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$$



Rachel S. McCrea and Byron J. T. Morgan

## Analysis of Capture-Recapture Data

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}

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\section*{Preface}

In this book we aim to cover the many modern developments in the area of capture-recapture and related models, and to set them in the historical context of relevant research over the past 100 years. The main area of application is ecology.

Much of the material of the book has been taught to students on the MSc course in Statistics at the University of Kent over several years. Parts of the book have also been covered in a number of workshops at both the University of Kent and St Andrews University, over many years, as well as in workshops for the National Centre for Statistical Ecology, at Cambridge, the British and Irish Region of the International Biometric Society at Rothamsted Experimental Station, the International Biometric Conference in Florence, Italy, at Point Reyes and Patuxent, USA, Radolfzel and Rostock, Germany and Dunedin, New Zealand.

The book may be used as an advanced undergraduate and higher-level textbook, for students with a knowledge of statistics and probability such as that typically provided in a second-year mathematics/statistics undergraduate course in the UK. Chapter 2 of the book provides a brief revision of the basic ideas of classical and Bayesian inference that are used and referenced in the later chapters. An appendix lists the distributions used in the book.

The book may also be used as a source of reference for quantitative ecologists as well as statisticians. Many of the methods described in the book have been devised in collaboration between statisticians and ecologists, notably through the series of successful Euring technical meetings over the past 20 years. Capture-recapture and related models are designed for particular types of ecological, social, epidemiological and medical data, and applications to real and simulated data sets provide fine examples of biometry and applied statistics at work.

One of the reasons that the capture-recapture area has seen a recent explosion of new applications and methods is the availability of free user-friendly computer software. Another reason is the appearance of important long-term data sets, as well as a wide range of new data resulting from technological advances in the marking, identification and tracking of wild animals. Several capture-recapture data sets now have classic status, and we include discussion and analyses of several of these. However, in order to provide continuity, where possible we illustrate methods on a single data set on Great cormorants, studied in Denmark.

In order to prevent the book becoming very large we have had to be selective. Supplementary material is provided in Exercises and on the book web site, www.capturerecapture.co.uk, which also contains data, computer programs, pictures, and an indication of how the book has been used as the basis of a lecture course.

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}

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\section*{Notation}

Where possible within the book we adopt the following notation.
\(S\) : survival probability
\(\phi\) : apparent survival probability
\(\lambda\) : recovery probability
\(p\) : capture probability
\(\psi\) : transition probability (in the context of multistate capture-recapture models, see Chapter 5)
\(\varphi\) : survival-transition probability
\(\psi\) : occupancy probability (in the context of occupancy models, see Chapter 6)
\(T\) : total number of capture occasions
\(N\) : population size
\(K\) : number of sites/states
\(G\) : number of groups
\(\epsilon\) : emigration probability
\(\rho\) : productivity
\(\boldsymbol{\theta}\) : model parameters
\(x\) : data
\(M(\boldsymbol{\theta})\) : model
\(L(\boldsymbol{\theta} ; \boldsymbol{x})\) : likelihood
\(\ell(\boldsymbol{\theta} ; \boldsymbol{x})=\log \{L(\boldsymbol{\theta} ; \boldsymbol{x})\}\)
\(\pi(\boldsymbol{\theta})\) : prior distribution
\(\pi(\boldsymbol{\theta} \mid \boldsymbol{x})\) : posterior distribution
\(\mathbf{U}=\partial \ell(\boldsymbol{\theta} ; \boldsymbol{x}) / \partial \boldsymbol{\theta}\) : scores vector
\(\boldsymbol{A}\) : Hessian matrix
\(\boldsymbol{J}=-\mathbb{E}[\boldsymbol{A}(\boldsymbol{\theta})]\) : Fisher information matrix
\(-\boldsymbol{A}(\boldsymbol{\theta})\) : observed Fisher information matrix
\(N_{d}\left(\boldsymbol{\theta}, \boldsymbol{J}^{-1}(\boldsymbol{\theta})\right)\) : multivariate normal distribution
\(\chi_{\nu}^{2}\) : chi-square distribution
\(-2 \log \lambda\) : likelihood-ratio test statistic
\(M\) : number of models in a model set
\(q(a, b)\) proposal function in Metropolis-Hastings
\(A I C\) : Akaike information criterion
\(\mathrm{AIC}_{c}: A I C\) adapted for small sample sizes
QAIC: AIC adapted for over dispersion
\(B I C\) : Bayesian information criterion
\(O_{i}\) : observed value
\(E_{i}\) : expected value
\(c^{2}\) : over dispersion coefficient
\(D(\mathbf{x}, \boldsymbol{\theta})\) : discrepancy statistic
\(\Lambda\) : population projection matrix
\(\boldsymbol{I}(\cdot)\) : indicator function
Generally, we will denote time-dependence of parameters by a subscript, state/site-dependence using a superscript and age-dependence will be denoted in parentheses. Note that when a parameter depends on a covariate, we will include this within the parentheses, and this will be made clear in the context of the example. Individual effects will also be denoted by a subscript and any further deviations from this notation will be described when introduced.
"Right from the beginning, I always strived to capture everything I saw as completely as possible."

Norman Rockwell

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\section*{Chapter 1}

\section*{Introduction}

\subsection*{1.1 History and motivation}

The Independent newspaper published in England on the \(6^{\text {th }}\) of May, 2010, contained an article with the title: "End of the Alaotra grebe is further evidence of sixth great extinction: species are vanishing faster than at any point in the last 65 million years." It is generally supposed that this loss of species is due to anthropogenic change, and there is great current concern regarding the consequent loss of biodiversity, which motivates the work of this book; see Kolbert (2014).

The aims of human demography and of population ecology are similar, with key demographic parameters relating to birth, death and movement in each case. The Births and Deaths Registration Act of 1836 resulted in all registrations of birth, death and marriage being kept centrally in England and Wales from the \(1^{\text {st }}\) of July 1837. As a result of such regulation, it is usually far easier to determine human mortality than that of wild animals, and the different data that arise for humans and animals require different methods of analysis.

An initial step in studying wild animals is often to ensure that they can be identified uniquely. When such animals are reencountered then this gives rise to different forms of capture-recapture data. For instance, an issue of the journal Ringing \(\mathcal{E}\) Migration, published in 2009, is devoted to celebrating 100 years of bird ringing in Britain and Ireland. The first paper in the issue, by Greenwood (2009), provides interesting background to the ringing scheme which is now administered by the British Trust for Ornithology (BTO). The bird rings have unique numbers, indicating when the rings were attached, and also contain an address. If a dead bird is found to have a ring, and the ring is returned to the address, then information is obtained on how long the bird lived; an illustration is on the book web site, www.capturerecapture.co.uk. This approach is generally regarded as having been initiated in Denmark in 1899, by Hans Chr. Mortensen, and is now used widely throughout the world.

Over the past 100 years a body of theory and methods has been developed for the analysis of capture-recapture data, and the area remains one of active research. Books on the subject include Williams et al. (2002), Amstrup et al. (2005), Royle and Dorazio (2008), Link and Barker (2009) and King et al.
(2010). In addition there are specialised computer packages such as Program Mark (White and Burnham 1999) and E-SURGE (Choquet et al. 2009) for model-fitting by maximum likelihood, and Gimenez et al. (2008) and Kéry and Schaub (2012) describe how WinBUGS may be used for Bayesian inference. Capture-recapture data also arise in medical, epidemiological and social areas, and we shall describe some of these applications-see Chao et al. (2001). The paper by Borchers et al. (2014) provides a modelling framework which links capture-recapture and distance sampling surveys (Buckland et al. 2001).

\subsection*{1.2 Marking}

Some animals can be identified by their physical characteristics, and this is true for example of the spot patterns of cheetahs, the belly patterns of great crested newts, (Figure 1.1(a)) and permanent marks produced by aggressive interactions between bottlenose dolphins. However, it is often the case that identifying marks have to be attached to wild animals. Marks may take the form of neck bands, leg rings, wing clips, ear tags, etc. Rings on the legs of cormorants are illustrated in Figure 1.1(c), and tags on the ears of ibex are shown in Figure 1.1(d). Butterflies may be marked using coloured marking pens, under standardised protocols. Also, more than one device may be used at the same time for any one animal, for instance colour rings for resighting live birds and metal rings with an address for the recovery of dead birds; this is the case for the cormorant study described in the next section. Double marking is sometimes also used if there is a danger of marks being lost or becoming illegible due to wear. It is usually assumed that the process of capturing animals and marking them does not affect their subsequent survival. Modern marking procedures also include radio-tagging such as the collar shown on a straw-coloured fruit bat in Figure 1.1(b), the use of passive integrated transponder (PIT) tags, like those used to identify animal pets, temperature depth recorder (TDR) tags, which can measure depth for marine animals, and miniature geolocators. In some cases genetic information can be gleaned from hair or fur deposited in the field on features such as barbed wire fences, and from faeces. In data analysis, account sometimes needs to be taken of the possibility of an animal losing a mark, of marks being damaged through wear and tear, and of misreporting of marks. It is often the case that marks from dead animals are reported soon after death, as otherwise the corpse may have decayed or been eaten. However, if marks are attached to shellfish, for example, then they can be discovered and reported a long time after death. We use the terms reencounter and recapture exchangeably, to cover recovery, recapture and resighting. There are often major differences in scale between the areas over which recoveries are reported and those for recaptures and resightings.


Figure 1.1 Examples of natural and applied markings: 1.1(a) shows the belly pattern of a Great crested newt, Triturus cristatus; 1.1(b) shows a Straw-coloured fruit bat, Eidolon helvum with a radio-transmitter collar; 1.1(c) shows a Great cormorant, Phalacrocorax carbo sinensis, with one ring on each of its legs and 1.1(d) illustrates an Alpine ibex, Capra ibex, with an ear tag.

\subsection*{1.3 Introduction to the Cormorant data set}

Throughout the book we shall consider applications to a range of different animals, however for continuity we shall demonstrate several methods using data from a population of Great cormorants, Phalacrocorax carbo sinensis. We have kindly been given permission to use these data collected by the National Environmental Research Institute at Aarhus University, Denmark. The data are part of a much larger ringing programme started in Denmark in 1977, which continues to the present day. Analyses have been provided by, for example, Frederiksen et al. (2001). There are many colonies of Great cormorants around Denmark and the data that we use in this book correspond to a period of population expansion (1981-1993) in six colonies located 32234 km apart. The location of the colonies is shown in Figure 1.2. The oldest of the six colonies, Vorsö (VO), was established (est.) in 1944 and along with Ormö (OR, est. 1972) and Brændegård Sö (BR, est. 1973) comprised the only colonies present in Denmark at the start of the ringing study. Colonies Toft Sö (TO), Dyreford (DY) and Mågeöerne (MA) were established during the study in 1982, 1984 and 1985 respectively. Nest locations vary between colonies: the
nests at colony MA are only located on the ground, whilst nests at BR are located both on the ground and in trees. Nests in the remaining four colonies are only found in trees.


Figure 1.2 Location of cormorant colonies in Denmark. Figure provided by T. Bregnballe.

For illustration, throughout the book we shall extract components of this substantial data set for particular examples. The multisite/state nature of the recapture data, and the multiple types of data collected, including live recaptures, dead recoveries and population counts makes this an ideal data set to demonstrate several of the modelling approaches of the book. Additional features, such as known age at capture, allow us to explore a wide range of complex model structures.

\subsection*{1.3.1 Capture-recapture-recovery data}

Chicks were ringed using a standard metal ring on one leg and a coloured plastic band with a unique combination of three alphanumeric characters on the other when they were between 25 and 38 days old. In this study recaptures are in fact resightings. Regular trips (often daily) are made to the colonies between February and October and attempts are made to resight and identify individuals; illustrative histories are shown in Table 1.1. We observe that within a single breeding season individuals can be resighted multiple times, and also that in some cases birds are not seen in a colony for several years after ringing. Generally, resighting is done from a distance; for example, at

Table 1.1: Extract of 1994 resighting data from colony VO.
\begin{tabular}{|c|c|c|}
\hline Individual Code & Date of Ringing & Dates of Resighting \\
\hline BL 089 & \(31 / 05 / 1986\) & \(13 / 06 / 1994\), \\
& & \(19 / 06 / 1994\), \\
GU 191 & \multirow{3}{*}{\(10 / 05 / 1980\)} & \(29 / 06 / 1994\) \\
& & \(10 / 03 / 1994\), \\
& & \(17 / 03 / 1994\), \\
HV 04L & \multirow{3}{*}{\(25 / 05 / 1992\)} & \(11 / 05 / 1994\), \\
& & \(10 / 05 / 1994\), \\
& & \(12 / 05 / 1994\), \\
& & \(19 / 05 / 1994\), \\
& & \(20 / 05 / 1994\), \\
& & \(23 / 05 / 1994\) \\
\hline
\end{tabular}
the largest colony, VO, this is conducted from an observation tower within the breeding cormorant population. Resightings are recorded only for individuals identified as breeders, and birds were considered breeders at VO if they had been observed copulating, incubating chicks or rearing chicks. The timing of onset of breeding varied among the years but 71-97\% of clutches that were laid at VO were initiated between 1 March and 19 April. This observation allowed criteria to be developed for identifying breeding cormorants at the other sites, where resighting intensity was not as high. Individuals at the remaining five colonies were judged to be likely breeders if they had been observed in the colony:
1. on a nest between 1 March and 19 April, or
2. between 1 March and 19 April and identified as a likely breeder in an earlier year, or
3. between 20 April and 30 June.

The birds were recovered dead within a large geographical area ranging from the United Kingdom to southern Algeria and from western Spain to eastern Romania, and separate data on recoveries of dead birds were provided by the Ringing Department at the Zoological Museum, Copenhagen. The approximate age of fledging is 30 days, and recoveries of birds found dead in their natal colony within this period were excluded; in addition, recovery information when only a ring was found within the natal colony less than 30 days after ringing was excluded.

Depending on the type of model we wish to fit, we may analyse information on several captures within a single year, or we may record data on an annual basis, and thereby develop an annual encounter history for an individual. We note that since individuals are ringed as non-breeders and not resighted until
they start to breed, we may decide to model the data using multiple states, where the state denotes the breeding status of an individual. Such modelling can allow us to estimate biological processes of interest, such as recruitment probabilities which describe when animals become breeders.

\subsection*{1.3.2 Nest counts and productivity}

Colony sizes were also estimated during each year of the study, by counting the number of nests in early May, which is the time of year when the nest numbers peaked; the data are given in Figure 1.3. The marked individuals make up a small proportion of the total population as the ringing of nestlings takes place in a small zone of each colony. Productivity is normally assessed through direct measurements, for instance through egg counting.


Figure 1.3 Cormorant colony size counts per colony, in terms of nests, between 1981 and 1992

\subsection*{1.4 Modelling population dynamics}

Estimates of annual survival probability and of productivity are important components of population dynamics models, and as we shall see below, they contribute to entries in what are called Leslie matrices. For example, suppose that we have a bird species in which we can detect 5 age-classes, and, ignoring the numbers of individuals in their first year of life, that \(N_{t}(1), N_{t}(2), N_{t}(3)\), and \(N_{t}(a)\) denote, respectively, the numbers of females aged one year, two years, three years, and greater than three years at time \(t\). We let \(S_{t}(j)\) denote the annual survival probability at time \(t\) of a bird in age class \(j\), where \(j\) takes
the values \(1,2,3,4\) and \(a\) (denoting \(4^{\text {th }}\) and older years of life) and denote productivity by the constant \(\rho\). If we assume that the process of birth in transition \((t-1, t)\) relates to year \(t-1\) and operates before the process of survival, and that only birds aged 2 and older reproduce, then we can write down the following transition equation, based on a Leslie matrix, relating the numbers of birds at time \(t\) in each of four age classes to those at the previous time.
\[
\left(\begin{array}{l}
N_{t}(1)  \tag{1.1}\\
N_{t}(2) \\
N_{t}(3) \\
N_{t}(a)
\end{array}\right)=\left(\begin{array}{cccc}
0 & \rho S_{t-1}(1) & \rho S_{t-1}(1) & \rho S_{t-1}(1) \\
S_{t-1}(2) & 0 & 0 & 0 \\
0 & S_{t-1}(3) & 0 & 0 \\
0 & 0 & S_{t-1}(4) & S_{t-1}(a)
\end{array}\right)\left(\begin{array}{c}
N_{t-1}(1) \\
N_{t-1}(2) \\
N_{t-1}(3) \\
N_{t-1}(a)
\end{array}\right)
\]

Applying this equation several times allows predictions to be made about the future behaviour of the population.

The Perron-Frobenius theorem states that for appropriate constant transition matrices \(\boldsymbol{\Lambda}\), if for some \(k\), all elements of \(\boldsymbol{\Lambda}^{k}\) are strictly positive, then there exists a real positive eigenvalue \(\lambda\) that is greater in absolute value (or in modulus, if some of the other eigenvalues are complex) than all other eigenvalues. The dominant eigenvalue \(\lambda\) represents the asymptotic growth rate of the population, and the normalised right eigenvector \(\boldsymbol{v}\) associated with \(\lambda\) represents the asymptotic proportion of every age class in the total population, called the stable age distribution; see Caswell (2001, p.83).

A simplifying feature of the model of Equation (1.1) is that it is deterministic, without any random components, and we shall consider stochastic transition equations, which allow for random variation, in Chapter 11.

\subsection*{1.5 Summary}

There is much current concern at the loss of biodiversity. We often study the behaviour of wild animals after giving them marks which identify them uniquely. It is usually assumed that marking does not affect their survival, although there is some evidence to the contrary in certain special cases. Marked animals may be found dead, or seen again alive, providing information on demographic features such as mortality and movement. Estimates of mortality and of productivity are used in models of population dynamics, which can provide understanding of how populations change, and provide predictions of future behaviour. The analyses in the book will frequently be illustrated by means of data on a particular population of cormorants. In certain cases, similar models are used in application areas such as epidemiology.

\subsection*{1.6 Further reading}

\subsection*{1.6.1 History and aspects of bird ringing}

The paper by Pradel (2009) provides graphs showing the increase in the use of methods of capture-recapture over time. A poster giving a time line for the main developments in the area of capture-recapture is on www. capturerecapture.co.uk.

Greenwood (pers com) observes that British and Irish ornithologists were ringing birds from 1890, and that in fact marking birds dates from medieval times. A wide-ranging review is provided by Lebreton (2001). The book by Balmer et al. (2008) provides an excellent introduction to bird ringing, and concludes with an interesting list of record breakers (for example, the species with the highest recovery probability, the oldest ringed bird (over 50 years), etc.). It is observed that there is a decline in the reporting of rings from dead birds in recent time; see Balmer et al. (2008, p.24). Some rings now also contain a web address; see Balmer et al. (2008, p.57). The paper by Saraux et al. (2010) found that flipper bands attached to penguins affected both the survival and reproduction of the birds. Although this is generally regarded as an extreme example, it should always be a consideration that marked animals might survive and reproduce differently from unmarked ones. The paper by Aebischer (1983) provides a way to determine ring numbers after their superficial features have been eroded. The effect of misreading marks is the topic of Schwarz and Stobo (1999); such errors can be a problem when using genetic information, see for example Link et al. (2010). Genetic information can reveal information other than just survival; see Okland et al. (2010). Goudie and Goudie (2007) give the history of marking fish.

\subsection*{1.6.2 Reviews, books and websites}

The book by Seber (1982) is a classical text in statistical ecology, and contains a wealth of applications and analyses of challenging and interesting data sets, as well as much historical material. There is for example discussion of ways of dealing with mark loss, on p.488. An early review of capture-recapture methods is provided by Pollock (1991). More recent work can be appreciated from Pollock (2000) and Schwarz and Seber (1999), Morgan and Thomson (2002), Senar et al. (2004) and Schaub and Kendall (2012). The volume by Williams et al. (2002) is encyclopaedic, and essential reading for statistical ecologists. The estimation of wild animal abundance is the subject of the book by Borchers et al. (2002). The book by Caswell (2001) is the classical reference for population dynamics modelling, and provides information regarding the formation of Leslie matrices. A modern approach to sensitivity analysis in population modelling is provided by Miller et al. (2011a). A wider ecological perspective is provided by references such as Morgan et al. (1997), Furness and Greenwood (1993), Clutton-Brock (1988), Clutton-Brock and Albon (1989) and Clutton-Brock et al. (1982).```

