CHAPTER 4

Capture—mark—recapture models

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4.1 Introduction

Demographic traits drive the dynamics of local populations and, at larger scales, of species ranges. Investigations of the impact of climatic factors on demographic traits are thus needed to address the process underlying the impact of climate change on population and range dynamics. Demographic traits are also fitness components. Their variation under the influence of climate change can thus provide important information on micro-evolutionary processes. Finally, because demographic traits define life histories, studying the impact of climatic factors on them could reveal selective pressures generated by climate change on life-history strategies.

Longitudinal data at the individual level gathered over long periods of time are needed in order to estimate most demographic traits and relate their variation to climatic factors (Williams *et al.*, 2002; Chapter 3). In this chapter we review the protocols, data, and statistical models for studying the impact of climatic factors on demographic traits from information at the individual level, and we present questions about the impact of climatic changes that can be addressed with these methods.

4.2 CMR protocols and data

4.2.1 Brief presentation of CMR protocols

Measuring demographic traits in bird populations implies setting up protocols for monitoring the states and fates of marked individuals. The monitoring methods that are most commonly used for birds are capture–mark–recapture (CMR) protocols where, at discrete occasions spread over time, birds occupying a focal area are captured and/or sighted (Sandercock, 2006). At each of these capture occasions, a mark is attributed to each bird encountered for the first time, which will allow identification in the future, and the re-encounters (recaptures or re-sightings) of individuals already marked at past occasions are recorded. In addition, phenotypic, physiological, parasitological, or behavioural characteristics of the birds encountered during a capture occasion can be measured and recorded. Finally, information, referred to as ring or band recovery data, on the date and place where ringed birds die can also be obtained when such birds are fortuitously recovered. These individual monitoring protocols produce histories of the states and fates of marked birds, which are incomplete because information is not recorded continuously through time, but only at discrete capture occasions, because not all individuals present in the area covered during a given capture occasion are encountered, and because the rates at which rings of dead birds are recovered and correctly reported are typically low.

4.2.2 Demographic traits that can be estimated with CMR data

The capture histories thus result from the combination of biological and observation processes, and ignoring the latter would produce flawed estimates of the former (Gimenez *et al.*, 2008). Specific statistical methods and models have thus been developed to disentangle these two types of processes and infer unbiased biological information from the analysis of capture histories. Depending on the design of the CMR protocol, a large variety of demographic traits can be estimated and monitored through time and possibly space (Table 4.1). These include survival, recruitment, population growth rates (Lebreton *et al.*, 1992; Pradel, 1996), breeding parameters (Lebreton *et al.*, 2009), and rates of dispersal among sub-populations (Lebreton *et al.*, 2009). When the protocol is undertaken at a stopover site of a migrating population, the probability of departure, the proportion of newly arrived birds, and stopover duration can be addressed (Schaub *et al.*, 2001). In all the abovementioned analyses, the monitored birds can be categorized according to phenotypic traits such as age or sex, determined in the field during capture occasions, and distinct estimates of the demographic traits can be obtained for each resulting category (Williams *et al.*, 2002).

4.3 CMR models where demographic traits are related to climatic factors

The important point from the perspective of evaluation of climatic impacts on birds is that the application of CMR protocols and models is an efficient and often the only way of obtaining time series of demographic traits. These time series can be related to that of climatic factors to infer how climatic variation impacts demographic processes and affect fitness components in birds. We only briefly describe the statistical techniques for studying the relationships between demographic parameters estimated from the analysis of CMR data and climatic factors. They have been reviewed more thoroughly by Grosbois *et al.* (2008).

4.3.1 CMR models

CMR models are a particular development of generalized linear models that allow the estimation and

Table 4.1 Demographic traits that can be related to climatic factors with CMR studies.

Demographic trait	Type of CMR data	Key sentence in ISI Web of Science[1]	Number of occurrences in Web of Science[2]
Juvenile survival rate	Single of multi-state capture–recapture and/or recovery data of birds marked at birth	(juvenile OR immature OR pre-breed*) AND (surviv* OR mortality)	15
Adult survival rate	Single of multi-state capture–recapture and/or recovery data	adult AND (surviv* OR mortality)	74
Recruitment of new breeders	Reversed single capture–recapture data Multi-state capture–recapture data with breeding status as states	recruitment	6
Population growth rate	Capture–recapture data	('population growth rate' OR lambda)	0
Probability of breeding of adults in intermittent breeding species	Multi-state capture–recapture data with breeding status as states	(breed* OR reproduct*) AND (propensity OR frequenc* OR proportion*)	3
Probability of dispersal between sites	Multi-state capture–recapture data with sites as states	(dispersal OR emigration OR immigration)	0
Stopover duration, probability of arrival and of departure at a migration stopover site	Capture recapture data at stopover sites	(stopover OR migrat*)	4

[1]All key sentences started with: (seabird* OR landbird* OR duck* OR goose OR geese OR bird* OR waterbird* OR passerine* OR aves OR avian OR raptor* OR wader*) AND (climate OR weather OR temperature OR rainfall OR precipitation OR snowfall OR ice OR NAO OR Nino) AND (capture OR mark) AND.

[2]The number of records found with ISI Web of Science was usually larger than the figure given here. However, many of the records turned out to be irrelevant after reading the abstract

modelling of biological and observation processes that generate capture histories. Models that describe variation in focal parameters specify linear relationships with covariates, and usually involve a link function to get in-range estimates (most often the logit function). These linear models are fitted to data using maximum likelihood or Bayesian techniques. Powerful, more or less user-friendly software such as MARK (White and Burnham, 1999), M-SURGE (Choquet *et al.*, 2004), and WinBUGS (Lunn *et al.*, 2000) are widely used to build CMR models and fit them to CMR data. They allow a wide variety of CMR data and models to be dealt with.

4.3.2 Building regression models in a CMR framework

Instead of opting for a two-step approach where standard CMR models are first used for obtaining a series of estimates of a demographic trait and standard linear regression techniques are then used to relate these estimates to climatic factors, it is advisable to build simple or multiple regression models directly within the CMR statistical framework (Grosbois *et al.*, 2008), where the sampling uncertainty associated with each estimate of the focal parameter is formally accounted for. The CMR regression framework allows the (1) identification within a set of candidate climatic factors of those that are likely to influence noticeably the focal demographic trait, (2) assessment of the statistical support for the existence of a genuine relationship between the focal trait and a climatic factor (i.e. a relationship that does not result from a coincidental similarity between their patterns of variation), (3) estimation of the magnitude of the impact of a climatic factor on the focal trait, (4) description of the sign and shape of the relationship between the focal trait and a climatic factor, and (5) assessment of whether the impact of a climatic factor and the focal trait and/or the shape of the relationship between them changes depending on individual characteristics such as age or sex or environmental conditions such as food abundance. A number of pitfalls have to be avoided when regression models relating a demographic trait to climatic factors are built. They are listed in Table 4.2 and described thoroughly by Grosbois *et al.* (2008).

4.3.3 Statistical relevance

In CMR regression models, statistics derived from the likelihood function are used to assess the statistical relevance of the effect of a climatic factor. Among these statistics, differences in values of the Akaike Information Criterion (AIC) and AIC weights are derived from information theory and are very powerful tools that allow multi-model comparisons and inferences (Burnham and Anderson, 2002). However, they can only be used when prior knowledge of the study system is sufficiently good so that most of the variation in the focal demographic or life-history parameter can be explained with a small set of candidate covariates and models. In the situation where a noticeable fraction of variation in the focal parameter remains unexplained because the mechanisms underlying it are too poorly understood, an analysis of deviance (ANODEV) approach or random-effect models should be preferred to assess the statistical relevance of the effect of climatic factors (Grosbois *et al.*, 2008). This is a frequent situation because temporal and/or spatial variation in demographic or life-history parameters addressed in CMR studies of bird populations often results from the interplay of a multitude of intrinsic, environmental, trophic, and anthropogenic factors, some of which are unavailable or even unsuspected by the investigator. Failing to incorporate unexplained residual variance may induce an overestimation of the precision with which the parameters describing the relationship between the focal demographic trait and a climatic factor are estimated (Barry *et al.*, 2003) and thus an increased risk of detecting effects of climatic factors that are spurious (i.e. risk of type I error).

Another concern about the assessment of the statistical relevance of the impact of climatic factors on a focal demographic trait arises when candidate climatic factors are plentiful (Grosbois *et al.*, 2008). The resulting multiple-hypothesis testing issue is usually either ignored, which results in increased risk of type I errors, or accounted for with procedures, such as Bonferroni corrections, that induce an important loss of statistical power. Although this

Table 4.2 Pitfalls encountered while conducting CMR studies.

Pitfall	**Consequence**	**Recommendation**
Poor fit of the model due to unaccounted heterogeneity in demographic or detection parameters	Increased risk of type I and/or type II errors (spurious detection of an effect of a climatic factor or failure to detect a genuine effect of a climatic factor)	Perform goodness-of-fit tests to detect heterogeneity and, if needed, use models that account for it or deviance inflation corrections
Poor fit of the model due to excessive residual temporal variation in demographic traits	Increased risk of type I (spurious detection of an effect of a climatic factor)	Use deviance inflation corrections and statistical tests that account for unexplained variance
High numbers of climatic factors tested	Inflated risk of type I error resulting from multiple testing	Use small sets of candidate covariates Combine correlated covariates using multivariate statistics techniques Apply corrections to *P* values for multiple tests
Non-linear relationship between the focal parameter and a climatic factor	Failure to detect the influence of a climatic factor with linear regression models Production of spurious predictions for climatic conditions outside the observed range	Test for quadratic relationships in linear regression models Use recently developed semi-parametric methods for fitting non-linear relationships
The focal demographic trait and the climatic factors show linear time trends	Increased risks of detecting spurious relationships because the effect of the climatic factor is confounded with the effect of any other factor showing a linear trend	Address the relationship between the de-trended time series
Climatic factors reflecting only imperfectly the real causal factor because of measurement errors or because it is a proxy such as the North Atlantic Oscillation (NAO)	Underestimation of the impact of climatic factors	Include local climatic factors in the set of candidate covariates

has to our knowledge never been done so far in a CMR framework, the application of recently developed procedures for discovering genuine relationships in multiple-hypothesis testing situations (e.g. Storey, 2007) would allow the risk of type I error to be maintained at low levels with limited statistical power loss.

4.3.4 Biological relevance

The effects of climatic factors on demographic traits should be characterized not only by measures of their statistical relevance (in the form of AIC or *P* values), but also by their estimated effect sizes. Effect sizes reflect the magnitude of the impact of climatic factors on the focal parameter. Effect sizes are needed for comparative studies and meta-analyses (Nakagawa and Cuthill, 2007). Furthermore, in exploratory studies that aim primarily at short-listing potentially influential factors, measures of effect sizes should be preferred over measures of statistical relevance for factor selection (Grosbois *et al.*, 2008). Indeed, in such studies, multiple test issues can reduce statistical power to such an extent that selection approaches based on statistical relevance become ineffective. Thus, whatever the objectives of a study where the influence of climatic factors on demographic traits is assessed, an important and often neglected point is to provide effect size measures. Ideally, effect size statistics that reflect both the change in the focal parameter expected for a given variation of a climatic factor (e.g. slopes or standardized slopes and the precision with which they are estimated) and the fraction of the variation in the focal parameter explained by the influence of a climatic factor (e.g. coefficient of determination) should be provided along with statistics, such as *P* values or AIC weights, that measure statistical relevance (Nakagawa and Cuthill, 2007). In the perspective that the results of small-scale studies should be exploitable for meta-analyses and other forms of syntheses, estimations of the mean and variance, over the study period, of the focal demographic parameter and of the climatic factors identified as influencing it should also be reported (Grosbois *et al.*, 2008).

4.3.5 Recent and future methodological developments

Although the standard CMR statistical framework already offers a large set of tools and possibilities to characterize influences of climatic factors on demographic traits, recently developed methods can greatly improve our understanding of climatic impacts on the population dynamics of birds.

In some studies of bird populations, distinct sources of information on variation of a demographic trait can be obtained. Integrated modelling techniques can be used to describe variation in a trait and identify factors underlying it from the simultaneous analysis of these different sources. For instance, CMR and ring recovery or population count data can be analysed simultaneously to obtain information about survival (Besbeas *et al.*, 2002; Schaub *et al.*, 2005). Information obtained with such integrated analyses is more precise than that obtained through the analysis of a single source, therefore improving the statistical power to detect the effect of climatic factors on a focal parameter.

Standard CMR methods have been developed in a frequentist statistical framework. Bayesian methods have recently been used to analyse CMR data to assess the impact of climate on vital rates (Barry *et al.*, 2003; Gimenez *et al.*, 2006; Grosbois *et al.*, 2008, 2009). They are very efficient for fitting complex models to quantify variation in a focal demographic trait that arises from the influence of unsuspected or unmeasured factors. Furthermore, although it has never been attempted, information available before the analysis about the effects of climatic factors considered as potentially influential on demographic parameters could be integrated in the form of prior distributions derived from experts' opinions or species with similar characteristics.

A method for simultaneously addressing several time series of a demographic trait with CMR data has recently been described by Grosbois *et al.* (2009). It allows the decomposition of total temporal variation in several time series of demographic traits over a given period into one component shared across series and one component independent among series. This method can be used to quantify synchrony among different demographic traits in a population or of one demographic trait in distinct populations of the same or different species. It also offers the possibility to assess the role of climatic and other types of factors in generating such synchrony. It has thus a great potential for addressing mechanisms (including climatic forcing) whereby variation in demographic traits generate population dynamics patterns in a given population or in several populations of a single or different species.

Regression models used in standard CMR studies offer limited options regarding the shape of the relationship between a demographic trait and a climatic factor. Recent adaptations of semi-parametric techniques to the CMR framework offer the possibility of describing relationships with non-linear shapes (Gimenez *et al.*, 2006), in the same spirit as generalized additive models that are used in other fields (e.g. species distribution or population trend modelling (e.g. Fewster *et al.*, 2000)).

As is generally the case for correlational studies, standard CMR methods allow the detection and quantification of the influence of a climatic factor, but not the depiction of the underlying mechanisms (i.e. whether the influence is direct, results from a more or less complex chain of causation, or is spurious because of a confounding effect). Although rigorous assessment of the mechanisms underlying the relationship between a demographic trait and climatic factors can only be obtained with experimental approaches, path analyses can produce some useful leads when information about the factors involved in one or several hypothetical causation chains is available. Path analysis allows the evaluation of the relative weight of evidence for each alternative hypothetical causation chain and estimation of the parameters of the best supported ones. With such analyses, one can, for instance, assess whether a climatic factor influences a demographic trait directly or through its impact on food abundance (Gimenez and Grosbois, unpublished results).

Statistical methods for combining the results from several studies (i.e. meta-analysis techniques) and for drawing predictions (i.e. cross-validation and external validity assessment techniques) from statistical analysis of empirical data have still not been adapted to the CMR framework. This might be the reason why conclusions that can be generalized across populations, species, geographical areas, and time periods in the study of climatic impacts on demography in bird populations are still scarce.

4.4 Biological questions, climate change, and demographic traits

4.4.1 Questions addressed so far in the literature

Most CMR studies of the impact of climatic factors on demographic traits published so far have aimed to identify influential climatic factors and estimate the magnitude of their impact on a single trait, which is usually survival probability (Table 4.1), of a unique focal population. The potential of CMR methods is still poorly exploited. Too few studies have so far addressed the influence of climatic factors on demographic traits other than survival (but see Table 4.1 and, for example, Lee *et al.*, 2007; Nevoux *et al.*, 2008; Votier *et al.*, 2008). Studies that consider the influence of climatic factors on variation of several demographic traits and therefore can deduce the consequences on dynamics of the population are also scarce (but see, for example, Frederiksen *et al.*, 2008; Altwegg and Anderson, 2009; Jenouvrier *et al.*, 2009a). That is also the case for studies where several populations of one or several species are considered and where inference on the impact of climatic factors on range or community dynamics can be obtained (but see Schaub *et al.*, 2005; Grosbois *et al.*, 2009; Jenouvrier *et al.*, 2009b).

4.4.2 Poorly addressed questions

Many precise questions about the impact of climatic factors on demographic traits could be addressed with CMR analyses. CMR analyses could be used to investigate interactions between climatic factors and other factors such as density or food abundance. Such investigations could reveal potential synergetic effects of climate and other factors. For instance, the hypotheses that high densities or low food abundance depress demographic traits only when climatic conditions are harsh and, vice versa, that harsh climatic conditions depress demographic traits only when they occur in conjunction with other detrimental conditions, could be addressed (Barbraud and Weimerskirch, 2003).

CMR protocols are sometimes undertaken on stopover sites along the migratory route of bird populations. Such protocols produce CMR data from which information on the phenology of migration can be obtained. Specific CMR models allow description of between and within year variation in probabilities of arrival and departure and in stopover duration. In particular, this variation can be related to between and within year variation in climatic conditions. Such studies could reveal influences of climatic variation and consequences of climate change on migratory behaviour (Péron *et al.*, 2007; Calvert *et al.*, 2009).

In some monitoring programmes of bird populations, in particular nest box populations, data on the breeding phenology of marked individuals are gathered. Individual histories with states reflecting the timing of breeding can then be built. The probabilities that the monitored individuals breed in different periods and the survival of individuals breeding in different periods can then be estimated from the analysis of such multi-state CMR data. By addressing the relationship between these parameters and climatic factors, the influence of climatic conditions on breeding phenology and the specific selection pressures generated by climate change on breeding phenology can be revealed. When monitored birds are marked at very young ages their date of hatching can be recorded. In such situations, the influence of climatic factors on fitness components of birds hatched at different times can be described and compared with CMR analyses. The selective pressures generated by climate change on breeding phenology through the fitness of offspring could thus also be evaluated.

Because demographic traits are fitness components, the investigation with CMR studies of the effect on demographic traits of interactions between individual behavioural and morphological or physiological characteristics on the one hand and climatic factors on the other could highlight selective pressures generated by climate change. Indeed, addressing such interactions would allow identification of phenotypic traits that vary among individuals and are associated with variation in the shape and the strength of the relationship between fitness components and climatic conditions. Such traits are likely to be subject to selective pressures related to climate change.

In studies of populations occupying areas where habitat characteristics show spatial variation, capture histories with the type of habitat (for instance breeding habitat) occupied by individuals considered as a state could be obtained. Effects on demographic traits of interactions between habitat characteristics and climatic factors could then be described with CMR models. As explained above for other phenotypic traits, such approaches could reveal selective pressures associated with climate change and affecting habitat selection.

Because demographic traits are life-history traits, the investigation with CMR methods of the impact of climatic factors on demographic traits could reveal selective pressures generated by climate change on life-history strategies (Doherty *et al.*, 2004). For instance, an increase in the frequency of extreme climatic events is expected in the next decades (Chapter 2). Such an increase in the frequency and the magnitude of climate-related environmental perturbations could generate selective pressures for shorter life histories or for strategies, such as facultative breeding or delayed recruitment, allowing for flexible life histories. Addressing such hypotheses would imply investigating the relationships between climatic factors and several demographic traits such as juvenile and adult survival, age of first breeding, probability of breeding and breeding success simultaneously. Although the statistical methods have now been developed and some bird population monitoring programmes have produced the type of CMR data required to do so (e.g. Lee *et al.*, 2007; Nevoux *et al.*, 2008; Votier *et al.*, 2008), climate change-related selective pressures on life-history strategies have so far never been addressed with CMR methods. Predicting micro-evolutionary processes on life-history traits triggered by climate change would also require estimation of heritability of life-history traits such as survival, age of recruitment, and breeding frequency and success. CMR methods are currently being developed for estimating the heritability of such traits from CMR data when information on relatedness of the monitored individuals is available.

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