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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, E., Link, W.A., Cooch, E.G., Monnat, J., Danchin, E., 2002. Individual covariation in life-history traits: seeing the trees despite the forest. Am. Naturalist, 159, in press]. 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

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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.

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., Service (2000), Cam et al. (2002), Link et al. (2002)).

Furthermore, as emphasized by van 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; Williams et al., 2002; Salinger et al., 2003). 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 (Coulson and Wooller, 1976; Coulson and Thomas, 1985; Thomas and Coulson, 1988; Cam et al., 1998; Cam and Monnat, 2000; Cam et al., 2002). 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 (Hogan and Laird, 1997; Wulfsohn and Tsiatis, 1999; Henderson et al., 2000). 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