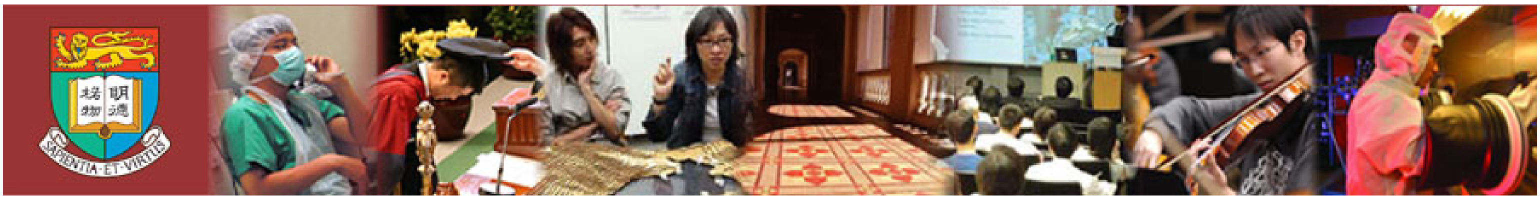

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Standardising terminology and notation for the analysis of demographic processes in marked populations

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Abstract

The development of statistical methods for the analysis of demographic processes in marked animal populations has brought with it the challenges of communication between the disciplines of statistics, ecology, evolutionary biology and computer science. In order to aid communication and comprehension, we sought to root out a number of cases of ambiguity, redundancy and inaccuracy in notation and terminology that have developed in the literature. We invited all working in this field to submit topics for resolution and to express their own views. In the ensuing discussion forum it was then possible to establish a series of general principles which were, almost without exception, unanimously accepted. Here we set out the background to the areas of confusion, how these were debated and the conclusions which were reached in each case. We hope that the resulting guidelines will be widely adopted as standard terminology in publications and in software for the analysis of demographic processes in marked animal populations.

Introduction

Recent decades have seen rapid developments in the analysis of demographic processes in marked animal populations (Senar, Dhondt & Conroy 2004, Morgan & Thomson 2002, Baillie, North & Gosler 1999, North & Nichols 1995, Lebreton & North 1993, North 1987, Morgan & North 1984). This has in large part been achieved through the successful collaboration of biologists, biometricians, statisticians and computer scientists. Thanks to partnerships across these disciplines, we have been able to advance our understanding through the development of new models and methods, better insights on how to design experiments and collect data (Schwarz 2002), and through the development of sophisticated software packages. These developments have revolutionized the way we conduct demographic analysis and the progress is clear to see, but the interdisciplinary nature of this field and the widespread uptake and implementation of these statistical models by biologists also brings with it challenges of communication between disciplines. This communication is not made easier when ambiguities, inaccuracies and redundancies in terminology and notation appear in the literature. In principle, provided terminology and notation are clearly defined, each author can exercise their right to use whatever notation and terminology are most suited to the issues upon which they are working, but there are many cases where authors have given different names to the same parameters, used the same name for different parameters, or used terminology which is not an accurate descriptor. In an effort to avoid confusion and make communication and comprehension easier, we tried to identify all places where there were problems or potential problems and by open debate and consensus we then tried to establish a series of accepted standards that we hope will be useful and widely followed in publications, software packages, and in all aspects of work in this field, until such time as further revision of terminology becomes desirable.

Methods

The EURING conferences constitute the premier forum for discussion and interaction on the subject of modeling demographic processes in marked populations, and it was through this medium that we tried to reach all involved in this field with a view to airing views and reaching consensus. All members of the EURING mailing list were contacted and asked to suggest topics where resolution and standardization would be beneficial, and they were asked to contribute their own views on what they felt would be the best standards to adopt. A particular effort was made to poll the views of those authoring software packages as they have particular influence on the way demographic analyses are approached and the terms and notation which are used. With the resulting agenda, all members of the list, and indeed in principle any other interested parties, were invited to attend a discussion forum at the EURING2003 conference in Radolfzell, Germany. Each of the points was discussed, and as far as was possible we tried to reach consensus on recommended standards. In most cases, it was possible to reach unanimous conclusions.

Results and Discussion

A summary of the recommended standards is given in table 1. In more detail, the issues were debated as follows:

'Apparent survival', 'local survival', 'true survival', Φ, and S

In many mark-recapture studies where intensive observations are made on small study sites, estimates of survival probabilities are valid under the assumption that animals do not permanently leave the area within which they can be encountered. In recognition of the fact that this assumption is rarely likely to hold, we often use the term 'apparent survival probability', Φ, the probability that an animal will not die and will not permanently leave the study site during the time period. By using the expression 'apparent survival probability', Φ, a clear distinction is made with 'survival probability', S. The survival probability can usually be estimated in mark-recovery models where dead birds can normally be found and reported even if they move some considerable distance from the point of marking. The link between apparent survival probability Φ and probability of survival S is usually through a probability of fidelity (Burnham 1993), and $\Phi = S \times \text{fidelity}$. The probability of permanent emigration is 1-fidelity.

There are two main sources of confusion in this area. Firstly, the term 'local survival' has also been used extensively to describe 'apparent survival', Φ. Secondly, some authors have used Φ to denote 'survival probability', S, in mark-recovery models, and S is sometimes used to denote apparent survival in mark-recapture models.

The forum felt that the term 'apparent survival' made a clearer acknowledgement that the estimated parameter was not a true survival probability, and that the term 'local survival' did not do this and could be interpreted as meaning simply that the survival probability was specific to a local area. We therefore chose unanimously to recommend only the use of the term ‘apparent survival’ and to discontinue use of the term ‘local survival’.

The forum further recommended that apparent survival should always and only be denoted Φ, and that survival probability should always and only be denoted S. It was emphasized that these parameters should be denoted by capital and not lower-case letters. Later it was added that if confusion may be caused by the use of capitals for the matrices used in multi-state models, then the matrices could be denoted with bold-face capitals.

During the discussions, the point was raised that a distinction should be made between ‘rates’ and ‘probabilities’ and since these models estimate probabilities they should be referred to as such and not as ‘rates’.

In other fields of statistics and demographic analysis, ‘survival’ often refers to survival from age zero, while mark-recapture and mark-recovery models typically concern survival through a specified time period conditional on being alive at the start of it. The forum agreed that the use of words to specify this time-period (e.g. ‘annual’ or ‘monthly’ survival) could help to clarify the meaning where there was potential for confusion.

‘Recovery probability’, ‘reporting probability’, f, λ, and r.

Brownie et al. (1985) used the term ‘recovery’ probability, *f*, to denote the probability that a marked animal alive at the start of the time period will be shot and have its mark reported. ‘*f*’ can be partitioned further to estimate the probability (‘reporting’ probability) that a hunter who has shot a marked bird will retrieve the mark and report it. ‘*f*’ is an index of hunting pressure and these models are popular for hunted populations in North America. Even when not hunted, marked birds are found dead and reported, and Seber (1970, 1971) used ‘Reporting’ probability λ to denote the probability that a marked animal that has died will be found and reported. This formulation has been popular in Europe where many non-hunted species are studied and where the probabilities of dead marked birds being found and reported are higher. Others have since referred to Seber’s ‘reporting’ probability as ‘Recovery’ probability and denoted it ‘*r*’ instead of ‘λ’. Despite the unfortunate ambiguities and redundancy here, these issues proved very difficult to resolve, and the only unanimous recommendation that could be made was that:

-even if standardisation can not be achieved, terms and symbols should be clearly defined in such a way that avoids confusion

As well as this, strong arguments were presented for adopting the terminology of Seber which had historical precedence. Seber did not in fact use ‘Recovery’ probability or ‘r’ in these papers. If Seber’s ‘Reporting’ probability λ is adopted then this avoids the confusion with the ‘recovery’ probability ‘*f*’, but we need to avoid confusion when using ‘reporting’ probability to refer to the probability that a hunter will report an animal he has shot.

In discussing these issues, two other points were raised and unanimous conclusions were reached. Firstly, the word ‘recovery’ should only be used to refer to dead re-encounters of marked animals. This is distinct from live ‘recaptures’ and ‘resightings’. The collective word for all of these is ‘re-encounters’, and particularly in analyses which combine different types of encounters, it makes sense to refer to ‘encounter histories’ as opposed to ‘capture histories’. The words ‘ring recoveries’ or ‘band recoveries’ are often used to describe all forms of re-encounter, but in the context of formal models we urge people not to use the word ‘recovery’ when referring to live animals.

Secondly, in demography, the symbols '*r*' and 'λ' are also both widely used to denote measures of population growth. The forum debated whether the notation we use for reporting probability could lead to confusion in this sense, but concluded that context would normally ensure there was no ambiguity in practice. With the increasingly integrated nature of demographic analyses, it is to be expected that population growth rate and reporting probability will increasingly be handled simultaneously in the same model (Pradel 1996, Besbeas et al. 2002), and care should be taken to avoid confusion when this is the case. In integrated models, the use of '*p*' to denote capture probability of live organisms could similarly lead to confusion with '*p*' for productivity, though currently this will normally be clear from context.

Multi-state models, Robust Design, 'temporary emigration', 'resighting' probability, and Ψ, γ, and c

In multi-state models, as well as the estimation of survival probabilities, we can estimate the probabilities of transition, Ψ, between states. These states could for example be distinct geographical sites, or they could be behavioural or physiological conditions such as breeding or non-breeding, healthy or diseased. While conventional open population mark-recapture studies involve single short trapping sessions at regularly spaced time intervals, Robust Design models can be used when each of these conventional trapping sessions are further divided into a short series of closely spaced repeat samples leading to a number of extremely short time periods, 'secondary sampling periods', as well as the conventional longer 'primary sampling periods'. The population can be assumed to be closed over these short secondary sampling periods and this makes it possible to estimate capture probability based on just a single trapping session. With a Robust Design, it then becomes possible to estimate not just survival and capture probabilities but also the probability that a bird will undergo transitions to and from an unobservable state, perhaps by opting in different years to establish a territory which is inside or just outside the study area.

A number of terminology issues were recognized as being problematic in these areas. Firstly, multi-state models are sometimes referred to as 'multi-strata' models even though 'strata' usually refers to fixed states between which transition is not possible. Secondly, the probability of transition to an unobservable state outside the study area and the probability of remaining there have traditionally been referred to with the terms 'temporary emigration' γ'' and 'temporary immigration' γ' even though there has been some discomfort that these terms do not describe well meaning of the parameters estimated. Thirdly, in Robust Design models a distinction is made between the probability of capture for the first time within a trapping session, and the probability of subsequent captures within the trapping session. The probability of capture of an animal that has already been captured once within a trapping session has been given a separate name, 'resighting' probability, and denoted *c*. This same term 'resighting' probability is also used in the models of Barker (1997, 1999) with a different meaning and refers there to the probability that an animal marked with a field readable ring can be encountered live in the course of the conventional (primary) sampling periods.

The forum felt that these areas of confusion could be resolved as follows, and was unanimous in these recommendations:

-where it is possible to make transitions between states, we should use the term 'multi-state models' and should discontinue the use of the term 'multi-strata models' because strata are typically states between which transition is not possible (Lebreton and Pradel 2002). The use of only one term will avoid confusion, and 'multi-state models' is a better descriptor.

-in Robust Design models, transitions to and from unobservable states should be labeled with the terminology and notation Ψ of multi-state models, and since these parameters are normally nuisance parameters anyway, terms based on 'temporary emigration' need not normally be used. If the transition has biological meaning, for example when only breeding birds can be observed and where birds periodically take sabbatical years as non-breeders, then accurate descriptive terminology can be used but normally the notation will suffice. As a standard Greek letter, 'γ' will always be used widely by mathematicians in various contexts, but within our field, discontinuation of the use of γ'' and γ' in Robust Design models should reduce confusion with the use of γ to denote seniority probability in the models of Pradel (1996)

-in Robust Design models, we see no need to create a new parameter 'resighting' probability or label it *c*; instead structure akin to modeling trap-dependence can be introduced whereby a distinction can be made between the capture probabilities of animals which have or have not previously been captured within the trapping session. This is more parsimonious and avoids all confusion with the 'resighting' probability of the Barker (1997) models.

In the context of resighting, the forum further suggested that rings which can be read in the field without capturing an animal should be referred to as 'field-readable rings'.

One further topic was raised during the discussions, namely the terminology which should be used when the exact age of trapped animals is unknown, but where the effects of age can crudely be built into the analysis by modeling the effect of 'time since marking'. Under some circumstances, this may be a good surrogate for age or it may otherwise have a clear biological meaning. For example, in cases where capture is impossible until animals recruit to the breeding population and where capture probabilities are high thereafter, 'time since marking' approximates time since recruitment, and this in turn approximates breeding experience. It was felt that some care should be exercised in using the term 'age' though, and under most circumstances it may be preferable to call these 'time since marking' models. In due course this issue may disappear if new models can be developed which estimate the effects of age on survival even when exact age of specific individuals is unknown.

Given that these recommendations have been established through open discussion and consensus, with the worthy goal of reducing confusion and simplifying communication and comprehension across our community, we hope very much that they will be adopted widely. We hope that these suggestions will not be blindly enforced or otherwise misused but that they will be taken up voluntarily and used intelligently to these ends. We urge authors of both manuscripts and software packages to be clear about what they mean, and we urge everyone not to invent new terms for established concepts when standard terminology and notation are already available.

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‘Apparent survival’, ‘local survival’, ‘true survival’, Φ and S

-we should discontinue use of the term ‘local survival’ and use instead only the term ‘apparent survival’
-we should denote ‘apparent survival’ with the Greek letter Φ (**<u>capital</u>** phi), and ‘true survival’ with capital S. This means we should not normally use Φ in dead-recovery models.
-these parameters should be denoted by capital letters in all cases
-if these parameters are ‘probabilities’ then they should be referred to as such and should not be referred to as ‘rates’.
- it enhances clarity when we make reference to time periods with terms such as ‘annual’ or ‘monthly’ survival probabilities etc.

‘Recovery probability’, ‘Reporting probability’, f, λ and r

A fully unanimous recommendation could not be reached on the core issues here, but
-the word ‘recovery’ should in any case only be used to refer to **<u>dead</u>** re-encounters of marked animals.
-even if standardisation can not be achieved, terms and symbols should be clearly defined in such a way that avoids confusion
As well as these unanimous recommendations, strong arguments were presented for adopting the terminology of Seber (1970, 1971) which in fact defines ‘reporting’ probability λ as the probability that a marked bird which has died will be found and reported.
The term ‘recovery’ probability f can then be used sensu Brownie et al (1985) to refer to the probability that a marked animal alive at the start of the time period will be shot and have its mark reported.
Reporting probabilities and population growth rates are mostly not yet modeled simultaneously, but care is needed to ensure clarity if they are as both are widely denoted with the same symbols.

‘Multi-state models’, ‘Robust design’, temporary emigration, resighting probability, Ψ, γ, c

-We should use the term ‘multi-state’ and not ‘multi-strata’ -In robust design models, transitions between the observable state inside the trapping area and the unobservable state outside it should be labeled with the terminology and notation (Ψ) of multi-state models -the terms ‘temporary emigration’ γ’ and ‘temporary immigration’ γ’’ need not normally be used -In robust design models, there is no need to introduce a new parameter ‘c’ or label it ‘resighting’ probability; instead structure akin to modeling trap-dependence can be introduced into the capture probability whereby a distinction can be made between probabilities of first and subsequent captures within sessions.

Table 1. Summary of conclusions and recommendations