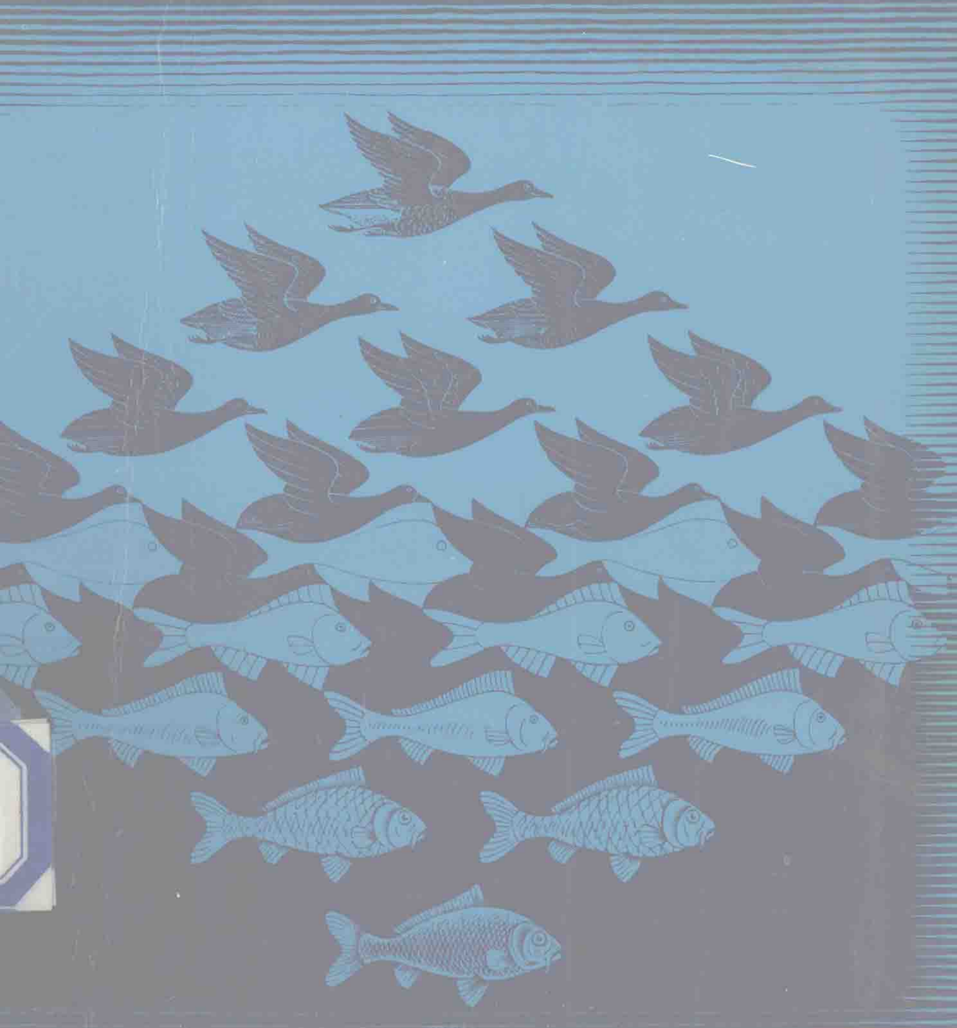
Investigating Animal Abundance

capture-recapture for biologists

Michael Begon



Investigating Animal Abundance:

capture-recapture for biologists

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Preface

Ecology is a subject which, by its very nature, must face up to the complexities of the living world. It is, therefore, fraught with problems concerning the quantification of its subject matter. One of these problems is the estimation, or more generally the investigation, of animal abundance.

Finding the solution to this problem, as is so often the case, has largely been the work of mathematicians or statisticians. But the potential users of the solution are biologists. My aims, therefore, are to communicate to biologists, at both student and research level, the essential simplicity of the mathematical techniques; and also to reassure them that it is their experience, *as biologists*, which can turn a sterile mathematical technique into a potent biological weapon. Both of these aims are, of course, pertinent to the conjugation of mathematics and biology generally.

It is a pleasure to thank Dr. J. A. Bishop and Dr. K. O'Hara for their help with the manuscript; and my wife, Sally, for her help in clarifying passages which, despite my good intentions, I had left obscure. I should like, also, to acknowledge my debt to the paper by R. M. Cormack (1973), which first awakened me to the proposition that mathematical techniques can be reduced to common sense. I have tried, in what follows, to convey this same message.

Liverpool, 1978 M.B.

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1 Context

Biologists all too often act as if mathematical techniques possess magical powers, transforming incomprehensible raw data into clear and precise scientific conclusions. Nothing could be further from the truth. Far from being magical, such techniques are, in fact, essentially sterile. They become potent only in the light of the biological problem to which they are applied, and the biological context in which they are interpreted. A consideration of mathematical techniques must, therefore, be preceded by a consideration of problems and contexts.

The roe-deer enjoys extreme popularity throughout most of Europe as an attractive member of the mixed-woodland community. Ironically, it is also a much-coveted hunting trophy. In 1962, for instance, Andersen reported that in Denmark alone around 25 000 roe-deer were being killed each year by more than 100 000 licensed sportsmen. Thus, the management of deer populations, and the policy regarding their shooting, must obviously be founded on a firm basis of biological fact. And especially important is the need for reliable information on the actual numbers of deer in particular woodlands (population size), or – what is essentially the same thing – knowledge of their absolute density (numbers per unit area).

Andersen described an attempt to measure the absolute density of roe-deer on the Danish Game Research Farm. The attempt was made by the forestry and game personnel, who had known the farm's woodlands for years, and spent part of every day there. No group could have been more experienced. They tried simply to count all the deer, and considered there to be about 70 present. But in the subsequent three months they managed to kill 213 deer in the same isolated woodland.

The experienced gamekeepers were incredulous at this discrepancy – but they should not have been. A simple count or census is justifiable – though not without difficulties – for an entirely visible and sedentary population. But roe-deer are continually, and unpredictably, on the move; and their ability to escape detection is obviously good enough to deceive even the most experienced census-taker. If a firm basis of biological fact is required for this mobile and cryptic mammal, then some more objective method of measuring absolute density is necessary.

Such information is urgently required – but only as a consequence of man's desire to exploit a part of his environment for his own pleasure. Frequently, however, the motivation behind population studies is much more humanitarian. Although nowadays we in the West are largely free from dangerous infectious disease, this is by no means world-wide. Dengue haemorrhagic fever, for instance, is a virus infection transmitted by the mosquito *Aedes aegypti*, which primarily affects young children. It was only recognized as a specific condition in 1953, but by the mid-1960's it had become a health problem in much of southern Asia.

In 1966, the World Health Organization established their Aedes Research Unit in Bangkok, the capital of Thailand. It had been noted there that the incidence of the disease showed a marked increase in the wet season, and that the outbreaks tended to be larger every second year. The presumption made by many researchers was that these cycles in the incidence of the disease were correlated with cycles in the density of the mosquitoes, or, perhaps, in their efficiency as vectors. The Aedes Research Unit set out to investigate whether there was any truth in these presumptions (Sheppard *et al.*, 1969). The aim was to control the disease. This could only be achieved by basing any plans on a proper understanding of mosquito ecology.

Among the relevant ecological parameters were the actual density of mosquito populations at different times of the year; the tendency of mosquitoes to move from one area (population) to another (which would affect the efficiency with which they located humans); and the life-expectancy of mosquitoes (which would also affect their efficiency as vectors). Life-expectancy can, of course, be quantified by measuring survival-rates: the higher a mosquito's chance of survival, the longer it can be expected to live.

It was essential that these parameters should be investigated under natural conditions: it was the dynamics of actual populations which were assumed to underlie the fluctuations in the disease's occurrence. The major problem facing the unit was, therefore, a practical one: to investigate the size, along with other parameters, of a population of actively mobile mosquitoes, in an urban environment large enough to support two million people – and to do this over an extended period of time, while the mosquitoes themselves passed through several generations: being born, maturing and dying.

Yet, if the ecology of the mosquitoes was to be properly understood, and an enlightened control plan instituted, this problem had to be solved. Progress towards the amelioration of dengue haemorrhagic fever was, therefore, crucially dependent on reliable information concerning the population parameters of the mosquitoes.

The mosquito and the roe-deer are both important to man. One we wish to control in order to alleviate suffering; the other we wish to exploit in order to increase pleasure. In both cases there is a requirement for information on the absolute density of non-cooperative populations, and on the processes leading to these densities: birth, death, emigration and immigration. Of course, such requirements are not confined to studies with an immediate application, as the following example shows.

Population genetics is essentially the study of the origin and dynamics of genetic variation within and between populations. In other words, the population geneticist seeks to account for the similarities and differences in gene frequencies between conspecific individuals, between conspecific populations, between closely-related species, and so on. In the past, there have been three classes of approach to this extremely daunting task: the theoretical, the laboratory and the field.

The theoretician identifies the processes which are potentially capable of affecting gene frequencies, and investigates their relative importance and combined action in a number of hypothetical circumstances. Many of these are themselves influenced by the ecological circumstances of the population in question. In spite of this, the theoretical population geneticist seeks to increase our understanding of the real world by considering idealized populations. This is the only way he can make any progress.

The population genetics fieldworker attempts to increase our understanding of the real world by studying the real world itself. Between him and the theoretician lies the laboratory worker. Laboratory work can uncover the potentialities of actual organisms. It can 'test' the models of the theoretician, and indicate to him what is biologically realistic; and it can provide the fieldworker with the results of controlled experiments to compare with any inference he may make. Ultimately, however, all population geneticists are interested in the real world. Yet, it is only by interpreting his results against a coherent theoretical background, that the fieldworker can hope to succeed in making the real world understandable. Fusing the different aspects of population genetics is obviously essential.

Towards this end the American geneticist Sewall Wright (1969) developed the concept of effective population size: essentially, the size of the ideal population with which an actual population can be equated genetically. In other words, by collecting the appropriate data from a natural population the effective population size can be estimated, and the results of the theoretician and laboratory worker applied to the field. As Wright himself has remarked, estimating effective population size is '. . . a practical necessity in dealing with natural populations'.

The quantification of absolute densities plays a crucial role in determining the effective size of a natural population. Yet the animals most often studied by population geneticists – butterflies, moths, fruit-flies, snails, and so on – are, once again, impossible to census by a direct count. It follows that the successful fusion of practical and theoretical aspects of population genetics is dependent on our ability to measure the absolute density of populations of animals, which are either mobile, cryptic or both.

It would be easy to follow example with example: the exploitation of freshwater fish for food; the destruction of verminous small mammals by poisoning; the protection of birds in disappearing parts of the environment; the removal of insect pests from crops; as well as the understanding of population dynamics for its own sake. All of these are areas where it is crucially important to measure the absolute density of populations of non-cooperative animals. Moreover, if we wish to exploit a fish population we will need to know the birth-rate; if we wish to destroy small mammals we will need to know the extent to which different populations intermix; and generally, if we wish to understand population dynamics we will need to study the forces underlying those dynamics: birth, death, immigration and emigration. Such an argument is easy to summarize: information on the absolute density of animal populations, and the forces determining density, is essential.

But the expressions–'information on' and 'measurement of' density – are unacceptably vague. The situation can be compared with a consideration of the length of the River Dee, or the volume of Lake Bala. Length, volume and number are all commonplace concepts, but there are cases (the River Dee, Lake Bala, and most animal populations) in which their measurement is by no means easy. Neither is it easy to say exactly where the River Dee begins or ends; or exactly what water level to assume in Lake Bala; or exactly where the limits of a population are. And finally, and by no means facetiously, for someone wishing to swim the Dee, it is only necessary to know if it is more or less than a mile or so long.

In other words, we must accept first of all that no population size can ever be specified exactly. But we must also accept that an exact specification is usually unnecessary. A geneticist measuring effective population size may only need to know whether his population is sufficiently small for genetic drift to be a potentially potent force. The Aedes Research Unit in Bangkok really only needed to know whether mosquito-density and disease-incidence were correlated. A Danish game-keeper may only need to know whether he should let 30 or 130 roe-deer be shot in a season. There are, of course, many situations where more precise information is required. But the basic point is the same: population sizes are measured in response to specific ecological questions, and the form of the question determines the precision and accuracy required of the answer.

In fact, one can go further. In an ideal world, precision and accuracy would always be maximized. But, in particular cases, time, money, personnel, and particularly technique may all be severely limited. In practice, therefore, precision and accuracy must be sacrificed in order to minimize the limitations of these other factors. The extent of the sacrifice is determined by the question in hand, and the circumstances of the study: context is all-important.

2 The Models

The first chapter established the interest of ecologists in estimating both the size of mobile animal populations and the strengths of those processes which determine the size. Operations designed to satisfy this interest will now be examined. All of the methods to be described involve marking, releasing and recapturing individuals. Most of them demand that these processes be repeated several times. A variety of generic names have been used for these methods: mark-release-recapture, release-recapture, multiple-recapture, and so on. I shall refer, in general, to capture-recapture methods and capture-recapture models.

The first chapter also established the importance of context in determining what methods should be used. This applies not only within the range of capture-recapture models, but also between capture-recapture and other models. There are undoubtedly situations in which the accuracy required of the answer, and the limitations in resources, suggest that some method other than capture-recapture is the most appropriate. Such methods will not be described here, because space is limited. No value judgement is implied.

2.1 The Petersen estimate

Even the most sophisticated models are directly descended from the simplest, which is the one first advocated by Petersen in 1896. It was also used by Lincoln in 1930 to estimate the size of the North American duck population, and is often called the Lincoln Index.

Imagine that we wish to estimate the size of a population into which there is neither birth nor immigration. On a first visit we catch a random sample of r individuals, mark them so that we can recognize them in future, and return them to the population. They remix perfectly with the unmarked individuals. Subsequently there is both death and emigration, to which, however, marked and unmarked animals are equally prone. The marked *proportion* remains the same as when the r marked individuals were initially released. On a second visit a further random sample is caught: total size n, of which m individuals are marked. If the size of the whole population immediately before the first visit was N, then it should be true that:

$$\frac{m}{n} = \frac{r}{N}$$

i.e. the marked proportion has remained the same, and our random sample of a perfectly mixed population reflects this.

We can now estimate N. The symbol $\hat{N}$ ('N-hat') denotes 'an estimate of N', and therefore:

$$\hat{N} = \frac{rn}{m}$$

This is the Petersen estimate.

Imagine that the population *is* subject to birth and immigration, but *not* to death and emigration. After the first visit, all of the r marked individuals would remain in the population, but there would be neither birth nor immigration of marks. The number of unmarked individuals, however, would increase steadily and the marked proportion steadily decline. The marked proportion in the second random sample would, therefore, reflect the situation *at that time*. In other words, $\hat{N}$ would refer not to the first, but to the second visit.

Of course, if there is neither birth, death, emigration nor immigration, the population size remains constant, and $\hat{N}$ refers to both first and second visits. In fact, this (most restrictive) case is the one usually envisaged for the Petersen estimate. For convenience it will be referred to as the 'simple Petersen estimate'.

In 1951, Bailey showed that, in cases where the numbers involved were small (m around 10, or less), the modified formula:

$$\hat{N} = \frac{r(n+1)}{(m+1)}$$

gave a more accurate (less biased) estimate. When numbers are large, the difference between the modified and unmodified formulae is negligible. The modified formula is, therefore, of more general application. Similar formulae will be used in most future calculations.

Bailey also derived a formula for the standard error of this estimate:

$$\mathrm{SE}_{\hat{N}} = \sqrt{\frac{r^2(n+1)(n-m)}{(m+1)^2(m+2)}}$$

The Petersen estimate is the simplest estimator of population size using marked individuals, but it is also the one of most restricted utility. There are two basic reasons for this. The first is that it involves just one release and one recapture; even the simplest alternatives improve upon it by using more data. The second is that there are marginally more assumptions implicit in the Petersen estimate than in most other models. These assumptions must now be examined.

2.2 Capture-recapture assumptions

1) The first, and almost trivial, assumption is that all marks are permanent, and are noted correctly on recapture. This, of course, refers only to the period of study: subsequent losses are irrelevant.
2) The second assumption is that being caught, handled and marked one or more times has no effect on an individual's subsequent chance of capture. This infers both that the inherent 'catchability' of an individual is unaffected by being caught; and that the position of marked individuals in the population, after sampling, is no different to that which would be expected if they had never been caught.
3) Thirdly, it is assumed that being caught, handled and marked one or more times has no effect on an individual's chances of dying or emigrating. Implicit in this assumption is another one: that all emigration is permanent, and therefore essentially indistinguishable from death.
4) Furthermore, it is assumed that all individuals–whether marked or not–have, inherently, an equal chance of being caught. This is tantamount to assuming that the population is sampled at random, without regard for the age, sex or physiological condition of individuals. Note that this assumption will still hold if, on a particular day, catchabilities are not equal, but individuals are assigned a catchability-class at random. In other words we are assuming that there is no *inherent* difference, *not* that on a particular day there is no difference at all. It follows from this that individuals from different classes within the population will be sampled in the proportion in which they occur.

   The analysis of a heterogeneous population will produce results which are applicable neither to the individuals or individual classes, nor to the population as a whole. Consequently this assumption can, and should whenever possible, be side-stepped by dealing with the different sexes, age-classes, etc. separately.
5) It is also assumed that all individuals – whether marked or not – have, inherently, an equal chance of dying or emigrating.

These five assumptions apply to almost all capture-recapture models. The exceptions will be indicated in the models concerned.

6) The Petersen estimate assumes either that there are no births or

immigrations, or that there are no deaths or emigrations, or that there are none of these. Most alternative models do not make any of these assumptions.

7) The final assumption – which applies to all models that do *not* assume that there is neither birth, death, emigration nor immigration – is that sampling periods are short in relation to total time. This is because birth, death, immigration and emigration are all processes which we may call quasi-continuous. That is to say we treat them as continuous, while recognizing that they are actually made up of a series of discrete, singular events. We know, for instance, that death affects one whole individual at a time, but we might still compute a death-rate of 0.05 individuals per minute. In other words, we recognize that there is a continuous *possibility* of death.

   Most capture-recapture models include these quasi-continuous processes, and many actually quantify them. If they are to be quantified, then they must be measured between two points in time. This means that sampling periods are assumed to *be* points in time. In fact, even if the processes are not quantified, population size is estimated for a sampling occasion on the assumption that the processes do not alter population size *during* the sampling occasion. Once again, a sampling period is assumed to be a point in time. Strictly speaking, this assumption can never hold – sampling can never be instantaneous – but attempts to conform as closely as possible to the assumption should still be made. Sampling periods should be short in relation to total time. This should lead, in turn, to the intervals between samples being discrete.

2.3 Notation

Before the individual models are examined, it will be useful to describe a common notation which will be employed throughout.

2.3.1 Sampling

In essence, all of the following methods involve taking a series of samples from the population under study. Most commonly, the intervals between these samples are one or more days, and sampling is said to occur on 'day *1*', 'day *2*' etc. Remember that a 'day *1* sample' refers to a sample taken over a short period during day *1*. Remember, also, that other time intervals are equally acceptable, and that 'days' refer to any discrete time interval. It follows from this that in practice it is always advisable, and in some methods essential, for samples to be taken at the *same* time each day. In this way all time intervals are the same, or, at worst, simple multiples of one another.

The size of each sample, the number caught, will be denoted by n. Thus, on day *1* n_1 individuals are caught; on day *2* n_2 individuals are caught; and, in general, on day i n_i individuals are caught.

Often, every one of these individuals will be marked and released. Sometimes, however, animals are harmed or damaged during handling, so that the number of marked individuals released on day i is less than the number originally caught (n_i). The number of marked individuals released on day i will be denoted by r_i.

2.3.2 *Marking*

A brief comment about marking is convenient here, although this will be examined again in Chapter 5. There are, essentially, three types of mark. The first is individual-specific, allowing each animal to be recognized individually, and providing the maximum amount of information on recapture. Such information is, however, largely superfluous in the present context. The second type is date-specific. On recapture, such marks allow the previous occasion or occasions on which the animal was caught to be noted. A single, individual-specific mark does, of course, have this same capacity. The third type of mark is neither individual- nor date-specific. It merely allows animals to be classified as marked or unmarked, providing the minimum amount of information.

Most of the following methods presume that marking is date-specific, and such marking is, therefore, to be recommended. When marking is individual-specific, the pattern of marks on each recaptured animal that *would* have resulted from date-specific marking must be imagined. This imaginary pattern must then be used.

On every day except the first a proportion of the sample will probably be marked. In those cases where the total number of marks caught on day i is required, this will be denoted by m_i. Often, however, it will also be necessary to partition m_i according to when the mark was given. For instance, of m_4 marks caught on day *4*, some will be from day *1*, some from day *2*, and some from day *3*. These will be denoted by $m_{4\,1}$, $m_{4\,2}$ and $m_{4\,3}$ respectively; and, in general, by $m_{i\,j}$ where i is the day of capture, and j the day of marking.

2.3.3 *Population size*

The most obvious, but by no means the sole, purpose of capture-recapture studies is the estimation of population size itself. The population size on day i will be referred to as N_i.

2.3.4 Death and emigration

Capture-recapture methods do not, in themselves, distinguish between death and emigration. They must, therefore, be considered together as 'loss'. L_i will be used to denote the *number* of individuals lost from a population between days i and $i+1$. (For instance, L_2 is the number of individuals either dying or emigrating between days *2* and *3*.)

Those individuals which are not lost survive, and it is often survival rather than loss which is measured. This, apart from anything else, avoids the disadvantage of equating death and emigration. In fact it is usual to consider survival-*rate*: the proportion of the population surviving from one occasion to the next, or the probability of any one individual surviving from one occasion to the next. ϕ_i ('phi'$_i$) will be used to denote the proportion surviving from day i until day $i+1$. Several methods calculate one survival-rate only, on the assumption that the rate of survival is constant. This will be denoted simply by ϕ.

2.3.5 Birth and immigration

Capture-recapture methods are also unable to distinguish between birth and immigration, and these too must be considered together – as 'gains' or 'additions'. B_i will denote the number of additions between days i and $i+1$, and b_i will denote the proportion of the day $i+1$ population that were added between days i and $i+1$. When b_i is assumed to remain constant from day to day it will be referred to as b.

2.3.6 'Marks at risk'

The simplest Petersen estimate rests on the assumption that the marks released on the first occasion represent the sum total of marks available for recapture on the second. All alternative methods, however, modify this assumption to some extent. Primarily, it is generally recognized that a proportion of the marks are subject to either death or emigration each day. But the consequent decline in the number of marks is usually opposed by the fact that fresh marks are regularly being added to the population.

These two factors combine to determine the 'marks at risk', M_i: the number of marks in the population which are available for sampling immediately before the day i sample. Obviously, additions to M_i can only be made with the experimenter's knowledge – by releasing a known number of marked individuals. Yet in other respects M_i is assumed to be a true sub-population of N_i: loss-rates in the marked and unmarked portions of the population are assumed to be the same, proportions captured of the marked and unmarked portions are assumed to be the same, and so on. In other words, the marked individuals are regarded as truly representative of the whole population. Measurements can be made on those marked individuals, because they are identifiable. These measurements are assumed to be equally applicable to the whole population.

It should be clear that M_i is analogous to the term r in the Petersen estimate. Not surprisingly, the estimation of M_i is a crucial part of most Petersen estimate derivatives.

2.3.7 Summation

Most of the terms introduced so far have had two components: the quantity which they measure, and the day to which they apply. For instance, m_3 refers to the number of marks caught – on day *3*. Many of the following methods require several of these terms to be added together. For instance, in a study lasting five days we may need to know the following sum: $r_1 + r_2 + r_3 + r_4$ – the total number of marked individuals released (none are released on day *5*). It is convenient to have a shorthand method of representing such sums, and the one generally used is:

$$\sum_{i=1}^{i=4} r_i$$

Put into words, this is the sum of the r_i's, where i takes all values from *1* to *4*.

Furthermore, in this particular case, since we know that marked individuals are released on all days except the last, it is really only necessary to write:

$$\sum_i r_i \text{ or even } \sum r_i$$

– the total number of marked individuals released.

The notation used in the models is tabulated in Table 2.1.

We are now in a position to consider the various capture-recapture models. In each case, the model itself will be described first, followed by a worked example, and then by a discussion of the model's utility. The description will concentrate on rationale. This should promote a critical appreciation of the model, but may do so at the expense of a superficial and rapidly-learnt ability to use it. For this reason, it is likely that an understanding of how to apply the model – as opposed to an understanding of the model itself – will be developed by considering the description and worked example together.

Many of the models include formulae for calculating the standard error of their estimates. Standard errors measure precision, and, at