

Appendix

Estimation of queen number by Bayesian methods

Mark-recapture methods are extensively used for the estimation of demographic parameters from natural populations (see e.g. Lebreton *et al.*, 1992; Schwarz and Seber, 1999). Most studies employ a version of the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965), which has the main focus on the estimation of survival parameters. The original CJS model assumes that all individuals have equal death rates and capture probabilities, but this assumption can be relaxed by modeling variability by fixed or random effects (e.g. Natarajan and McCulloch, 1999; Newman, 2003). We follow here this line of research by assuming a random effect model with nest and census specific variation in capture probability.

The model

We assume that a set of N nests has been included in the mark-recapture study, and that the nest i has been sampled m_i times. We denote by n_i the (unknown) number of queens in nest i . For capture time j and nest i , we denote by g_{ij} the capture probability, which we assume to be equal for unmarked and marked individuals. We model the capture probability by $\text{logit}g_{ij} = a + \varepsilon_{ij}$, where ε_{ij} represents random variation (e.g. due to weather conditions) in the capture probabilities. We assume that the ε_{ij} follow a normal distribution, $\varepsilon_{ij} \sim N(0, \sigma^2)$ with standard deviation σ to be estimated. We thus assume that there are no systematic differences in the capture probabilities among nests. If there were differences with for example a higher capture rate in smaller nests, part of the variation should be included in random effects ε_{ij} .

The full posterior distribution is given by

$$p(a, \varepsilon, \sigma, n|y) \propto p(y|a, \varepsilon, n)p(a)p(\sigma)p(n)p(\varepsilon|\sigma),$$

where $p(a), p(\sigma), p(n), p(\varepsilon|\sigma)$ represent the prior distributions (see below), $n = (n_i)$ is a vector of the nest i specific queen numbers, $\varepsilon = (\varepsilon_{ij})$ contains all the random effects, and the likelihood of the data is given by

$$p(y|a, \varepsilon, n) \propto \prod_{i=1}^n \prod_j^{m_i} \binom{n_{ij}}{y_{ij}} (g_{ij})^{y_{ij}} (1 - g_{ij})^{n_{ij} - y_{ij}}.$$

Here y_{ij} denotes the number of individuals (unmarked or marked) captured at time j from nest i , and n_{ij} the number of all individuals (unmarked or marked) present at time j in nest i . We note that n_{ij} may differ from n_i as some of the queens were removed for genetic analyses.

The prior distributions

We assume the prior distributions $a \sim N(0, 10)$ and $\sigma^2 \sim \text{Inv} - \chi^2(\nu_0, \sigma_0^2)$ with $\nu_0 = -1$ and $\sigma_0 = 0$, where the latter is the standard noninformative prior distribution for variance components which is uniform on σ (Gelman, 2006). To construct a prior for n , we considered the data presented by Brown and Keller (2000), which include queen number estimates for 38 nests. These estimates are derived from relatedness estimates based on genetic data. Unfortunately, genetic data do not allow precise estimation of queen number when relatedness values are low. Indeed, for 11 out of the 38 nests, the relatedness estimates were negative leading to an infinite estimated number of queens. In another nest the relatedness value was very close to zero leading to an estimate of 187.5 queens. The negative relatedness estimates demonstrate that very high queen numbers are possible. We chose a conservative strategy, in which we assumed that the number of queens in the nests with a negative relatedness estimate was of the same order as in the nest with largest estimated value of 187.5 queens. In the remaining 26 nests the relatedness values were not close to zero leading to reliable estimates of queen number between 1 and 68 (mean = 14.55). To account for both the well estimated values and the tail, we constructed a prior which gave 26/38 weight for a distribution that mimics the reliable part of the data, and 12/38 weight for the tail (representing the 11 nests with negative relatedness estimates and the nest with 187.5 queens). These two sub-distributions were chosen to be $1 + \text{NegBin}(1/14.55)$, and $1 + \text{NegBin}(1/200)$, where the value 14.55 is identical to the mean of the reliable estimates, and 200 represents our a priori impression of the mean of the tail.

The Metropolis-Gibbs algorithm

In order to sample the posterior distribution, we utilized a Metropolis-Gibbs algorithm, in which each parameter is updated in turn, conditional on the current values of the other parameters (Gelman *et al.*, 2004). We ran the Markov Chain for 30000 steps, out of which the first 10000 were treated as a transient. We next describe how samples from each full-conditional distribution were drawn.

1. The full conditional posterior distribution of n is given by $p(n|a, \varepsilon, \sigma, y) \propto p(y|a, \varepsilon, n)p(n)$. We drew a sample from this distribution by updating each n_i separately with the Metropolis algorithm using a discrete uniform proposal distribution ranging from $n_i - V_i^n$ to $n_i + V_i^n$, where n_i is the present value and V_i^n was chosen to be $V_i^n = 10 + 1.5z_i$, where z_i is the number of different queens that were found from colony i . The proposal distribution was chosen in this manner to obtain roughly a 30% accept ratio.

2. The full conditional posterior distribution of ε is given by $p(\varepsilon|a, \sigma, n, y) \propto p(y|a, \varepsilon, n)p(\varepsilon|\sigma)$. We drew a sample from this distribution by updating the ε_{ij} 's in blocks, one block corresponding to the captures to one nest. We used the Metropolis algorithm with a multinormal proposal distribution centered at the present value, with variance-covariance matrix $V^\varepsilon I$, where I is the identity matrix and we set $V^\varepsilon = 0.3$ to obtain roughly a 30% accept ratio.

3. The full conditional posterior distribution of σ is given by $p(\sigma|a, \varepsilon, n, y) \propto p(\varepsilon|\sigma)p(\sigma)$. Based on the use of a conjugate prior distribution, a sample from this distribution can be obtained directly as $\sigma^2 \propto Inv - \chi^2(\nu_1, \sigma_1^2)$,

$$\text{where } \nu_1 = \nu_0 + \sum_i m_i \text{ and } \sigma_1^2 = \frac{\nu_0 \sigma_0^2 + \sum_{i,j} \varepsilon_{ij}^2}{\nu_0 + \sum_i m_i}.$$

4. The full conditional posterior distribution of a is given by $p(a|\varepsilon, \sigma, n, y) \propto p(y|a, \varepsilon, n)p(a)$. We used the Metropolis algorithm with a normal proposal distribution centered at the present value, with standard deviation set to 0.1 to obtain roughly a 30% accept ratio.

Model fit

We assessed the model fit by comparing the posterior predictive distribution against the real data. To do this, we drew a set of parameters from the posterior distribution and generated simulated data sets assuming the same number of visits to the nests as in case of the real data set. We used two different methods. First, we drew all the model parameters (a , ε , and n) from the posterior distribution (Method 1). Second, we drew the parameters (a , σ , and n) from the posterior distribution, and

randomized the random effects from $\varepsilon_{ij} \propto N(0, \sigma^2)$ (Method 2). The difference between these two methods is that Method 1 generates simulated data using the recapture-specific estimates for capture probabilities, whereas Method 2 randomizes these by using information only on the estimated variance σ^2 . We calculated the number of unmarked and marked queens present at the nest for each census by using information on the total number of queens (the estimated value of n), the number of marked queens and number of queen removed during that census. We then randomized the number of observations based on the estimated capture probability given by $\text{logit}(a + \varepsilon_{ij})$.

Figures S1a and S1b reveal that the posterior predictive distribution generated by Method 1 fits well with the numbers of unmarked queens captured in the real data set, a result that is expected given that we used nest and census specific parameters for capture probability. The data presented on the figure may also reveal if there is a difference in capture probability between marked and unmarked queens. The 95% confidence intervals of Fig. S1b overlap with the real data, but the data are so sparse that we cannot exclude that marked queens have a different capture probability than unmarked ones. The total number of unmarked queens captured is 1551 in the real data, which is consistent with the posterior predictive distribution giving a mean of 1535 (95% highest posterior interval: 1438–1636). The number of marked queens recaptured was 19, whereas the posterior predictive distribution gives a significantly greater value: 37 (22–53). This mismatch may have at least two reasons. First, it may be that the recapture probability of marked queens is lower. Second, it may be that marked queens had a higher mortality or were more likely to move to another nest (note that neighboring nests were not sampled). To discriminate between these two explanations, we compared the real and predicted numbers of marked queens for the first and last three censuses to each nest. During the first three censuses there were 11 marked queen captured, which is not statistically different from the model prediction of 7.9 (3–14). For the last three days there were 14 captures (the periods overlap for some of the nests), which is significantly smaller than the model prediction of 27.1 (15–40). Hence the overestimation of marked queens occurred mainly for the last period of the study, suggesting that marked queens are more likely to die or move between nests. However, we note that the numbers of marked queens recaptured is too low to conclusively determine the source of the bias.

Figures S1c and S1d illustrate the model fit assuming Method 2, in which the capture probabilities were randomized independently for each nest and census. In this case the number of captured queens in the large nests are apparently overestimated with the effect that even if there is no statistically significant difference for any individual nest, the summed estimate (2868, CI: 1882–4221) is significantly greater than the real number of 1551. The pattern is similar for recaptures of marked queens,

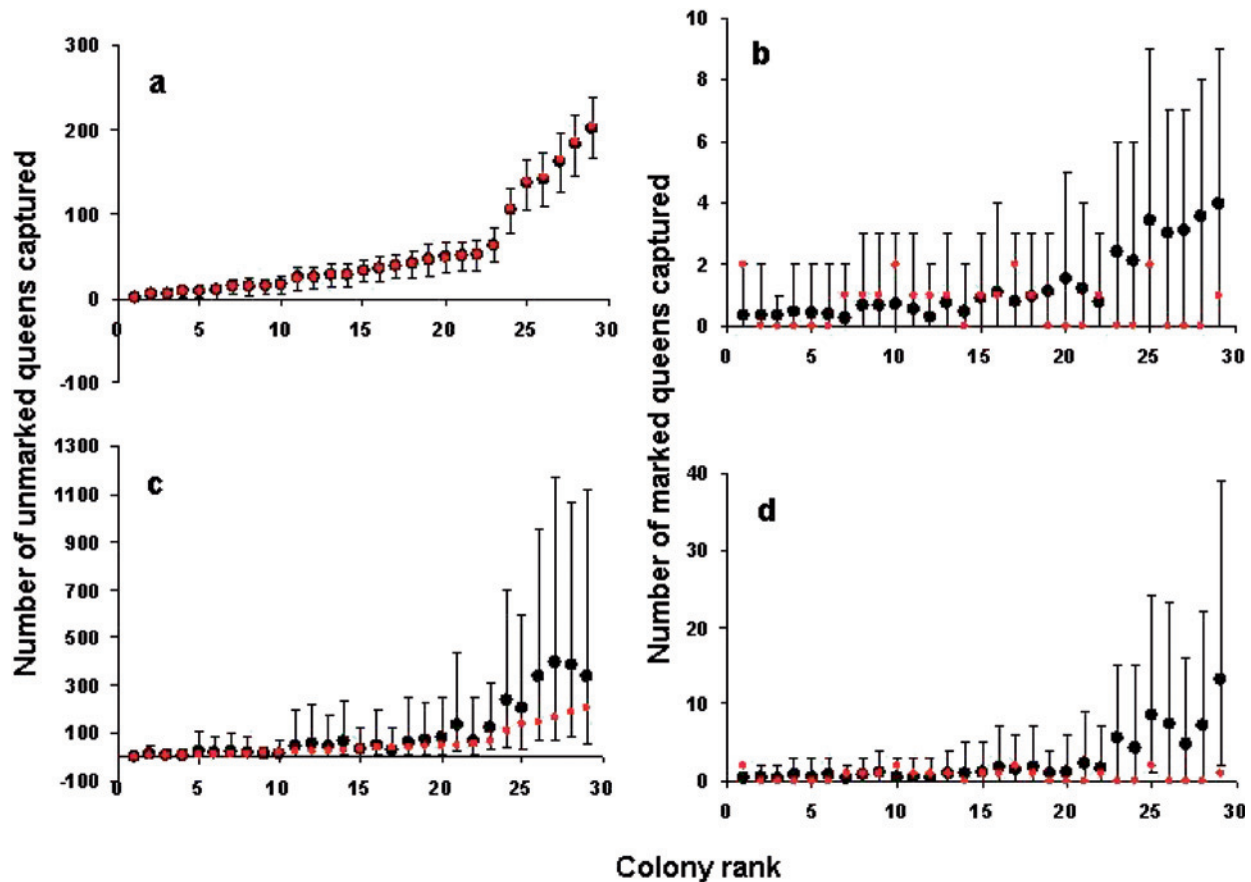


Fig. S1 An assessment of model fit. Black dots with error bars depict the 95 % HPDIs (highest posterior density intervals) of the posterior predictive distributions and the red dots depicts the real data. Panels a and c show the number of unmarked queens captured, whereas panels b and d show the number of marked queens captured. Upper panels (a and b) correspond to Method 1 and lower panels (c and d) to Method 2.

for which the estimate 73 (44–115) is greatly higher than the true number of 19. Thus we conclude that the capture probability is somewhat smaller for large nests (the mismatch in Fig. S1c and S1d), but the random effects in our model is able to capture this difference (there is no mismatch in Fig. S1a and S1b).

References

- Brown W.D. and Keller L. 2000. Colony sex ratios vary with queen number but not relatedness asymmetry in the ant *Formica exsecta*. *Proc. R. Soc. Lond. B. Biol. Sci.* **267**: 1751–1757
- Cormack R.M. 1964. Estimates of survival from sighting of marked animals. *Biometrika* **51**: 429–438
- Gelman A. 2006. Prior distributions for variance parameters in hierarchical models (Comment on article by Browne and Draper). *Bayesian Analysis* **1**: 515–534
- Gelman A., Carlin J.B., Stern H.S. and Rubin D.B. 2004. *Bayesian data analysis*, 2nd Edition Chapman & Hall/CRC: Boca Raton, Florida
- Jolly G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52**: 225–247
- Lebreton J.D., Burnham K.P., Clobert J. and Anderson D.R. 1992. Modeling survival and testing biological hypotheses using marked animals – a unified approach with case-studies. *Ecol. Monogr.* **62**: 67–118
- Natarajan R. and McCulloch C.E. 1999. Modeling heterogeneity in nest survival data. *Biometrics* **55**: 553–559
- Newman K.B. 2003. Modelling paired release-recovery data in the presence of survival and capture heterogeneity with application to marked juvenile salmon. *Statistical Modelling* **3**: 157–177
- Schwarz C.J. and Seber G.A.F. 1999. Estimating animal abundance: Review III. *Statistical Science* **14**: 427–456
- Seber G.A.F. 1965. A note on multiple-recapture census. *Biometrika* **52**: 249–259

To access this journal online:
<http://www.birkhauser.ch/IS>
