_{i=1}^{k} y_i} \cdot e^{-n\lambda}\lambda^{\sum_{i=1}^{n} y_i}. \end{aligned} \tag{2}$$

The forms of the priors for either λ or θ were chosen based on the conjugate prior property. A conjugate prior is a family of prior probability distributions that has the property that the posterior probability distribution also belongs to that family (Gelman *et al.* 2003).

These priors were chosen by algebraic convenience, since we had no other possible criteria to describe them. However, it can be found in the literature several articles that use similar approach with respect to the prior specification. Thygesen and Zwinderman (2006) model the variance in SAGE (Serial Analysis of Gene Expressions) data using a hierarchical Poisson model with a gamma prior. Chien and Huang (2003) present a Bayesian speech duration modeling and learning for hidden Markov model (HMM) based on speech recognition with focus on sequential learning of HMM state duration. In order to exploit sequential learning they used a poisson duration model incorporated with gamma prior density. Rodrigues et al. (2001) estimated the number of species in a population using a hierarchical Bayesian model. The authors used a poisson-gamma prior distribution for the unknown number of species.

In this present work we assumed, for simplicity, independent priors over k, θ, and λ such that k follows a discrete uniform distribution, i.e., k~uniform{1,…,n} and θ, and λ follow distinct gamma distributions with parameters *a1* and *b1*, and *a2* and *b2*, respectively, i.e.,

θ~Gamma(a1, b1) and λ~Gamma(a2, b2).

The values of the hyperparameters *a1*, *b1, a2* and *b2* were fixed low (to be discussed in Section 4) in order to describe vague priors for λ and θ, since small values of theses parameters correspond to weak prior beliefs. However, it is possible to formulate a hierarchical Bayesian model by assigning distributions to the hyperparameters. It is also possible to specify some dependency structure between θ and λ by describing a bivariate joint prior distribution for θ and λ with a given variance-covariance matrix. However, in the present problem we have no previous knowledge, of any kind, that allows such specification.

Considering the prior independence assumption among the model parameters, the joint posterior distribution involving the set of parameters (θ,λ,*k*) is given by expression (3) from which can be derived the full conditional posteriors of each parameter:

$$\begin{aligned} p(\theta,\lambda,k|\mathbf{Y},a_1,a_2,b_1,b_2) &\propto L(\mathbf{Y}\mid\theta,\lambda,k)\cdot P(\theta,\lambda,k|a_1,a_2,b_1,b_2) \\ &\propto L(\mathbf{Y}\mid\theta,\lambda,k)\cdot P(\theta|a_1,b_1)\cdot P(\lambda|a_2,b_2)\frac{1}{n}. \end{aligned} \tag{3}$$

The full conditional posterior of θ is given by

$$\begin{aligned} p(\theta|\lambda,k,\mathbf{Y},a_1,b_1) &\propto L(\mathbf{Y}\mid\theta,\lambda,k)\cdot P(\theta|a_1,b_1) \propto e^{-\theta k}\theta^{\sum_{i=1}^{k} y_i}\cdot\theta^{a_1-1}e^{-b_1\theta} \\ &\propto \frac{(k+b_1)^{\left(a_1+\sum_{i=1}^{k} y_i\right)}}{\Gamma\left(a_1+\sum_{i=1}^{k} y_i\right)}\theta^{\left(a_1+\sum_{i=1}^{k} y_i\right)-1}\ e^{-\theta(k+b_1)}. \end{aligned} \tag{4}$$

Therefore, the full conditional distribution of θ, likewise its prior, follows a gamma distribution,

$$\theta|\lambda,k,\mathbf{Y},a_1,b_1 \sim gamma\left(a_1+\sum_{i=1}^{k} y_i; k+b_1\right).$$

Similarly, the full conditional distribution of λ is given by

$$\lambda|\theta,k,\mathbf{Y},a_2,b_2 \sim gamma\left(a_2+\sum_{i=k+1}^{n} y_i; b_2+n-k\right).$$

Finally, the full conditional posterior of k is as follows:

$$p(k|\mathbf{Y},\lambda,\theta)=\frac{L(\mathbf{Y}\mid\theta,\lambda,k)P(k)}{\sum_{h=1}^{n}L(\mathbf{Y}\mid\theta,\lambda,h)P(h)}=\frac{e^{(\lambda-\theta)k}\left(\frac{\theta}{\lambda}\right)^{\sum_{i=1}^{k} y_i}}{\sum_{h=1}^{n}e^{(\lambda-\theta)h}\left(\frac{\theta}{\lambda}\right)^{\sum_{h=1}^{n} y_h}}. \tag{5}$$

Those full conditional distributions can be easily sampled using the Gibbs sampler scheme presented before to obtain samples from the joint posterior distribution of the parameters of interest.

A change-point model is an especial case of the Hidden Markov Models (HMMs). A HMM is characterized by an **unseen state process** (which promotes shifts of some kind) often a finite state Markov process, and an **observation process**, a random function of the state. The observations are conditionally independent and identically distributed given the

state sequence. HMMs are special stochastic systems in which the transition from state to state, and state to observation, can be separately described. The estimation of the unseen state of a Hidden Markov Model is, in general, the target problem in applications, requiring the estimation of the unknown dynamics of the HMM. Some useful references about this sort of models are Churchill (1989), Rabiner (1989) and Rabiner and Juang (1993). Such class of models allows for the description of multiple change points. However, these models are data hungry not being suitable for small data sequences.

4 Data description

According to Martins *et al.* (2006b), the Brazilian *Gracilinanus microtarsus* is a small (20-45 g), sexually dimorphic in size (females: 20-30 g; males: 30-45 g), short-lived (1-2 years), solitary, arboreal, nocturnal, insectivorous, and seasonally breeding Neotropical didelphid marsupial inhabiting the Atlantic rain forest and the highly seasonal cerrado biomes of southeastern Brazil. Using capture-recapture sampling techniques the G. microtarsus has been monitored in a cerrado remnant (about 73 ha) from August 2000 to February 2003, with the period between January 2001 to February 2002 defining what they have called as Cohort 2000, and the period between December 2001 to February 2003 as Cohort 2001.

Capture-recapture data for Cohort 2000 are composed of 14 sampling occasions (months), of which 7 corresponded to the premating (January-July 2001) and 7 to the postmating period (August 2001-February 2002). For Cohort 2001, capture-recapture data are composed of 15 sampling occasions (months), of which 8 corresponded to the premating (December 2001-July 2002) and 7 to the postmating period (August 2002-February 2003). However, the cutoff point that determined the premating and postmating periods have been chosen based on field observation and some subjective arguments.

The data used in the change-point analysis are shown in Table 1. Based on these data, for Cohorts 2000 and 2001, the profiles described by the number *mt* of recaptures at time *t* for the males and females are displayed in Fig. 1. As it can be observed, for both cohorts, the females profiles are rather uniform as opposed to the males ones which presented a similar pattern for Cohorts 2000 and 2001, being first increasing till reaching a maximum point being then steadily decreasing.

Table 1 - Number m_t of recaptures of males and females at time t for Cohorts 2001 and 2003

Cohort 2000 (January/2001 to February/2002)														
Month	jan	feb	mar	apr	may	jun	jul	aug	sep	oct	nov	dec	jan	feb
Females	0	3	3	2	2	3	1	1	2	3	5	1	1	1
Males	0	3	4	6	5	6	5	8	3	4	2	1	1	1

Cohort 2001 (December/2001 to February/2003)															
Month	dec	jan	feb	mar	apr	may	jun	jul	aug	sep	oct	nov	dec	jan	feb
Females	0	3	4	4	5	5	5	6	6	3	5	4	5	5	4
Males	0	4	7	6	7	7	7	5	3	3	1	2	1	5	1

5 Results

For the males data in Cohort 2001 some diagnosis details of the MCMC generated samples for the change-point variable k are presented. The convergence of the MCMC procedure was verified by Gelman and Rubin´s (1992), Heidelberger and Welch´s (1983), and Geweke´s (1992) convergence diagnosis techniques available in the software CODA.

In order to perform the diagnostic, two sequences with 100,000 elements each were generated using the procedures described above. We also considered a burn-in of 10,000 observations and thinning of 50 observations. Some **sensitivity analyses** for the parameters λ and θ are presented in Table 2. For such purpose, two sets of fixed values for the hyperparameters were considered for λ and θ respectively: $a1=1$ and $b1=1$, and $a2=1$ and $b2=1$ and $a1=0.5$ and $b1=0.5$, and $a2=0.5$ and $b2=0.5$. Such small values for those parameters describe vague priors for λ and θ.

Table 2 - Summary of the MCMC diagnostics considering two chains of 100,000 iterations each; thinning of 50 observations; burn-in of 10,000 observations and two sets of hyperparameter specifications – Cohort 2001

Hyperparameter	Maximum Autocorrelations Lag 50	Heidelberger and Welch stationarity test in each of the chains	Gelman and Rubin shrink factors (50% and 97.5%)	Maximum of the absolute value of Geweke's criterion
λ ($a1=1$; $b1=1$)	0.057	passed	1.00; 1.00	0.512
θ ($a2=1$; $b2=1$)	0.029	passed	1.00; 1.00	1.020
k	0.059	passed	1.00; 1.00	0.540
λ($a1=0.5$;$b1=0.5$)	0.083	passed	1.05;1.02	0.773
θ($a2=0.5$;$b2=0.5$)	0.090	passed	1.00; 1.00	0.744
k	0.0914	passed	1.02;1.03	0.178

As one can observe from Table 2, considering lag of size 50, the **autocorrelations** are pretty low. Each of the two chains passed in the **Heidelberger and Welch's** stationarity test for all the parameters and choices of priors. Besides that, **Gelman and Rubin's** shrink factors in each of the chains is around 1.00 for both the 50% and 97.5% quantiles of the sampling distribution for a scale reduction (shrink factor). According to Gelman and Rubin (1992) if both quantiles are approximately 1.0, effective convergence may be diagnosed. **Geweke's** maximum z-scores are very moderate providing no evidence against convergence for each of the parameters. Altogether, there is no evidence of lack of convergence.

For one of the MCMC generated samples for the data in Cohort 2001, a graphical summary of the iterates for the change-point variable k and the other parameters is displayed in Fig. 2. The traces for each of the generated sequences are shown in the left hand side panels while the estimated density/distribution for each of the parameters are shown in the right hand side panels. A little bump can be observed in the posterior distributions of the parameters. As we already described from the diagnostic analyses presented above, those bumps do not cause any problem in the chain convergence.

The reason why the bump occurs is due to the way the data are collected rather then a real change in the biological regime of the recaptures at the beginning of the sampling occasions. The experiment initiates with no recaptures (that is why we have 0 frequency in January and in December of the Cohorts 2000 and 2001 respectively). Some animals are then captured, for the first time, say in January of 2000. Then, in February, there happen to be 3 animals recaptured. Such a jump in the recapture frequencies alone explains the little bump. When one removes the data from January of Cohort 2001, the result is an extraordinarily well behaved posterior distribution with no little bump (see Fig. 3). Such analysis represents only an exercise to allow for a better understanding of the impact of the first, null frequency, in the posterior distributions.

Table 3 shows some summary statistics that help to characterize the posterior distribution of k and the other parameters for Cohort 2001. Since the dataset available for analysis was very small, the posterior standard deviations were large as well as the width of the 95% credibility intervals that can be described by the 2.5% and 97.5% quantiles. As it can be observed, the mean and median (Bayesian point estimators considering a quadratic or absolute loss function, respectively) of k is around time k =10 (mode) for the males in **Cohort 2001**, meaning that a shift in the recaptures regime occurred **in September of 2002**. For the males in **Cohort 2000** (see Table 4) the referred shift occurred around time k=11 (**November of 2001**). We observe from Tables 3 and 4 that inferences are reasonably insensitivity to the choice of the vague priors for λ and θ.

Table 3 - Summary statistics characterizing the posterior distributions for the single point change-point model of the males in Cohort 2001

Cohort 2001 Hyperparameter	mode	mean	s.d.	Quantiles				
				2.5%	25%	50%	75%	97.5%
λ ($a1$=1 ; $b1$=1)	-	4.299	1.291	0.197	3.970	4.482	5.000	6.126
θ ($a2$=1 ; $b2$=1)	-	1.680	0.802	0.632	1.160	1.522	1.958	4.021
k	10	8.821	2.566	1	8	9	10	12
λ($a1$=0.5 ; $b1$=0.5)	-	4.484	1.393	0.078	4.142	4.703	5.268	6.426
θ($a2$=0.5 ; $b2$=0.5)	-	1.763	0.843	0.615	1.206	1.597	2.078	4.135
k	10	8.655	2.514	1	8	9	10	12

Table 4 - Summary of the MCMC diagnostics considering two chains of 100,000 iterations each; thinning of 50 observations; burn-in of 10,000 observations and two sets of hyperparameter specifications – Cohort 2001

Hyperparameter	Maximum Autocorrelations Lag 50	Heidelberger and Welch stationarity test in each of the chains	Gelman and Rubin shrink factors (50% and 97.5%)	Maximum of the absolute value of Geweke's criterion
λ ($a1$=1 ; $b1$=1)	0.057	passed	1.00; 1.00	0.512
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λ($a1$=0.5;$b1$=0.5)	0.083	passed	1.05;1.02	0.773
θ($a2$=0.5;$b2$=0.5)	0.090	passed	1.00; 1.00	0.744
k	0.0914	passed	1.02;1.03	0.178

6 Discussion

In this paper we have described a Bayesian change-point model aimed to estimate the time when the male's recapture process suffered a shift due to *G. microtarsus* partial semelparity. Our goal was to obtain a model based, rather than a subjective determination, of the cutoff point between the premating and postmating periods.

One of the most important motivations for using a Bayesian approach instead of a frequentist one is the fact that the Bayesian estimation of uncertainty (like variances and confidence intervals) is not based on asymptotic sampling arguments that requires the availability of larges samples.

In this work we used independent prior for θ and λ. However, it is also possible to specify some dependency structure between those parameters by describing a bivariate joint prior distribution for θ and λ with a given variance-covariance matrix. A problem that looms larger is the complete lack of previous information, preventing us to specify any biologically reasonable model accounting for such dependencies. Since the sample sizes are too small, the posterior inferences could be seriously affected by the choice of a very informative prior. That would be even worse if such prior would represent a bad guess. Maybe in the future, when we have more data, we could do something about specifying prior **dependencies among the parameters.**

Another limitation of the methods used in this work is the implicit assumption that the recaptures were independent. Unfortunately, again, the small amount of data available prevented the use of more complex models accounting for possible **dependencies among the observations,** such as Hidden Markov Models (HMMs), as well as the use of more parametrized models involving both males and females.

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- RESUMO: A sobrevivência pós-reprodutiva define a posição de uma dada espécie, em uma escala de tempo contínua, que vai da *semelparidade*, uma condição em que os machos morrem após a primeira estação de acasalamento, enquanto as fêmeas sobrevivem para uma segunda ocasião de acasalamento, à *iteroparidade*, uma condição em que os machos têm múltiplas oportunidades de acasalamento no decorrer de suas vidas. Baseado em um estudo de captura-recaptura para populações abertas, foi estabelecido que o gambá cuíca (Gracilinanus microtarsus) é *parcialmente semélparo*, uma condição em que a mortalidade, após a primeira estação de acasalamento, é alta, mas distribuída ao longo do tempo, com uma fração dos machos sobrevivendo a uma segunda estação de acasalamento. Neste trabalho utiliza-se um modelo Bayesiano de Ponto de Mudança para detectar uma mudança de regime na disponibilidade dos

machos ao longo do tempo, devida à semelparidade parcial. Tal metodologia permite que sejam feitas especificações mais precisas sobre o inicio da ocasião de pós-acasalamento.

- PALAVRAS-CHAVE: Métodos Bayesianos; modelos de ponto de mudança; MCMC; pequenos mamíferos.

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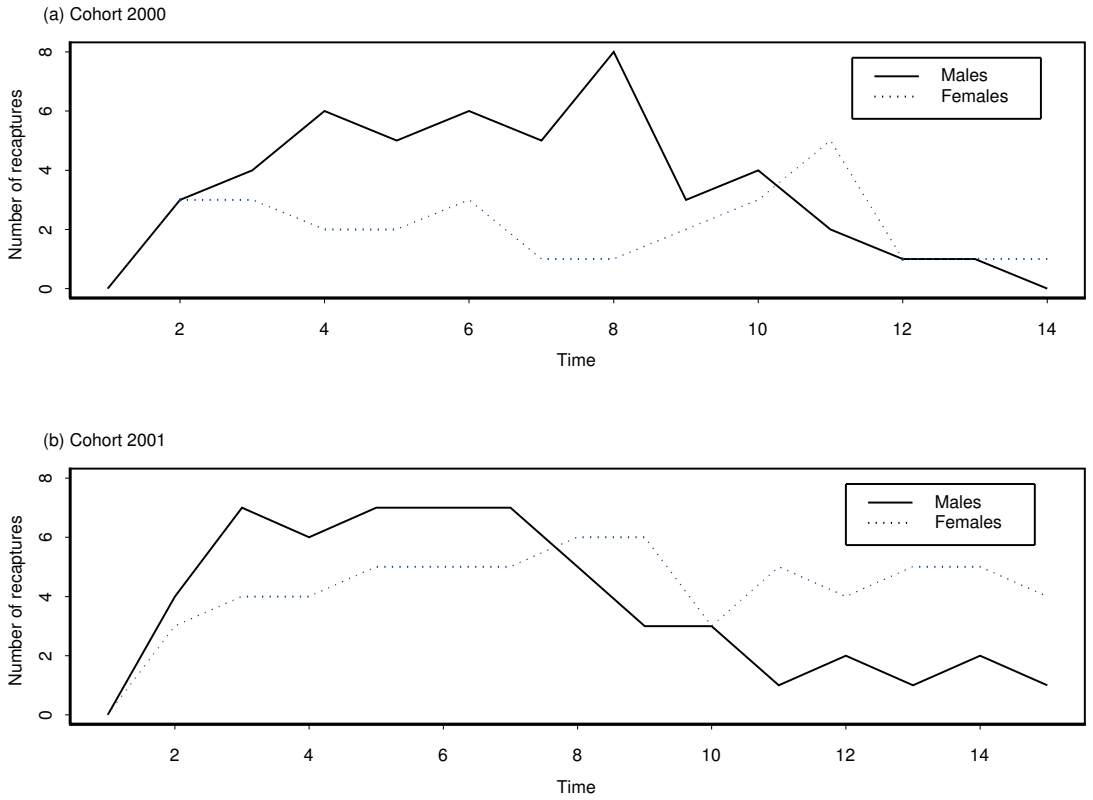

Fig. 1 Profiles described by the number m_t of recaptures of males and females at time for the Cohorts 2000 and 2001

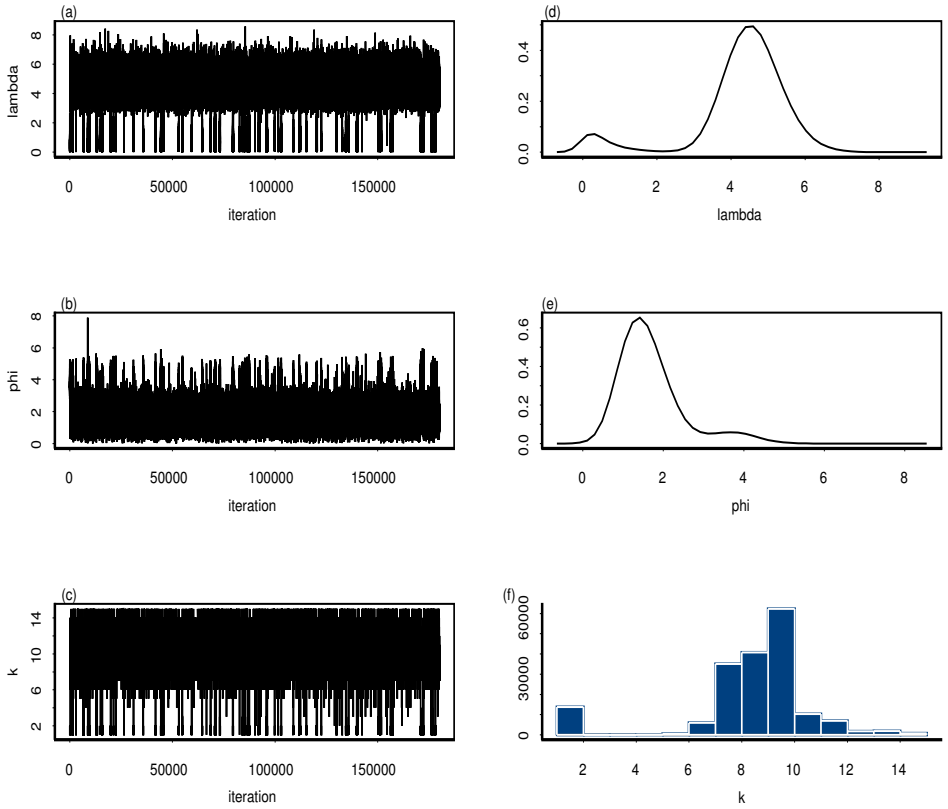

Fig. 2 Graphical summary of the MCMC output for the model parameters - Male data in Cohort 2001

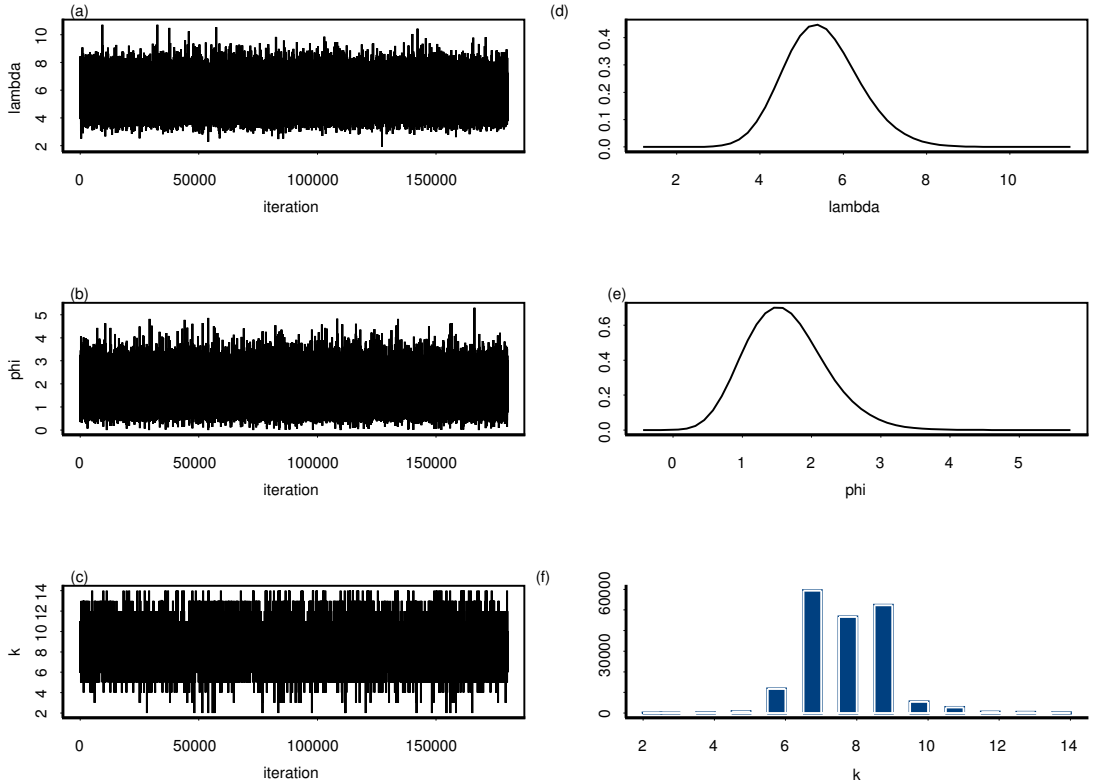

Fig. 3 Graphical summary of the MCMC output for the model parameters - Male data in Cohort 2001 - first time removed