

Individual heterogeneity in studies on marked animals using numerical integration: capture–recapture mixed models

O. GIMENEZ¹ AND R. CHOQUET

Centre d'Ecologie Fonctionnelle et Evolutive, Campus CNRS, UMR 5175, 1919 Route de Mende, 34293 Montpellier Cedex 5, France

Abstract. In conservation and evolutionary ecology, quantifying and accounting for individual heterogeneity in vital rates of open populations is of particular interest. Individual random effects have been used in capture–recapture models, adopting a Bayesian framework with Markov chain Monte Carlo (MCMC) to carry out estimation and inference. As an alternative, we show how numerical integration via the Gauss-Hermite quadrature (GHQ) can be efficiently used to approximate the capture–recapture model likelihood with individual random effects. We compare the performance of the two approaches (MCMC vs. GHQ) and finite mixture models using two examples, including data on European Dippers and Sociable Weavers. Besides relying on standard statistical tools, GHQ was found to be faster than MCMC simulations. Our approach is implemented in program E-SURGE. Overall, capture–recapture mixed models (CR2Ms), implemented either via a GHQ approximation or MCMC simulations, have potential important applications in population biology.

Key words: *capture–recapture mixed models; CR2M; European Dippers; finite mixture models; generalized linear mixed models; likelihood-ratio test; mark–recapture models; random effects; Sociable Weavers; survival estimation; WinBUGS.*

INTRODUCTION

Estimation of demographic parameters (e.g., survival, reproductive success, or dispersal) involves the analysis of individual monitoring data. In the wild, these are obtained from a capture–recapture protocol (CR; Williams et al. 2002), in which individuals are captured, marked, and released in their environment. CR models allow inferring demographic processes in spite of the practical impossibility to detect all individuals at each sampling session. Because they allow addressing important questions in ecology, management and evolution while accounting for the uncertainty of detection, CR methods have become extremely popular in the field of population biology.

Besides estimating vital rates, biologists are often interested in explaining individual variations in demographic parameters. If individual characteristics such as age or phenotype are measured in the field, it is relatively easy to incorporate them in CR models (Pollock 2002), using a framework inspired by generalized linear models theory (Lebreton et al. 1992). However, there are important situations in which the information cannot be measured at the individual level, and yet, individual variation still needs to be accounted for and quantified. Ignoring between-individual heterogeneity generated by individuals having contrasted performances over life may mask senescence or hamper the understanding of

life history trade-offs (Cam et al. 2002), or may decrease the viability of small populations (Conner and White 1999). Moreover, failing to incorporate unexplained residual variance may induce bias in parameter estimates (Barry et al. 2003) and lead to detecting an effect of the individual covariate more often than it should be: an inflated type I error rate (Lin 1997).

How is individual heterogeneity usually incorporated in situations with perfect detectability? Nonlinear and generalized linear mixed models (Pinheiro and Bates 2000) are often used, which extend classical models by including random or subject-specific effects in addition to the (traditional) fixed effects in the structure for the mean response. Mixed models have long been used in the fields of social sciences, medicine, and agriculture. This has been facilitated in part by their implementation in popular statistical programs such as SAS with its procedure MIXED, or R with its package LME4. Whereas applications of mixed models are currently rapidly developing in ecology and evolution (Bolker et al. 2009), traditional CR models remain fixed-effect models.

Pledger et al. (2003) developed capture–recapture (CR) models in which individual heterogeneity was modeled according to a finite mixture of individuals. Recently, a proposal was made for incorporating individual heterogeneity in open CR models via a continuous mixture using random effects (Royle 2008; see also Clark et al. 2005, Gimenez et al. 2006a). A state–space formulation of the Cormack–Jolly–Seber (CJS) model (Lebreton et al. 1992) was adopted, in line with previous work (Clark et al. 2005, Gimenez et al. 2007).

Manuscript received 14 October 2009; revised 22 October 2009; accepted 28 October 2009. Corresponding Editor: K. B. Newman.

¹ E-mail: olivier.gimenez@cefe.cnrs.fr

Because the resulting likelihood was high dimensional with no closed form, estimation and inference were accomplished in a Bayesian framework using Markov chain Monte Carlo (MCMC). However, the Bayesian approach using extensive MCMC simulation methods remains difficult to implement (Gimenez 2008). First, some nonbasic knowledge is required, such as a training in Bayes theory and in the use of MCMC algorithms, as well as programming skills. Second, fitting a model can be very time consuming, if not intractable when a model selection step involving several candidate models is at stake.

We offer an alternative to MCMC methods for the incorporation of individual heterogeneity in open CR models. We refer to this class of models as capture-recapture mixed models (CR2Ms) as they include both fixed and random effects. When estimating the parameters of mixed models, the marginal likelihood is obtained by integrating out the random effects. To cope with this issue, several methods have been proposed in the literature, MCMC algorithms being one of them (Evans and Swartz 1995). Noteworthy, standard statistical software have not adopted Bayesian methods to incorporate random effects (e.g., SAS or R). They rather have favored frequentist methods, including quasi-likelihood methods (Breslow and Clayton 1993) and numerical integration (Liu and Pierce 1994). The latter has been used in the context of closed CR models (Coull and Agresti 1999), but never to our knowledge for approximating the likelihood of open-population CR models. We show here that this approach is particularly efficient to handle with individual random effects as only one- or two-dimensional integrals are involved. When compared to the Bayesian approach using MCMC algorithms, numerical integration has appealing advantages: (1) the computational speed is often faster, and convergence criteria are well defined and easily implemented in an automatic way; (2) it relies on the well-established standard maximum-likelihood theory; and, last but not least, (3) because it requires only slight modifications of the likelihood and the use of standard optimization methods, it opens an avenue for the implementation of individual random effects in existing frequentist CR programs like MARK (White and Burnham 1999; note that this program implements a simple MCMC algorithm, which does not allow incorporating individual effects) or E-SURGE (Choquet et al. 2009). We aim at investigating these advantages in the context of open-population CR models.

We describe how individual random effects can be incorporated in a frequentist framework using numerical integration. We compare our results with that of a MCMC analysis on the European dipper data using the CJS model with heterogeneity in the survival and recapture probabilities. We consider another example on Sociable weaver data using a mixed-effect structure on survival probabilities, with an individual covariate and a random effect to cope with unexplained variability.

In both case studies, we compare our approach with finite-mixture models developed by Pledger et al. (2003).

HETEROGENEOUS CORMACK-JOLLY-SEBER MODELS

Assume we have K capture occasions and N individuals. Let the encounter history for individual i be $h_i = (\delta_{i1}, \dots, \delta_{iK})$ where δ_{ik} denotes whether individual i is observed ($\delta_{ik} = 1$) or not ($\delta_{ik} = 0$) at time k . Let e_i be the occasion where individual i is captured for the first time, l_i the last occasion where individual i is recaptured. Then the likelihood component corresponding to individual i is

$$L(p_{i2}, \dots, p_{iK}, \phi_{i1}, \dots, \phi_{i(K-1)}; h_i) = \left\{ \prod_{k=e_i}^{l_i-1} \phi_{ik} \right\} \left\{ \prod_{k=e_i+1}^{l_i} p_{ik}^{\delta_{ik}} (1 - p_{ik})^{1-\delta_{ik}} \right\} \chi_{il_i} \quad (1)$$

where p_{ik} is the probability of recapture at time k of individual i ($p_{ie_i} = 1$ as the likelihood is conditional upon the first capture), ϕ_{ik} is the probability of survival over the interval $(k, k + 1)$ of individual i , and χ_{ik} the probability that animal i , alive at time k , is not subsequently recaptured, calculated recursively as $\chi_{ik} = 1 - \phi_{ik} \{1 - (1 - p_{i(k+1)})\chi_{i(k+1)}\}$, with $\chi_{iK} = 1$ (Lebreton et al. 1992). Assuming independence among individuals, the likelihood is the product of the probabilities of all individual encounter histories given by $\prod_{i=1}^N L(p_{i2}, \dots, p_{iK}, \phi_{i1}, \dots, \phi_{i(K-1)}; h_i)$. Assuming the same survival and recapture parameters for all individuals (homogeneity assumption), this likelihood corresponds to the CJS model $\{\phi(t), p(t)\}$ in which both survival and recapture probabilities are time dependent.

We consider individual heterogeneity in the CJS model by incorporating an individual random effect on survival and/or recapture probabilities. We now show how to write down the likelihood of the resulting models. Following Royle (2008), we assume

$$\text{logit}(p_{ik}) = a_k + \alpha_i \quad (2)$$

$$\text{logit}(\phi_{ik}) = b_k + \beta_i \quad (3)$$

where a_k and b_k are fixed yearly effects, and α_i and β_i are independent random effects, with $\alpha_i \sim \mathcal{N}(0, \sigma_p^2)$ and $\beta_i \sim \mathcal{N}(0, \sigma_\phi^2)$. By integrating out the random effects, we obtain the marginal likelihood of model $\{\phi(t + h), p(t + h)\}$ adopting notation as in Royle (2008):

$$\prod_{i=1}^N \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} L(a_2, \dots, a_K, b_1, \dots, b_{K-1}, \alpha_i, \beta_i; h_i) \times f(\alpha_i | \sigma_p) f(\beta_i | \sigma_\phi) d\alpha_i d\beta_i \quad (4)$$

where $f(\cdot | \sigma)$ is the density function of $\mathcal{N}(0, \sigma^2)$. If we consider no individual heterogeneity on the recapture probabilities, i.e., $\alpha_i = 0$ in Eq. 2, then the likelihood in Eq. 4 simplifies to:

$$\prod_{i=1}^N \int_{-\infty}^{+\infty} L(a_2, \dots, a_K, b_1, \dots, b_{K-1}, \beta_i; h_i) f(\beta_i | \sigma_\phi) d\beta_i \tag{5}$$

which corresponds to model $\{\phi(t + h), p(t)\}$. The marginal likelihood of model $\{\phi(t), p(t + h)\}$ is easily obtained in the same way by setting $\beta_i = 0$ in Eq. 3:

$$\prod_{i=1}^N \int_{-\infty}^{+\infty} L(a_2, \dots, a_K, b_1, \dots, b_{K-1}, \alpha_i; h_i) f(\alpha_i | \sigma_p) d\alpha_i. \tag{6}$$

The likelihoods in Eqs. 4, 5, and 6 involve integrals that cannot be evaluated analytically due to the complexity of the CR model likelihood. To circumvent this issue, Royle (2008) uses MCMC algorithms which directly generate random values from a Markov chain whose stationary distribution is the posterior distribution of the parameters under interest. In the next section, we show how this problem can be tackled using numerical integration.

RANDOM EFFECTS WITH NUMERICAL INTEGRATION

Numerical integration aims at getting an approximation to the integral by building a grid of points at which to evaluate the function, this function being the likelihood here. We use the Gauss-Hermite quadrature (GHQ), which is known to work well for a large class of problems, at least for low-dimensional integrals and a Gaussian distribution for the random effects (e.g., Butler and Moffit 1982, Hedeker and Gibbons 1994).

Formulas 4, 5, and 6 involve integrals of the form

$$I = \int_{-\infty}^{+\infty} g(z) \exp(-z^2) dz \tag{7}$$

pending a change of variable we make explicit below. The integral of Eq. 7 can be approximated using a GHQ by a weighed sum

$$I \approx I_Q = \sum_{q=1}^Q w_q g(z_q) \tag{8}$$

where Q is the number of quadrature points, the z_q are the zeros of the Q th order Hermite polynomial, and the w_q are corresponding weights. The quadrature points (or nodes) z_q and the weights w_q are tabulated (Abramowitz and Stegun 1964). The precision of the GHQ approximation is discussed in Appendix A. Throughout the paper we used $Q = 15$.

We focus on the model $\{\phi(t + h), p(t)\}$. Let $\beta_i = \gamma_i \sqrt{2} \sigma_\phi$, then Eq. 5 becomes

$$\prod_{i=1}^N \frac{1}{\sqrt{\pi}} \int_{-\infty}^{+\infty} L(a_2, \dots, a_K, b_1, \dots, b_{K-1}, \gamma_i \sqrt{2} \sigma_\phi; h_i) \times \exp(-\gamma_i^2) d\gamma_i \tag{9}$$

which has the same form as Eq. 7. As a consequence, the

marginal likelihood of the model $\{\phi(t + h), p(t)\}$ can be approximated by

$$\prod_{i=1}^N \frac{1}{\sqrt{\pi}} \sum_{q=1}^Q w_q L(a_2, \dots, a_K, b_1, \dots, b_{K-1}, z_q \sqrt{2} \sigma_\phi; h_i). \tag{10}$$

Posing $\alpha_i = \eta_i \sqrt{2} \sigma_p$ in Eq. 6, we also get an approximation of the marginal likelihood of model $\{\phi(t), p(t + h)\}$ of the same form, and a similar reasoning leads to an approximation of the marginal likelihood of model $\{\phi(t + h), p(t + h)\}$ (Appendix B). We obtain maximum-likelihood estimates (MLEs) of the model parameters by maximizing the GHQ approximate marginal likelihood using a quasi-Newton algorithm. Approximate standard errors (SEs) are obtained from the inverse Hessian calculated from a standard finite-difference scheme.

TESTING INDIVIDUAL HETEROGENEITY

Royle (2008) tested the heterogeneity components by calculating posterior probabilities of the models considered above. In a frequentist framework, considering the model $\{\phi(t + h), p(t)\}$, we need a test of the null hypothesis of homogeneity $H_0: \sigma_\phi^2 = 0$ vs. the alternative hypothesis of heterogeneity $H_1: \sigma_\phi^2 > 0$. This can be accomplished by calculating the likelihood ratio test (LRT) between models $\{\phi(t + h), p(t)\}$ and $\{\phi(t), p(t)\}$. However, because H_0 is on the boundary of the parameter space, classical inference no longer holds (Self and Liang 1987). The asymptotic null distribution of the LRT is a 50:50 mixture of χ^2 distributions with 0 and 1 degrees of freedom (Stram and Lee 1994). In the general case, Shapiro (1988) showed that if H_0 and H_1 involves q and $q + q'$ uncorrelated random effects, then the null LRT distribution is a mixture of the form

$$\sum_{r=0}^{q'} 2^{-q'} \binom{q'}{r} \chi_r^2. \tag{11}$$

If we want to test for heterogeneity in both survival and recapture probabilities, we need a test of $H_0: \sigma_\phi^2 = 0$ and $\sigma_p^2 = 0$ vs. $H_1: \sigma_\phi^2 > 0$ and $\sigma_p^2 > 0$, which requires a LRT between models $\{\phi(t + h), p(t + h)\}$ and $\{\phi(t), p(t)\}$ with null distribution a 25:50:25 mixture of χ^2 distributions with 0, 1, and 2 degrees of freedom.

Once the structure of the random effects has been selected via LRTs, one can then use standard model selection procedures using the Akaike information criterion (AIC) to determine a structure on the fixed effects, as illustrated in the next section.

EXAMPLE 1: THE EUROPEAN DIPPER DATA

We consider data on the European Dipper (*Cinclus cinclus*) that were collected over seven years (1981–1987) in France, and consist of 255 individuals. A detailed analysis by Lebreton et al. (1992) showed that a flood

TABLE 1. Maximum-likelihood estimates (MLEs) and associated standard errors (SEs) for the 15-node Gauss-Hermite quadrature (GHQ) approximation as well as Markov chain Monte Carlo (MCMC) results (posterior modes and standard deviations [SDs] are given) for the model $\{\phi(\text{flood} + h), p(h)\}$ applied to the European Dipper data.

Parameter	GHQ analysis MLE (SE)	MCMC analysis mode (SD)
ϕ_{flood}	0.480 (0.045)	0.477 (0.050)
$\phi_{\text{non-flood}}$	0.614 (0.034)	0.616 (0.036)
p	0.959 (0.038)	0.957 (0.033)
σ_p	2.083 (1.276)	2.041 (1.105)
σ_ϕ	2.872×10^{-5} (2.623×10^{-6})	0.104 (0.192)

Note: The parameters ϕ and p are the survival and detection probabilities respectively; h stands for heterogeneity; σ_p and σ_ϕ are the standard deviations of the individual random effects on the detection and survival probabilities, respectively.

during the breeding season in 1983 had a negative impact on survival. The model best supported by the data incorporated two distinct survival probabilities, one for the two flood periods 1982–1983 and 1983–1984, and another for the remaining non-flood periods. Here, we considered individual heterogeneity on both the recapture and survival probabilities. Parameter estimates for model $\{\phi(\text{flood} + h), p(h)\}$ are provided in Table 1. For the Bayesian analysis, we used the same priors as in Royle (2008), in particular a $U(0, 8)$ (where U stands for the uniform distribution) for the standard deviation of the individual random effects. Following Royle (2008), we generated three chains of length 65 000, discarding the first 5000 as burn-in and produced MCMC posterior summaries using WinBUGS (Spiegelhalter et al. 2003). We also calculated MLEs and SEs using the GHQ. The estimation results are very similar for the two methods, although there is a discrepancy for σ_ϕ which may be due to the sensitivity of the Bayesian analysis to the prior on σ_ϕ and the uncertainty in the variance estimation. To understand this difference in the magnitude of σ_ϕ , we simulated data according to the MCMC model results (Table 1), and the frequentist and Bayesian methods were applied to that simulated data. We found that the discrepancy disappeared, with similar results for the frequentist (MLE = 0.121, SE = 0.189) and the Bayesian (posterior mean = 0.152, SD = 0.124) analyses.

The MCMC simulations took approximately 42 minutes vs. 37 minutes for the GHQ on a PC (2Go RAM, 2.6 GHz CPU) for the model $\{\phi(\text{flood} + h), p(h)\}$. The difference in the computational costs was more pronounced for model $\{\phi(\text{flood}), p(h)\}$, with approximately 30 minutes for the MCMC approach vs. 2 minutes for the GHQ approximation.

We tested the null hypothesis of homogeneity, which favors the model with no heterogeneity (LRT $\{\phi(\text{flood}), p\}$ vs. $\{\phi(\text{flood} + h), p(h)\}$, $0.25\chi^2(0) + 0.5\chi^2(1) + 0.25\chi^2(2) = 2.803$, $P = 0.109$). Heterogeneity in survival was less likely (LRT $\{\phi(\text{flood}), p\}$ vs. $\{\phi(\text{flood} + h), p\}$, $0.5\chi^2(0) + 0.5\chi^2(1) = 0.000$, $P = 0.5$) than heterogeneity in recapture (LRT $\{\phi(\text{flood}), p\}$ vs. $\{\phi(\text{flood}), p(h)\}$, $0.5\chi^2(0) + 0.5\chi^2(1) = 2.803$, $P = 0.047$). In brief, in agreement with Royle (2008), we found evidence of

heterogeneity in recapture but not in survival. Keeping heterogeneity in the recapture, the comparison of $\{\phi(\text{flood}), p(h)\}$ with models having time-varying ($\Delta\text{AIC} = 7.77$) or constant ($\Delta\text{AIC} = 3.91$) survival probabilities showed the importance of the flood effect (Appendix C: Table C1). Finally, we fitted finite-mixture models (Pledger et al. 2003) with two classes of individuals on the recapture, on the survival or on both. We found that models using random effects were overall better supported by the data ($\Delta\text{AIC} = 6.05$, Appendix C: Table C1). Note that, among finite-mixture models, we still found evidence for heterogeneity in recapture but not in survival (Appendix C: Table C1).

EXAMPLE 2: THE SOCIABLE WEAVER DATA

In the previous example, we did not attempt to explain sources of heterogeneity. Here, we consider a modification of the CJS model with heterogeneity where an individual covariate is thought to influence survival probability. We use a data set on the relationship between body mass and survival of Sociable Weavers (*Philetairus socius*) in South Africa. The data were collected over eight years in South Africa and consist of 977 individuals that were weighed as adults. A detailed analysis is provided by Covas et al. (2002) using fixed-effects CR models, in which survival was assumed to be completely determined by individual body mass. In a subsequent analysis, Gimenez et al. (2006a) adopted a Bayesian approach similar to that of Royle (2008) and showed that, accounting for an individual effect on survival, a cubic relationship with no time effect was appropriate. We consequently modified Eq. 3 in the following way:

$$\text{logit}(\phi_{ik}) = \kappa_0 + \kappa_1 x_i + \kappa_2 x_i^2 + \kappa_3 x_i^3 + \beta_i \quad (12)$$

where the κ 's are fixed-effects regression parameters, x_i is the body mass of individual i , and β_i is a random effect, with $\beta_i \sim \mathcal{N}(0, \sigma_\beta^2)$. The κ 's capture the effect of the covariates on survival for the average individual in the population, while β_i modifies the average response to make it specific to individual i . Recapture probabilities were constant over time with no individual heterogeneity. Parameter estimates for this mixed model, denoted

TABLE 2. Maximum-likelihood estimates (MLEs) and associated standard errors (SEs) for the 15-node Gauss-Hermite quadrature (GHQ) approximation as well as Markov chain Monte Carlo (MCMC) results (posterior modes and standard deviations [SDs] are given) for model $\{\phi(x + x^2 + x^3 + h), p\}$ applied to the Sociable Weaver data.

Parameter	GHQ analysis MLE (SE)	MCMC analysis mode (SD)
κ_0	0.509 (0.117)	0.500 (0.116)
κ_1	0.016 (0.131)	0.020 (0.139)
κ_2	-0.268 (0.088)	-0.275 (0.091)
κ_3	0.081 (0.044)	0.093 (0.048)
p	0.427 (0.023)	0.431 (0.023)
σ_ϕ	0.824 (0.163)	0.835 (0.170)

Note: The κ 's are the regression parameters to be estimated; p is the detection probability; σ_ϕ is the standard deviation of the individual random effect on the survival probability.

$\{\phi(x + x^2 + x^3 + h), p\}$, are given in Table 2. We calculated MLEs and SEs using the GHQ. For the Bayesian analysis, we used a $U(0, 1)$ for p , a $N(0, 100)$ for the regression coefficients κ 's, and a $U(0, 8)$ for σ_ϕ . To compare our results with the MCMC analysis, we used WinBUGS (Spiegelhalter et al. 2003) to generate two chains of length 50 000, discarding the first 10 000 as burn-in. The results of the GHQ and MCMC analyses are quite similar. The MCMC simulations took approximately 2.3 hours while in comparison the GHQ took only 10 minutes. We performed a likelihood ratio test of the null hypothesis of homogeneity, which showed that the heterogeneity term σ_ϕ was needed ($0.5\chi^2(0) + 0.5\chi^2(1) = 11.710, P < 0.001$). Note that, to get the P value of this test, using the mixture of distributions $0.5\chi^2(0) + 0.5\chi^2(1)$ corresponds to halving the P value from using the $\chi^2(1)$ distribution.

Keeping heterogeneity in the survival, the comparison of model $\{\phi(x + x^2 + x^3 + h), p\}$ vs. a model without body mass $\{\phi(h), p\}$ ($\Delta AIC = 10.57$) showed the importance of the covariate (Appendix C: Table C2). Finally, we fitted finite-mixture models (Pledger et al. 2003) with two classes of individuals on the survival. Individual heterogeneity in survival was better captured by two classes of individuals than a random effect ($\Delta AIC = 10$; Appendix C: Table C2). This might be due to the fact that we did not incorporate the gender in our analyses, while males and females might experience different selection pressures on body mass. Note that using a two-class mixture, we still found an effect of body mass on survival ($\Delta AIC = 4.99$; Appendix C: Table C2).

DISCUSSION

Modeling individual heterogeneity in demographic parameters is crucial in evolutionary ecology and conservation biology. Royle (2008) developed models in which heterogeneity was handled with individual random effects, while Pledger et al. (2003) used finite mixtures. We propose a maximum-likelihood implementation of Royle's approach using GHQ to carry out estimation and inference about individual heterogeneity in open CR models.

The GHQ was found to be faster than the MCMC algorithm used by Royle (2008). This discrepancy in the computational burden was marked in the Sociable Weaver example as there were about four times as many individuals as in the European Dipper example. When random effects were considered for both survival and recapture probabilities as in the European Dipper case study, the GHQ approximation was slower than when individual heterogeneity was applied to only one of these parameters, but yet faster than the MCMC algorithm.

To test homogeneity, we relied on the null hypothesis testing framework using LRT. We acknowledge that the AIC is often preferred in CR analyses. Nevertheless, the use of AIC in testing random effects is still the object of research. It is not clear to what extent AIC suffers from the boundary issue described in Section 4. Besides, counting the number of parameters is problematic, some authors using the number of fixed effects and variance components (marginal AIC; Wager et al. 2007), others using an "effective degrees of freedom" (conditional AIC; Vaida and Blanchard 2005). While the latter would need to be adapted to CR2Ms, the former is straightforward to implement since numerical integration provides an approximation of the likelihood. Inference based on the marginal AIC was qualitatively similar to LRT results (see Appendix C), with a marginal effect of individual heterogeneity on recapture of European Dippers ($\Delta AIC = 0.8$ between models $\{\phi(\text{flood}), p(h)\}$ and $\{\phi(\text{flood}), p\}$), and strong individual heterogeneity on survival of Sociable Weavers ($\Delta AIC = 9.7$ between the models $\{\phi(x + x^2 + x^3 + h), p\}$ and $\{\phi(x + x^2 + x^3), p\}$).

Our approach has some limitations. First, if the random effects have large variance, GHQ may perform poorly (Lesaffre and Spiessens 2001). Adaptive GHQ (AGHQ; Liu and Pierce 1994) has been proposed to overcome this issue. For the variances we encountered in the examples, GHQ performed well. Second, the GHQ approximation may be time consuming for integrals with more than two dimensions. This is the case when heterogeneity is to be combined with other random effects. For example, one might want in the European Dipper analysis to consider the yearly effects as random

(Barry et al. 2003), or in the Sociable Weaver analysis to consider a nonlinear relationship (Gimenez et al. 2006a), which requires a mixed effect formulation (Gimenez et al. 2006b). Because the total number of nodes increases at an exponential rate with the number of dimensions, product-rule formulas cannot be used as in *Random effects with numerical integration*. One promising solution is to use sparse grids integration (Heiss and Winschel 2008) which combines one-dimensional quadrature as does the product-rule technique but in a different way such that it decreases computational costs in high dimensions. The use of sparse grids is the object of ongoing work.

We envisage several extensions to our approach, which may help in relaxing the assumption of perfect detectability that is often made to analyze CR data with individual random effects. First, we assumed independent random effects in the European Dipper analysis although there exists an interest for considering multivariate distribution for the random effects to study relationships among parameters. Cam et al. (2002) incorporated a possible correlation between individual effects on both survival and reproduction, while Cam et al. (2004) considered a correlation between breeding and success probabilities before and after dispersal, resulting in a 2×2 and a 4×4 covariance matrix respectively. To deal with multivariate distributions, one can apply a transformation to obtain uncorrelated random effects, then apply standard univariate GHQ (Todem et al. 2007). Second, rather than accounting for between-individual variability, one may be interested in dealing with clusters of individuals. For example, Cohas et al. (2007) investigated the effect of offspring type (extra-pair young vs. within-pair young) on juvenile survival using "family" as a random effect to specify the same between-individual variance among all members of a same cluster. Because clusters are independent, the likelihood turns out to be a product of one-dimensional integrals for which the GHQ can be applied. Third, if one is interested in inference about the random effects (the breeding values in a quantitative genetic analysis, for example), the Bayesian approach is quite convenient as posterior distributions are easily obtained. Interestingly, these quantities can also be obtained using an additional round of GHQ.

Based on generalized linear models, Lebreton et al. (1992) proposed a unified framework for analyzing CR data which has had a strong influence. Inspired by generalized linear mixed models, we call for a move forward from fixed-effects to CR mixed models (CR2Ms). We hope that the Bayesian approach using MCMC simulations developed by Royle (2008) and the frequentist approach using numerical integration proposed here will motivate further developments of CR models, with important applications in population biology. In that spirit, we implemented GHQ and its adaptive version in program E-SURGE (Choquet and Gimenez, *in press*). (Program E-SURGE [Choquet et al.

2009] is *available online*.)² We also provided a step-by-step illustration of a typical E-SURGE analysis in Appendix D using the Sociable Weaver data.

ACKNOWLEDGMENTS

The authors thank R. Pradel for helpful discussions, M. D. Anderson, C. R. Brown, and R. Covas for making the Sociable Weaver data available, and G. Marzolin for sharing the European Dipper data. This research was supported by a grant (reference: ANR-08-JCJC-0028-01) from the "Jeunes Chercheuses et Jeunes Chercheurs" program of the French ANR to work on CR2Ms.

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² (<http://www.cefe.cnrs.fr/BIOM/logiciels.htm>)

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APPENDIX A

Precision of the Gauss-Hermite quadrature approximation (*Ecological Archives* E091-067-A1).

APPENDIX B

Approximating the marginal likelihood of models $\{\phi(t), p(t+h)\}$ and $\{\phi(t+h), p(t+h)\}$ using a Gauss-Hermite quadrature approximation (*Ecological Archives* E091-067-A2).

APPENDIX C

Model selection in the Sociable Weaver and European Dipper case studies (*Ecological Archives* E091-067-A3).

APPENDIX D

Incorporating individual random effects using program E-SURGE (*Ecological Archives* E091-067-A4).