Statistical modelling of repeated and multivariate survival data

Wintrebert, C.M.A.

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CHAPTER 3

Joint Modelling of Breeding and Survival in the Kittiwake Using Frailty Models

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Abstract

Assessment of population dynamics is central to population dynamics and conservation. In structured populations, matrix population models based on demographic data have been widely used to assess such dynamics. Although highlighted in several studies, the influence of heterogeneity among individuals in demographic parameters and of the possible correlation among these parameters has usually been ignored, mostly because of difficulties in estimating such individual-specific parameters. In the kittiwake (Rissa tridactyla), a long-lived seabird species, differences in survival and breeding probabilities among individual birds are well documented. Several approaches have been used in the animal ecology literature to establish the association between survival and breeding rates. However, most are based on observed heterogeneity between groups of individuals, an approach that seldom accounts for individual heterogeneity. Few attempts have been made to build models permitting estimation of the correlation between vital rates. For example, survival and breeding probability of individual birds were jointly modelled using logistic random effects models by Cam et al. (2002). This is the only example in wildlife animal populations we are aware of. Here we adopt the survival analysis approaches from epidemiology. We model the survival and the breeding probability jointly using a normally distributed random effect (frailty). Conditionally on this random effect, the survival time is modelled assuming a lognormal distribution, and breeding is modelled with a logistic model. Since the deaths are observed in year-intervals, we also take into account that the data are interval censored. The joint model is estimated using classic frequentist methods and also MCMC techniques in Winbugs. The association between survival and breeding attempt is quantified using the standard deviation of the random frailty parameters. We apply our joint model on a large data set of 862 birds, that was followed from 1984 to 1995 in Brittany (France). Survival is positively correlated with breeding indicating that birds with greater inclination to breed also had higher survival.

3.1 Introduction

Assessment of the dynamics of populations is central to population ecology. Matrix population models have been widely used to investigate the dynamics of structured populations (e.g., Linacre and Keough (2003)) in studies with management and conservation implications or in studies of life history evolution (Caswell, 2001). Specification of such models requires demographic data and estimation of relevant demographic parameters (Oli, 2003). As emphasized by Grist and des Clers (1999) or Pitt et al. (2003) population models have often been criticized because of unrealistic assumptions (e.g., identical individuals). There has been an increasing awareness of the importance of individual heterogeneity in the life history process to population dynamics (Holmes and Sherry, 1997; Pontier et al., 2000).

Age- and stage-based matrix population models have enhanced our ability to account for such heterogeneity. However, the mathematical difficulties raised by complex models partly explain why the population-level consequences of individual variability has seldom been investigated. The importance of individual heterogeneity should not be underestimated. Simulation studies have shown that individual heterogeneity may enhance the viability of small populations, which is likely to have consequences in terms of conservation (Conner and White, 1999). In addition, several researchers have emphasized that observable heterogeneity (i.e., individual characteristics that can be directly assessed or measured) seldom accounts for individual heterogeneity in a satisfactory manner in demographic models (e.g., Hougaard (1991)). This led to the development and use of random effects models accounting for individual heterogeneity without grouping individuals (e.g., Cam et al. (2002); Link et al. (2002); Service (2000)).

Furthermore, as emphasized by Tienderen (1995) population models need to account for the possible covariation among demographic parameters, which highlights the need for models permitting estimation of the correlation among these parameters (e.g. Cam et al. (2002)). Such models can prove difficult to fit using classical approaches (Link et al., 2002), but very few attempts have been made. Parameter estimation has long been recognized as central to ecological modelling (Jorgensen, 1997; Salinger et al., 2003; Williams et al., 2002). Our main objective is to develop a new parametrization for a model to estimate the survival and breeding probability jointly using data from a long-lived species (the kittiwake). We also assess two approaches to fitting the model (a frequentist and an objective Bayesian approach).

In the kittiwake (Rissa tridactyla), a long-lived seabird species differences in survival and breeding probabilities among individual birds are well documented (Cam et al., 1998, 2002; Cam and Monnat, 2000; Coulson and Thomas, 1985; Coulson and Wooller, 1976; Thomas and Coulson, 1988). Several approaches have been used in the animal ecology literature to establish the association between survival and breeding. The vast majority of these approaches use discrete groups of individuals. In addition, survival and breeding probability of individual birds were jointly modelled applying logistic random effects models (Cam et al., 2002). This is the only example of such a model in wildlife animal populations, we are aware of. As emphasized by the authors, fitting these models can prove difficult (see also Link et al. (2002)). In human epidemiology a number of technical and more complicated methods have also often been used to estimate the correlation between survival and a repeated measured covariable (Henderson et al., 2000; Hogan and Laird, 1997; Wulfsohn and Tsiatis, 1999). Here, we adopt these survival approaches from human epidemiology to assess the correlation between the survival of the birds and repeated breeding attempts of the birds. We model the association between survival and breeding probability jointly using a normally distributed random effect (frailty). We use this approach with data from a long-term study of kittiwakes. Since the death events are observed in yearly intervals, we also take into account that the data are interval or right censored. The joint model is estimated using a classic frequentist method and also MCMC samplings in WinBugs (Spiegelhalter et al., 1996). As emphasized by Link et al. (2002) MCMC has widely been used in the statistical literature, but there are still relatively few examples in wildlife-related applications. Here we use this statistical tool to fit a model designed to assess the correlation between reproduction and survival that has never been used with data from wild animal populations. Estimation of the correlation between vital rates is of central interest in evolutionary ecology (Stearns, 1992), and in studies with conservation management implications (Tienderen, 1995).

This chapter is organized as follows. In Section 3.2 we give a description of the data set and develop the methods. The classic frequentist method and the Bayesian approach are given in detail. Section 3.3 describes the results and we conclude with a discussion in Section 3.4.

3.2 Material and Methods

3.2.1 The data set

Data from 862 individually marked birds were collected in Brittany (France) from 1984 to 1995, and truncated capture-recapture histories of all individuals birds were gathered including survival and breeding attempt in each year during the breeding season. Since recapture probability is very close to one (Cam et al., 1998), we assumed that individuals that were missing at recapture died. So we need not to take the recapture probability into account in our analysis. In our analysis, we retained the individuals that have been recruited and bred at least once, adult birds. This is because young (not yet breeders) birds are more difficult to capture and to count, and so their recapture probability is not equal to one.

3.2.2 Methods

Cam et al. (2002) modelled jointly survival and breeding probability of individual birds applying logistic models. They used individual random effects for the survival in year t and for the conditional breeding probability in year $t+1$ and they assumed that these two random effects were bivariate normally distributed to assess the correlation between the survival and the breeding probability. We consider the survival in another way and show that only one frailty, the same for the survival model and for the breeding attempt model is needed to assess this correlation and explain why. Conditionally on this single random effect, the survival time is modelled assuming a parametric distribution, and breeding is modelled with a logistic model. We select the lognormal survival distribution, but several parametric models are fitted. In WinBugs we also use the semi-parametric Cox model. Since the deaths are observed in yearly intervals, we take into account that the data are interval or right censored: an individual alive in year x, and dead in year $x+1$, is interval censored between x and $x+1$, and an individual alive at the last recapture is right censored in that year.

Model description

The probability that a bird, indexed i, attempted breeding in year j $(Y_{ij}=1)$ is modelled using a logistic model

$$p_{ij} = Pr(Y_{ij} = 1 \mid X_{ij}, w_i) = (\exp(\beta^T X_{ij} + w_i))(1 + \exp(\beta^T X_{ij} + w_i))^{-1},$$

where X_{ij} is a vector of covariate values associated with year j, β is a vector of (unknown) regression weights. w_i is a random effect representing the inclination of bird i to attempt breeding. Statistically, w_i, random effect of bird i is assumed to account for the correlation between his repeated breeding attempts. This correlation can be explained by important unknown covariates of the breeding attempts.

We assume that given w_i, Y_{ij} and Y_{ik} for any j and k are independent. Our set of covariates is limited to gender of the bird, the animal's age, age-squared in year j, and calendar year.
The date of death (failure time) of bird i, T_i , is modelled using a frailty model, and given the frailty w_i, $\log(T_i)$ is assumed to be normally distributed with expectation $\mu_i = \beta^{T*} X_i + \alpha w_i$, and variance-parameter σ_T^2 . We choose the lognormal model for sake of convenience, but we check its marginal fit, and that is satisfactory. We include w_i in the model for survival to evaluate the association between survival and breeding. We assume that the breeding attempts of animal i are independent of its survival given w, and we further assume that w is normally distributed with expectation zero, and variance σ_w^2. The parameter α determines the association between the survival and the breeding processes: if α equals zero survival is independent of the breeding inclination. In this part of the model, the set of covariates we consider was gender and year of birth of the birds.

We also estimate the logistic model and the lognormal model apart. In that case the frailty term in the lognormal model is not identifiable, since a bird dies only once and we need repeated measurements to be able to identify random effects.

Only one frailty estimable

In the lognormal-frailty model only one frailty parameter is estimable. This is easily understood as follows. Suppose we consider two frailty parameters, w_{i1} and w_{i2}, to model the association between survival and breeding:

$$\begin{aligned} log(T_i \mid X_i, w_{i1}) &= \beta^{\star T} X_i + w_{i1} + f_i \\ f_i &\sim N(0, \sigma_T^2) \\ logit(p_{ij}) &= \beta^T X_{ij} + w_{i2} \\ (w_{i1}, w_{i2}) &\sim N((0,0), \Sigma) \end{aligned}$$

where
$\Sigma = \begin{pmatrix} \sigma_1^2 & \sigma_{12} \\ \sigma_{12} & \sigma_2^2 \end{pmatrix}.$

We then rewrite w_{i1} as $w_{i1} = \alpha w_{i2} + e_i$, where e_i and w_{i2} are independent. It is always possible to find a constant α such that $e_i = \alpha w_{i2} - w_{i1}$ and w_{i2} are independent. This is achieved when $\alpha = \sigma_{12}/\sigma_2^2$. Then, the formulation of the survival component of the model becomes

$$log(T_i|X_i, w_{i2}, e_i) = \beta^{\star T} X_i + \alpha w_{i2} + e_i + f_i$$

illustrating the fact that e_i and f_i are fully confounded and consequently that the frailty w_{i1} is not attainable in its entirety. However, one can still estimate α and σ_2^2 and thus the covariance $\sigma_{12} = \alpha\sigma_2^2$ between the two frailties. Thus, writing the survival part of the model as

$$log(T_i|X_i, w_{i2}, e_i) = \beta^{\star T} X_i + \alpha w_{i2} + f_i'$$

as we will do in the sequel is in no way restrictive. It is merely acknowledging that part only of the general model is estimable. In particular it by no means implies that the survival and breeding frailties are proportional (because αw_{i2} is just one part of the w_{i1} frailty, the other part being absorbed in f_i'). We may also remark that the choice of a one-parameter distribution for $log(T_i)$ (e.g. the exponential distribution) renders the w_{i1} frailty identifiable. However, we would rather opt for a distribution that better describes the phenomenon and be content with the estimation of the covariance between the two frailties.

For the semi-parametric Cox regression model Elbers and Ridder (1982) showed that a frailty parameter is identifiable in some cases. This can, however, be interpreted as a reflection of violation of the proportionality assumption of the model (Keiding et al., 1997), and need not reflect individual differences in the underlying hazards.

Parameter estimation: classic method and likelihood

Let $G(w)$ be the distribution function of the normal distribution, then the likelihood of the data of animal i equals

$$\begin{aligned}
L_i &= Pr(T_i \geq t_i, Y_{i1} = y_{i1}, ..., Y_{it_i} = y_{it_i}) \\
&= \int Pr(T_i \geq t_i, Y_{i1} = y_{i1}, ..., Y_{it_i} = y_{it_i} \mid w_i) dG(w) = \\
&= \int (F(\log(t_i)) - F(\log(t_{i-1})))^{d_i} (1 - F(log(t_i)))^{1-d_i} \star \\
& \prod_{j=1}^{t_i} \exp(y_{ij}(\beta^T X_{ij} + w_i))(1 + \exp(\beta^T X_{ij} + w_i))^{-1} dG(w)
\end{aligned}$$

where t_i is the age of the bird i at the last observation time, and d_i is an indicator-variable indicating whether bird i dies $(d_i = 1)$ between t_{i-1} and t_i or is still alive at t_i $(d_i = 0)$, and F(.) are the cumulative distribution function associated with $log(t_i)$. The unknown parameters of this joint model $(\beta, \beta^*, \sigma_T^2, \alpha, \sigma_w^2)$ are estimated in two ways, namely (1) by maximisation of the loglikelihood using Gauss-Hermite approximation of the integral involved, and (2) by a MCMC approach using WinBugs.

We first give some details of the maximum likelihood approach. The likelihood contribution of animal i can be written as

$$\begin{aligned}
L_i = \int & (F_w^*(\log(t_i)) - F_w^*(\log(t_{i-1})))^{d_i} (1 - F_w^*(log(t_i)))^{1-d_i} \star \\
& \prod_{j=1}^{t_i} (\exp(y_{ij}(\beta^T X_{ij} + w_i)))(1 + \exp(\beta^T X_{ij} + w_i))^{-1} g(w) dw,
\end{aligned}$$

where $g(w)$ is the density function of the normal distribution with mean zero and standard deviation σ_w, and $F_w^*(.)$ is the distribution function of the normal distribution with expectation $\mu_i = \beta^{*T} X_i + \alpha w_i$ and variance σ_T^2. The integral could be approximated to any desired degree of precision using the Gauss-Hermite rule:

$$\begin{aligned}
L_i = \sum_l & (F_w^*(\log(t_i)) - F_w^*(\log(t_{i-1})))^{d_i} (1 - F_w^*(log(t_i)))^{1-d_i} \star \\
& \prod_{j=1}^{t_i} (\exp(y_{ij}(\beta^T X_{ij} + \sigma_w q_l)))(1 + \exp(\beta^T X_{ij} + \sigma_w q_l))^{-1} r_l,
\end{aligned}$$

where q_l and r_l are fixed known constants (Abramowitz and Stegun, 1965). The unknown parameters $(\beta, \beta^*, \sigma_T^2, \alpha, \sigma_w^2)$ can be easily estimated by maximizing the corresponding loglikelihood. This was done by the Gauss routine maxlik (GAUSS, 2002). Since (σ_T^2, σ_w^2) are required to be positive we estimate $(\log(\sigma_T^2), \log(\sigma_w^2))$.

Bayesian approach and modelling

We also take a Bayesian approach to estimate the unknown parameters of this joint model $(\beta, \beta^*, \sigma_T^2, \alpha, \sigma_w^2)$. We use Monte Carlo Markov Chains techniques with the WinBugs package (Spiegelhalter et al., 1996). For each quantity of interest, a stream of simulated values is generated which converges to the posterior distribution, instead of calculating exact or approximate estimates.

First, we construct a graphical representation of the model where the specifications of the model quantities and their qualitative conditional independence structure are given.

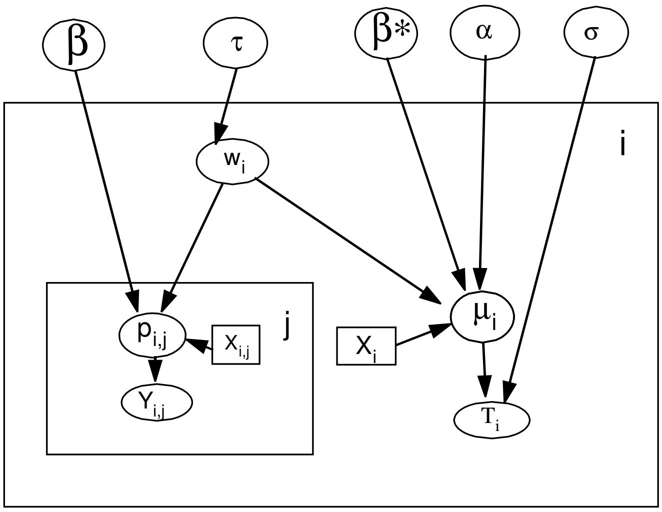

FIGURE 3.1: *Directed acyclic graph*

Figure 3.1 shows a directed acyclic graph (DAG) representing the model assumptions and structure. Circles represent all unknown quantities, little rectangles indicate observed data. Then, to provide the likelihood terms in the model, we specify the parametric form of the direct relationships between the model quantities. These likelihood terms in our model are :

$$
\begin{aligned}
Y_{ij} &\sim Bernouilli(p_{ij}) \\
logit(p_{ij}) &= \beta^T X_{ij} + w_i \\
T_i &\sim lognormal(\mu_i, 1/\sigma_T^2) \\
\mu_i &= \beta^{T*} X_i + \alpha w_i \\
w_i &\sim normal(0, 1/\sigma_w^2)
\end{aligned}
$$

Finally, to complete our Bayesian model specifications, we choose the following prior distributions. The fixed effects β, β^*, α are assumed to follow vague independent Normal distributions with mean zero and low precision of 0.001. The precision of the frailty $(1/\sigma_w^2)$ and the precision of the lognormal distribution $(1/\sigma_T^2)$ are assumed to arise from non-informative gamma priors, namely

$$
\begin{aligned}
\beta, \beta^*, \alpha &\sim Normal(0, 0.0001) \\
1/\sigma_w^2, 1/\sigma_T^2 &\sim Gamma(0.001, 0.001)
\end{aligned}
$$

We choose the gamma priors for sake of convenience since $\sigma_w^2 > 0$, and $\sigma_T^2 > 0$.

In the analysis we take into account right and interval censored data with the help of the WinBugs function $I(upper, lower)$.

To improve convergence and stability of the samples, good parameterizations of the parameters are found to be important. The convergence of the algorithm is checked by using the Gelman and Rubin (Gelman and Rubin, 1992a,b) convergence test. Their test is based on two or more parallel chains: each started from different initial values which are overdispersed with respect to the true posterior distribution.

Using a Bayesian approach, lead also to pay attention for the burn-in. The burn-in represents how many initial iterations need to be discarded in order that remaining samples are drawn from a distribution close enough to the true stationary distribution to be usable for inference and estimation.

3.3 Results

3.3.1 Description of the sample

Data from 862 animals are used for analysis: 395 females, and 434 males and of 33 birds gender can not be ascertained. Age at first observation varies from 2 to 8 years with mean 4.1 (SD=0.92), and age of first reproduction also varies from 2 to 8 years with mean 4.0 (SD=0.92). Observation period starts in 1984 and continues until 1995; there are 98 birds observed in 1984, 162 in 1985, and between 200 and 305 in the other years.

3.3.2 Survival

A total of 249 (29.9%) birds are still alive at the end of the follow-up period: median live-lengths is 6 years (Figure 3.2).

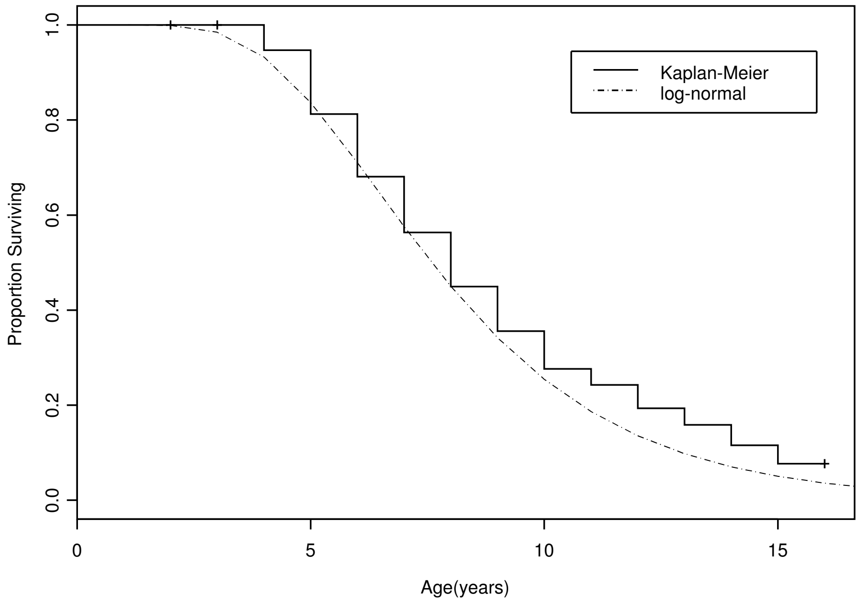

FIGURE 3.2: *Lognormal model and Kaplan-Meier.*

Several parametric models are fitted using classic methods, see Table 3.1.

The lognormal model shows a satisfactory fit to the survival data when compared to the non-parametric Kaplan-Meier (Andersen et al., 1993) estimate (Figure 3.2).

There is no significant difference between male and female birds: expected life-length is 1.02 times larger for female birds with 95% confidence interval $CI : [0.94 - 1.11], p = 0.58$. This is consistent with the results of a previous study of the influence of sex on survival (Cam and Monnat, 2000). There are small $(p = 0.02)$ differences among animals that are observed for the first time in the different calendar years. The deviance of the lognormal survival model is 2260. Model comparison can be done

TABLE 3.1: *Loglikelihood of several parametric models for the survival*

model	loglikelihood	df	AIC	Δ AIC [1]
Kaplan-Meier	-1172.0	12	2368	–
weibull	-1175.8	2	2355.6	12.4
extreme	-1273.9	2	2551.8	183.8
normal	-1189.9	2	2382	14
logistic	-1196.5	2	2397	29
lognormal	-1129.9	2	2263.8	104.2
loglogistic	-1140.8	2	2285.6	82.4

[1] Δ AIC is the difference of the AIC compared to the fully non-parametric model of Kaplan-Meier.

using Akaike Information Criterion (AIC): the lognormal survival model outperforms the others. Using breeding as a time-dependent covariate, we find that breeding attempt in the previous year is significantly ($p < 0.001$) associated with death-risk at age t with relative risk 0.67 (95% CI: 0.52 - 0.86).

3.3.3 Breeding attempts

Out of 2373 observation-years in total, breeding attempts are made in 2086 cases (87.9%). There is a highly significant effect of age ($p<0.001$), and this effect is illustrated in Figure 3.3.

In addition, there are significant differences between calendar years; in particular breeding is attempted much less in 1988 when compared to other years: 68% of the birds attempted breeding in 1988 while this percentage varied from 85% to 93% in other years. There is no significant difference between male and female birds. The standard deviation σ_w is estimated as 1.12 (p=0.001), which corresponds to a correlation of about 0.3 between the repeated breeding attempts of the same bird. The deviance of the logistic breeding frailty model is 1569.3.

3.3.4 The joint model

The aim of this joint model is to estimate the correlation between the survival and the breeding attempts of the birds.

Estimation of the parameters

The maximum likelihood and Bayesian approaches to the estimation of the parameters in the joint model are similar. We therefore report, for the estimation of the parameters,

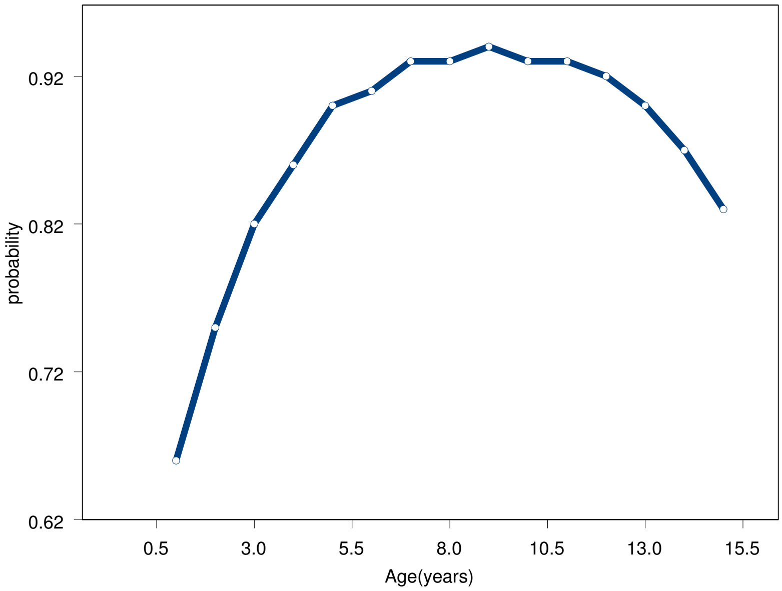

FIGURE 3.3: *Marginal probability of a breeding attempt.*

the results of the Bayesian approach only. In the Bayesian approach, we use a 500 burn-in iterations and 49500 thereafter. Updates takes approximately 2 hours to complete. The posterior mean with confidence interval for each regression coefficient and for the frailty parameters are shown in Table 3.2.

The posterior distributions in general are symmetric, both for the regression parameters (β, β^*, α), and for the variances (σ_t^2, σ_w^2). This is illustrated in Figure 3.4 for α and σ_w. The process converges beautifully, as illustrated by the traces for α and σ_w in Figure 3.4.

Indeed we can observe that the traces follow a normal distribution. The trace also gives information on the number of iterations it takes to stabilize.

Gelman-Rubin propose a convergence test based on 2 or more parallel chains, each started from overdispersed initial values. Here we simulated two Markov Chains. Their method is based on a comparison of the within and between chain variances for each variable. This comparison is used to estimate the factor by which the scale parameter of the marginal posterior distribution of each variable might be reduced if the chain were run to infinity. Best results are obtained for parameters whose marginal posterior densities are approximately normal. This is here the case for the estimated parameters. These are the median and the 97.5% quantiles (also called Gelman-Rubin diagnostics) of the sampling distribution for this shrink factor.

In the graphs on Figure 3.5, the Gelman-Rubin diagnostics are plotted. These quantiles are estimated from the second half of each chain only. If both quantiles are approximately 1.0, effective convergence may be diagnosed. We can observed convergence on the graphs. (In other words, samples from the second half each chain may be assumed to have arisen from the stationary distribution. In this case, summary statistics and density estimates may be calculated by combining the latter 50% of iterate from all chains.) The estimates of the parameters in Table 3.2 show similar conclusions for effects of age, gender, and birth year on reproduction and survival as are found in the separate models. Most interesting is that the posterior mean of α is 0.13 with posterior standard error 0.057. This indicates that birds with a higher inclination to breed also have a longer life-span.

The classical approach permits us to check the fit of the joint model versus the separate models. The loglikelihood of the joint model was -1909.5, whereas the loglikelihood of the model assuming independence of survival and breeding ($H_0 : \alpha = 0$) was -1914.3. The likelihood ratio statistic was therefore 9.6 (df=1), and p-value 0.002.

3.4 Discussion

Our analysis provides evidence of a positive correlation between the survival and the breeding probabilities in kittiwakes. This result is consistent with the one of Cam et al. (2002) using the same data set but using other models from ecology. In population ecology of vertebrates survival and breeding probability are usually modelled using logit models (Williams et al., 2002). This indicates that we can adapt techniques from human epidemiology to solve ecological problem with an appropriate data set. Up to now, frailty models have been used in an extremely limited number of cases in population ecology, in spite of the growing appreciation of their usefulness in related areas of research in humans (e.g. demography Hougaard (1991)). An interesting point of our models is that we use only one frailty in both models for the survival and for the breeding, resulting in a more parsimonious model than the one employed by Cam et al. (2002). We assess the fit of separate models for survival and breeding attempts, as well as a joint model for both processes, and the best model is the joint lognormal-logistic model by far. Our results provide evidence of a positive correlation between survival and reproduction using a model different from those previously used (Cam et al., 1998, 2002).

One of the motivations for the development of our approach to modelling is that there is growing interest in individual variation in population ecology (Caswell, 2001; Conner and White, 1999; Grist and des Clers, 1999; Pontier et al., 2000). In addition, much of the focus in evolutionary ecology is quantifying and understanding the sources and consequences of individual variation in fitness and trait values. Our results provided unambiguous evidence of substantial heterogeneity in demographic parameters in this population. One of the explanations for heterogeneity may be the influence of genetic differences on survival and breeding. The relationship between the genetic and individual effects is an interesting question about which virtually nothing is known. Approaches based on individual effects are used in agronomics for animal or vegetable reproduction, as for instance described in the book from Littell et al. (1996). The interpretation of individual differences in evolutionary ecology due to the existence of genetical differences is still an important question.

Many classical ecological models are based on the assumption that populations consist of identical individuals or homogeneous groups of individuals. Here for instance, by including an individual effect in our model, we provide evidence of senescent decline in survival. This cannot be achieved when analyzed using classic approaches to the effect of age on survival (Cam et al., 2002). In clinical biostatistics, models that take into account individual variation are extensively used, and research is advanced. This has been very rarely addressed in wild animal populations. Although senescence has been well documented in humans and in domestic and laboratory animals, evidence for its occurrence and importance in the wild remains limited and equivocal. Knowledge of age-specific patterns of variation in survival is usually limited by the small number of older individuals in populations. Studies of age-related variations in survival also require large numbers of individuals marked as young, and have to be long in duration. Our sample was apparently of sufficient size, and duration. Senescence was also seen in wild populations of common sterna (Nisbet and Cam, 2002); see Bennett and Owens (2002) for a review in birds.

In ecology, individual heterogeneity has important implications for population management and conservation. For instance, individual heterogeneity of the demographic parameters influences population viability (Conner and White, 1999). Theoretical and management implications of individual heterogeneity are explained in details in Link et al. (2002).

TABLE 3.2: *Estimation of the parameters of the joint lognormal-logistic model.*

parameters		estimation	(CI)
breeding attempt:	intercept	3.781	(2.776 ; 4.891)
	age	0.4958	(0.2746 ; 0.7215)
	age^2	-0.2678	(-0.3915 ; -0.1451)
	sexe	-0.2488	(-0.5939 ; 0.08651)
	year 1984	0.00	(-)
	1985	-0.6156	(-1.619 ; 0.3227)
	1986	-0.6935	(-1.683 ; 0.2214)
	1987	-0.6699	(-1.653 ; 0.227)
	1988	-2.464	(-3.469 ; -1.582)
	1989	-0.4615	(-1.521 ; 0.5401)
	1990	-0.5893	(-1.653 ; 0.401)
	1991	-0.3836	(-1.435 ; 0.5958)
	1992	-0.4623	(-1.5 ; 0.4981)
	1993	-0.457	(-1.496 ; 0.4998)
	1994	-0.4019	(-1.448 ; 0.5666)
	1995	-0.9341	(-1.953 ; -0.007969)
survival:	intercept	2.199	(1.882 ; 2.548)
	year 1980	0	(-)
	1981	-0.08403	(-0.4254 ; 0.2405)
	1982	-0.1275	(-0.4553 ; 0.1828)
	1983	-0.2225	(-0.5552 ; 0.09107)
	1984	-0.2143	(-0.562 ; 0.1154)
	1985	-0.1957	(-0.5324 ; 0.1221)
	1986	-0.2602	(-0.6082 ; 0.07065)
	1987	-0.005138	(-0.3532 ; 0.3251)
	1988	-0.09743	(-0.4404 ; 0.2296)
	1989	-0.1445	(-0.495 ; 0.1927)
	1990	-0.078	(-0.4693 ; 0.308)
	1991	-0.3662	(-0.7329 ; -0.01282)
	1992	-0.111	(-0.4904 ; 0.2698)
	1993	0.7014	(-0.4621 ; 1.817)
	1994	0.4361	(-1.439 ; 2.324)
	sexe	0.00089	(-0.07586 ; 0.07578)
	σ_T	0.4135	(0.3665 ; 0.4554)
association between survival	α	0.1335	(0.04253 ; 0.266)
and breeding attempt:	σ_w	1.103	(0.7795 ; 1.438)

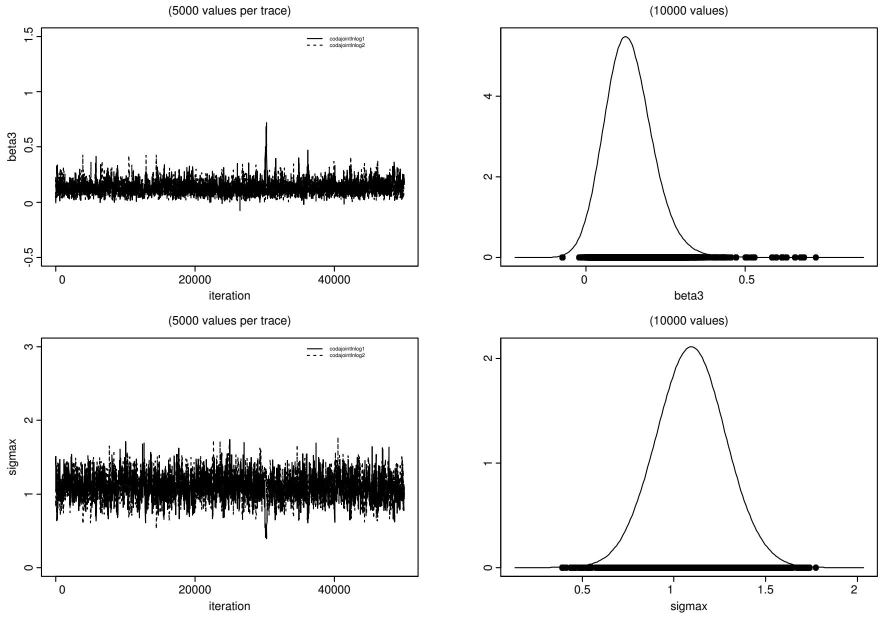

FIGURE 3.4: *Traces and density of* α *and* σ_w.

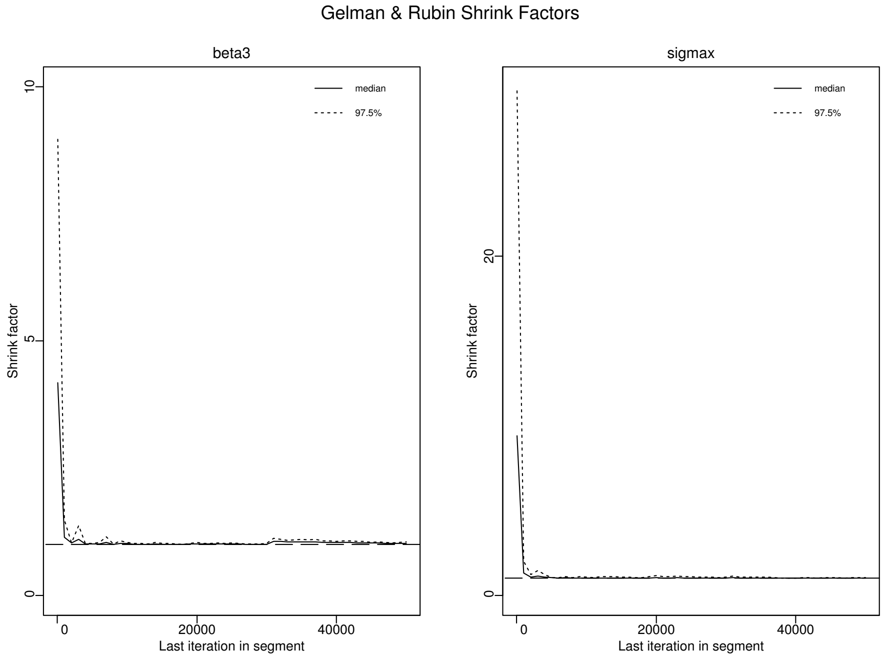

FIGURE 3.5: *Gelman and Rubin statistic for* α*(beta3) and* σ_w*(sigmax)*