Evolution of quantitative methods for the study and management of avian populations: on the importance of individual contributions

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Abstract

Evolution of quantitative methods for the study and management of avian populations: on the importance of individual contributions.— The EURING meetings and the scientists who have attended them have contributed substantially to the growth of knowledge in the field of estimating parameters of animal populations. The contributions of David R. Anderson to process modeling, parameter estimation and decision analysis are briefly reviewed. Metrics are considered for assessing individual contributions to a field of inquiry, and it is concluded that Anderson's contributions have been substantial. Important characteristics of Anderson and his career are the ability to identify and focus on important topics, the premium placed on dissemination of new methods to prospective users, the ability to assemble teams of complementary researchers, and the innovation and vision that characterized so much of his work. The paper concludes with a list of interesting current research topics for consideration by EURING participants.

Key words: Animal population dynamics, David R. Anderson**,** EURING meetings, Individual contributions, Management, Science.

Resumen

Evolución de los métodos cuantitativos para el estudio y gestión de las poblaciones de aves: sobre la importancia de las contribuciones individuales.— Los congresos EURING y los científicos que asistieron a los mismos han contribuido de forma significativa al aumento de conocimientos en el campo de la estimación de parámetros de las poblaciones animales. En el presente estudio se revisan brevemente las aportaciones de David R. Anderson a la modelación de procesos, la estimación de parámetros y el análisis de toma de decisiones. Se consideran los distintos modos en que se puede cuantificar la contribucion realizada por un investigador al desarrollo de un campo de la ciéncia, llegándose a la conclusión de que las contribuciones de Anderson han resultado fundamentales. De entre las destacadas características de Anderson y su carrera cabe mencionar su capacidad para identificar temas clave y centrarse en los mismos, la importancia que le da a la diseminación de los nuevos métodos entre los posibles usuarios, la capacidad para formar equipos de investigadores complementarios, y la innovación y visión estratégica que caracterizan gran parte de su trabajo. El estudio concluye con una interesante lista de temas de investigación actuales para que los participantes de EURING tomen en consideración.

Palabras clave: Dinámica poblacional de los animales, David R. Anderson, Reuniones de EURING, Contribuciones individuales, Gestión, Ciencia.

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Introduction

At the first EURING meeting I was able to attend, held in Montpellier in 1992, George M. Jolly (1993) presented the introductory lecture on the topic of "Instinctive Statistics". In this lecture, he reviewed the contributions to biometry in general, and to studies of marked animals in particular, of four "original thinkers", A. Quetelet, C. H. N. Jackson, R. A. Fisher, and P. H. Leslie. In more recent history, and especially over the last two decades, participants in the EURING conferences have included many of the original thinkers and primary contributors to methods for studying population dynamics using marked animals. In fact, these participants, and the EURING conferences themselves, have played an important role in the rapid growth in capture–recapture and band recovery methodologies over the last two decades. This year marked the retirement of one such participant, Dr. David R. Anderson. Although it is extremely unlikely that his contributions will end with his retirement, this event does provide an appropriate motivation for reviewing his contributions to our field.

In this paper, I will thus try to trace the modern evolution of studies of band recovery and capture–recapture methods through the contributions of David Anderson, one of the truly original thinkers in our field. As strongly emphasized in several of the presentations in EURING–03, views of estimation for population dynamics are expanding to include integration of marked–animal data with observation–based approaches. Thus, the contributions of Anderson to perhaps the most important observation–based estimation approach, distance sampling, will also be briefly reviewed. Throughout this methodological review, I will emphasize a general approach developed by Anderson to introduce biologists and managers to new classes of methods and to expedite assimilation of such methods into the fields of population ecology and management. I also emphasize the Anderson theme of striving to permit flexibility, as provided by multiple models, and his efforts to confront the resulting problem of model selection.

I note that although EURING conferences have focused on estimation issues, it is important to recall that estimation is not a "stand–alone" activity or an inherently useful endeavor and attains value primarily in the context of a larger process, such as science or management. Population modeling can be viewed as a class of methods required for the conduct of science and management, and decision–theoretic and optimization methods are also essential to informed management. Anderson has made important contributions to both of these classes of methods, and these will be briefly reviewed as well. I briefly explore the nature of individual contributions to a field and discuss the personal and research attributes that separate the exceptional contributors from the rest of us. In particular, I propose hypotheses about characteristics of Anderson's research program that set it apart from other programs. Finally, I offer some opinions about the current state of our field and note some of the opportunities and possibilities that seem to be especially useful and exciting.

Band recovery models

The use of data from individually banded birds that have been recovered as shot or found dead have a long history of use for estimation of annual survival and, for hunted species, indices to hunting mortality rate (see reviews in Lebreton, 2001; Nichols & Tautin, in press). Modern approaches to estimation are often traced back to Haldane (1953, 1955), with the first general (permitting time–specific estimates), stochastic models attributed to Seber (1970) and Robson & Youngs (1971). When these latter two papers appeared, Anderson was working with the U.S. Fish and Wildlife Service studying the population dynamics of the mallard *Anas platyrynchos* in North America. He immediately recognized the utility of these new models and wanted to extend them to multiple age classes. Thus, he developed software for implementing the Seber–Robson–Youngs model (Anderson et al., 1974) and funded D. S. Robson and C. Brownie, at Cornell University, to develop age–specific extensions.

Anderson and colleague K. P. Burnham, together with Brownie and Robson, produced an impressive body of methodological work, much of which was incorporated into the monograph, "Statistical Inference from Band Recovery Data – A Handbook" (Brownie et al., 1978). This monograph described a set of models to be fit to band recovery data in order to draw inferences about survival rates and band recovery rates (indices to harvest rates). Estimators and associated variances and covariances were presented for models permitting closed form expressions, and computer programs were described for computing estimates and test statistics for goodness–of–fit and between–model tests. The software corresponded to single–age (ESTIMATE) and 2–age (BROWNIE) models designed for data from a single banding period each year. However, the monograph also described models for 3 age classes and models for designs with two banding periods per year. Test statistics were recommended for drawing inferences about sources of variation in underlying survival and recovery rate parameters, and a chapter was devoted to the design of studies, including necessary sample sizes.

The Brownie et al. (1978; 2nd addition in 1985) handbook is simply the most influential publication ever written on band recovery models for drawing inference about avian survival and recovery rates. Beyond that distinction, I believe it to have been a landmark publication for two other reasons. The first reason is the suggestion that multiple models be fit to the same data sets. The second reason is that the monograph provided a model for the introduction of statistical inference methods to biologists and managers.

With only a few exceptions (e.g., Darroch, 1958), the history of parameter estimation for animal populations prior to the work of Brownie et al. (1978) had been characterized by the development of single, general models. General models were a focus because of the greater likelihood that model assumptions would be met, so such models were viewed as most likely to be useful. The basic, general models in the sets introduced by Brownie et al. (1978) included time–specific survival and recovery rates for 1–age (Seber, 1970; Robson & Youngs, 1971) and 2–age (Brownie & Robson, 1976) data. The model sets also included even more general models in which adult recovery rates the first year after banding differed from adult recovery rates in subsequent years following banding. These models were developed to incorporate the biological realism of high recovery rates following initial banding, a phenomenon encountered by Anderson in his analyses of mallard data sets. The model sets also included models in which parameters (survival and/or recovery rates) were constrained to be constant over time.

The consideration of multiple models leads to the question of how to select the "best" model for a given data set. Brownie et al. (1978) presented a clear discussion of the principle of parsimony, recommending use of the simplest model that fits the data adequately. All of the models in their model sets were nested, so Brownie et al. (1978) recommended using sequential hypothesis–testing as a selection procedure. The user began with the most general model and assessed model fit. Conditional on fit of the general model, a likelihood ratio test statistic can be computed between the general model and the next most general model, and this procedure can be repeated for all neighboring pairs of models in the sequence going from most general to most restrictive. If a likelihood ratio test between two models is judged to be "significant", then it is concluded that the extra parameters of the more general model are needed to describe the variation in the data (i.e., the simpler model is not adequate). If the likelihood ratio test is not significant, then this is taken as evidence that the extra parameters of the more general model are not really needed, so the user selects the less general model for estimation, as associated estimates will be more precise than those of the more general model.

In addition to introducing multiple models and the concept of model selection to biological readers, Brownie et al. (1978) provided an extremely successful model for the introduction of new statistical inference procedures to biologists and managers. An important component of the model was a monograph written for a biological readership. Although it was detailed and rigorous, Brownie et al. (1978) was not written in the terse manner typical of statistical contributions, but included descriptions designed to be understandable to biologists and wildlife managers. Another component was the presentation of model sets that provided the user with unprecedented flexibility. This flexibility included the ability to fit very general models motivated by biological realism (the models with different direct and indirect recovery rates), as well as reduced–parameter models designed for parsimonious estimation. Perhaps the component of the Brownie et al. (1978) model most responsible for the rapid assimilation of the methods into biological research and management was the accompanying software. BROWNIE and ESTIMATE were user–oriented, and their output was described in comprehensive worked examples in the monograph itself. All estimates, summary statistics, and test statistics needed for inference were computed by the software, and it was not necessary for the user to perform any secondary computations. A final component of the model for introducing statistical methods to biologists and managers was the conduct of accompanying workshops and short courses. Anderson and Burnham recognized that the monograph contained many new concepts that might require additional explanation for some readers, so they taught a number of 2–5 day workshops for the purpose of introducing potential users to the models and underlying concepts of their methods. The workshops included multiple computer exercises designed to familiarize attendees with software use. As will be noted subsequently, Anderson and colleagues have used this basic model repeatedly for the introduction of new statistical estimation methodologies to biologists.

Following the publication of Brownie et al. (1978), Anderson collaborated on papers that clearly demonstrated the superiority of these band recovery models to estimators based on different approaches that had dominated the literature prior to publication of the handbook (Anderson et al., 1981, 1985; Burnham & Anderson, 1979). He also worked on issues involving bias expected to result from failure of underlying model assumptions (Anderson & Burnham, 1980; Nelson et al., 1980). The next major step in the evolution of band recovery models was the development of software facilitating estimation under user–defined models (White, 1983; Conroy & Williams, 1984; Conroy et al., 1989). This step can be viewed as a logical extension of Anderson's emphasis on modeling flexibility exemplified by the model sets of Brownie et al. (1978). Now, instead of the statistician providing model sets consisting of a relatively small number of models, the practitioner was given the ability to tailor models to specific situations and questions of interest. This ability included the fitting of ultrastructural models in which survival and recovery parameters were themselves modeled as functions of relevant covariates (North & Morgan, 1979). This emphasis on increased flexibility has continued and is now exemplified by program MARK (White & Burnham, 1999).

The modeling flexibility made possible by developments in the 1980s has resulted in many useful extensions of band recovery models. For example, recovery rate estimates can be used to estimate harvest rates with the addition of information about band reporting rate. Such information can be obtained from reward band studies (e.g., Henny & Burnham, 1976). Flexible modeling software permitted the development of models that could be used for direct estimation and inference about reporting and harvest rates (e.g., Conroy & Blandin, 1984; Conroy et al., 1989; Nichols et al., 1991, 1995; Pollock et al., 2001). Special models similar to those initially discussed by Brownie et al. (1978) were developed for hunted species that were banded at multiple times per year (Conroy & Williams, 1984; Conroy et al., 1989). Such models have been used to draw inferences about seasonal survival rates (e.g., Blohm et al., 1987), survival rates of young birds between hatch and the time of fledging (e.g., Hestbeck et al., 1989), and harvest mortality rates (Hearn et al., 1998). Band recovery models dealing with movement among banding and recovery strata have been developed (Schwarz et al., 1988, 1993). Important models have been developed for nonharvested species as well, including the special case in which all birds are banded as juveniles (e.g., Seber, 1971; North & Cormack, 1981; Catchpole et al., 1998) and the situation where numbers of banded birds are unknown (Burnham, 1990). This list of advances and extensions is not intended to be complete (see Williams et al., 2002 for other developments) but provides evidence of substantial development built upon the base provided by Brownie et al. (1978).

Capture–recapture models

Closed–population models

David Anderson moved to the Cooperative Fish and Wildlife Research Unit at Utah State University in 1975 and began a project on capture–recapture models for estimating abundance when populations are closed to gains and losses between sampling periods. Collaborators on this project were D. L. Otis, K. P. Burnham and G. C. White, and the group recognized that there was an opportunity to provide a synthetic treatment of the different models and estimators that had been developed since the early work of such investigators as Petersen (1896), Lincoln (1930) and Schnabel (1938). Key efforts to be included in the synthesis were the constant and time–specific models for capture probability developed by Darroch (1958), the model and jackknife estimator for the case of individual heterogeneity in capture probability developed by Burnham & Overton (1978), and the synthetic treatment of sources of variation in capture probability, including trap response, found in K. H. Pollock's (1974) Ph. D. Thesis.

The monograph resulting from this work (Otis et al., 1978) provided an extremely valuable synthesis of models for closed populations. Instead of searching through various papers scattered throughout the literature, the biologist interested in these models could go to a single authoritative source. Otis et al. (1978) provided a conceptual framework for thinking of different models in terms of hypotheses about the sources of variation in capture probability that they incorporated. There was a constant capture probability model, models with single sources of variation (time, behavior, heterogeneity) and all possible combinations of sources. Estimation was not possible with all models, but they were all included in the model set, thus retaining Anderson's emphasis on flexibility.

Multiple models again led to the question of model selection, but this question could not be addressed using sequential hypothesis tests between nested models, because the closed population models were not all nested. Otis et al. (1978) thus developed a clever approach to the problem by simulating data under the various models, computing the goodness–of–fit and between–model tests that could be conducted, and using the probabilities associated with these tests to build a discriminant analysis classification function. The various test statistics are then computed for an actual data set and used in the discriminant function to compute a score that is the basis for model selection (Otis et al., 1978).

The Otis et al. (1978) monograph adhered to the approach taken by Brownie et al. (1978). Although it provided statistical detail, it was written with a biological readership in mind. Otis et al. (1978) included numerous worked examples, as well as important sections on study design and sample size. The monograph was accompanied by program CAPTURE, user–oriented software that could be used to fit the models and provide estimators under most of the models. As with the band recovery methods, Anderson and colleagues conducted workshops introducing biologists and managers to the models and associated software. Apparently, some biologists found the monograph intimidating despite the authors' efforts, so the authors wrote an additional monograph (White et al., 1982) explaining the general modeling and design concepts without the statistical detail of Otis et al. (1978). Once again Anderson and his group placed a premium on explaining the methods to a relatively naïve user group.

The Otis et al. (1978) monograph represents another landmark publication, and although additional useful developments have followed its publication (Chao & Huggins, in press), these developments always refer back to the monograph framework. Subsequent work has included models for capture probability as functions of covariates (e.g., Pollock et al., 1984; Huggins, 1989, 1991). A great deal of effort has been expended on estimators for dealing with heterogeneity models. These efforts include different moment–based estimators (e.g., Pollock & Otto, 1983; Chao, 1987), estimators based on sample coverage (e.g., Chao et al., 1992; Lee & Chao, 1994), finite mixture models (e.g., Norris & Pollock, 1996; Pledger, 2000), and models based on continuous mixtures (Dorazio & Royle, 2003). Stanley & Burnham (1998) have investigated both model selection procedures and model–averaged estimators. Program CAPTURE has been updated to include some of these estimators

(Rexstad & Burnham, 1991) and program MARK (White & Burnham, 1999) can be used to fit a variety of user–defined models.

Open–population models

Although David Anderson had used capture–recapture estimators for data from open populations (e.g., Anderson & Sterling, 1974), his first major effort to contribute to this methodology involved work on experimental data collected for the purpose of drawing inferences about survival. The emphasis was thus not simply on estimation, but on drawing inferences about the effects of specific treatment factors on short and long–term survival. Despite the more narrow focus than the band recovery and closed model monographs, Anderson recognized a need for synthesizing a variety of topics relevant to open–population capture–recapture models.

Anderson and colleagues K. P. Burnham, G. C. White, C. Brownie, and K. H. Pollock built on the initial open capture–recapture models developed by Cormack (1964), Jolly (1965) and Seber (1965) and on subsequent work to assess model fit (Pollock et al., 1985) and to introduce age–specificity (Pollock, 1981), capture history dependence (Pollock, 1975; Sandland & Kirkwood, 1981; Brownie & Robson, 1983), and reduced–parameter models (Jolly, 1982; Brownie et al., 1986). Anderson's vision of the kind of synthesis possible with open capture–recapture models was colored by his recognition that these models could be viewed as generalizations of band recovery models.

The resulting monograph (Burnham et al., 1987) contains a nice development of theory underlying open–population capture–recapture models, including data structures, modeling, goodness–of–fit testing, and between–model testing. Important ancillary topics such as quasi–likelihood, variance components, and bias approximation are developed nicely as well, and the monograph is literally filled with useful methods and information for capture–recapture practitioners. The core of the monograph deals with a nested set of models that differ from each other in the number and kinds of parameters (time–specific survival and capture probabilities) that are shared by, as opposed to modeled separately for, two or more groups. Sequential likelihood ratio tests are used to address questions about treatment effects and also to select the most appropriate model for use with the data.

This monograph once again followed the model of Brownie et al. (1978) in several important ways. It included statistical development, yet was written for a biological readership. It contained several worked examples and an important chapter on study design. User–oriented software, program RELEASE, accompanied the monograph and computed estimates, between–model test statistics and goodness–of–fit test statistics for the most general model. The experimental situation involved multiple groups (treatments), and modeling flexibility was provided by development of models representing different groups of shared parameters. Model selection and tests for treatment effects were accomplished by sequential between–model tests. Anderson and colleagues once again held workshops on the use of program RELEASE to implement the models presented in the monograph.

While completing the Burnham et al. (1987) monograph, Anderson became aware of flexible software, SURGE, developed by J.–D. Lebreton and colleague J. Clobert (e.g., Clobert & Lebreton, 1985), to implement user–defined open–population capture–recapture models. Early uses of SURGE emphasized the important ability to model survival and capture parameters as functions of time–specific covariates. Because of his emphasis on flexible modeling, Anderson was quite interested in this work to the extent that he and Burnham joined Lebreton and Clobert in a collaborative project on modeling capture–recapture data for open populations. This collaboration resulted in another landmark monograph that followed the Brownie et al. (1978) model in many ways.

Lebreton et al. (1992) presented a thorough development of open–population capture–recapture models and data structures, with instructions about how to fit the models in SURGE. This software was not quite as flexible as SURVIV (White, 1983) but was more user friendly. Few limits were placed on the SURGE user, and a wide variety of user–defined models could be fit to the data. Because the models did not have to be nested, the problem of model selection became very important. Possible models were not specified *a priori* as with the closed models of Otis et al. (1978), so the discriminant function approach to model selection was not appropriate. Burnham and Anderson (1992) had been exploring the use of Akaike's Information Criterion (AIC; Akaike, 1973) for the purpose of model selection and indeed recommended this approach in Lebreton et al. (1992). AIC treated model selection not as a problem in sequential hypothesis testing but as a direct optimization problem. The optimization criterion involved the magnitude of the likelihood and the number of model parameters, and was based on the principle of parsimony. The Lebreton et al. (1992) monograph was written for biologists and contained several worked examples with actual data sets. All of the authors were involved in subsequent workshops to explain the methods and software to biologist practitioners.

The foundation provided by Burnham et al. (1987), Lebreton et al. (1992) and some other key publications (e.g., Pollock et al., 1990) led to rapid development of modeling capture–recapture data from open populations. Anderson and Burnham became very interested in model selection. They used simulation to investigate the properties of open–population estimators based on models selected by AIC and other competitor approaches to model selection (Anderson et al., 1994; Burnham et al., 1994, 1995) and then wrote two books on the topic of model selection (Burnham & Anderson, 1998, 2002). Anderson has also maintained interest in software development, collaborating with White and Burnham on the enormously useful program MARK (White et al., 2001).

Other developments in open–population capture–recapture modeling cannot be reviewed here (see Williams et al., 2002), but I will note a few representative developments. Different models of capture history dependence have been presented including the trap response model of Pradel (1993) and the transient model of Pradel et al. (1997). Models and corresponding software for use in estimating parameters as functions of individual animal covariates were developed by Skalski et al. (1993) and Smith et al. (1994). Multistate models were developed in the 1970s by Arnason (1972, 1973), but lay dormant until the 1990s (Brownie et al., 1993; Schwarz et al., 1993) and are now seeing substantial use (Lebreton & Pradel, 2002; Fujiwara & Caswell, 2002a). These models can be implemented in programs MSSURVIV (Hines, 1994), MARK (White & Burnham, 1999) and MSURGE (Choquet et al., 2003). Open models permitting estimation under certain forms of temporary emigration have been recently developed (Fujiwara & Caswell, 2002b; Kendall & Nichols, 2002). Alternative parameterizations of the Jolly–Seber likelihood permit direct inference about recruitment and rate of population change based on open–model data (Pradel, 1996; Schwarz & Arnason, 1996; Nichols et al., 2000). These approaches can be implemented using program MARK (White & Burnham, 1999) and program POPAN (Schwarz & Arnason, 1996).

Models for multiple data sources on marked animals

Some studies yield different kinds of encounters for marked animals, and it is sometimes useful to tailor models to this situation. To my knowledge, David Anderson was the first person to publish the idea that different encounter types might provide information that could be used to draw inferences about parameters that could not be studied using traditional methods and models. Anderson & Sterling (1974) obtained both band recoveries and recaptures of molting drake pintails (*Anas acuta*) banded at a study site in Saskatchewan. Anderson recognized that the complements of survival rate estimates based on band recoveries reflected only mortality, whereas the complements of capture–recapture survival estimates included both death and permanent emigration. Anderson & Sterling (1974) presented an *ad hoc* estimator for the probability of permanent emigration using both capture–recapture and band recovery survival estimates. This basic idea was later formalized by Burnham (1993; also see Barker, 1997), and his model is now widely used to estimate both survival and fidelity.

The robust design of Pollock (1982) combines capture–recapture data from open– and closed–population sampling, permitting robust estimation of the usual open model parameters as well as permitting inference about other processes such as temporary emigration (Kendall et al., 1997) and potential problems such as uncertain state assignment (Kendall et al., 2003). Barker (1997) considered models in the situation where observations of animals could be recorded between formal sampling periods. His models permit more precise estimation of standard parameters and sometimes provide inferences about movement as well. The combination of band recovery data and recapture data from both closed– and open–population time scales permits separate estimation of true survival and both temporary and permanent emigration (Lindberg et al., 2001).

Observational data and distance sampling

During work on his M. S. degree at Colorado State University in the 1960s, Anderson and fellow graduate student, R. S. Pospahala, worked on waterfowl production in the San Luis Valley in southern Colorado. They walked line transects looking for duck nests and took perpendicular measurements to each nest to use in estimation. Anderson & Pospahala (1970) provided an intuitive development for a nonparametric approach to nest density estimation using distance sampling. Burnham & Anderson (1976) then formally developed the framework for distance sampling, presenting a general density estimator that provides the basis for both parametric and nonparametric modeling.

Building on the early parametric modeling of Hayne (1949) and subsequently Gates et al. (1968) and Eberhardt (1968), and on their own seminal work (Burnham & Anderson, 1976), Burnham and Anderson proceeded to develop various modeling approaches for use in analysis of distance data (e.g., Anderson et al. 1978, 1979a, 1979b; Burnham, 1979; Burnham et al., 1979). They recognized the need for synthesis and produced yet another landmark monograph, Burnham et al. (1980).

Burnham et al. (1980) provided a thorough conceptual development for distance sampling, and recommended a robust estimation approach based on Fourier series. The Anderson theme of flexibility was again emphasized, as the user was to decide on the number of terms to be included in the Fourier series based on goodness–of–fit and sequential likelihood ratio tests. Various parametric models were also described and investigated. The model of Brownie et al. (1978) for dissemination of described methods was followed, as Burnham et al. (1980) was again written for biologists. It included many worked examples and substantial discussion of design considerations. The monograph contained a description of a comprehensive computer program, TRANSECT, designed to fit models, compute estimates, compute test statistics, and carry out necessary computations. Anderson has remained heavily involved in research on distance sampling and has been a collaborator on the two major synthetic books written to update the state of distance sampling methods and modeling (Buckland et al., 1993, 2001). He has also been associated with the comprehensive software package, DISTANCE, written to replace TRANSECT.

In addition to these seminal contributions to traditional distance sampling, Anderson is responsible for another innovation in the use of these methods. He considered application of this approach to trapping data. As there is no natural gradient in capture probability on standard trapping grids, Anderson et al. (1983) recommended a web configuration of traps designed to induce such a gradient and thus permit analysis using distance sampling methods. The trapping web is an ingenious idea that permits direct estimation of density from trapping data and that appears to work well in practice (Parmenter et al., 2003).

Methods for the conduct of science and management: estimation in context

The focus of the EURING meetings over the past two decades has been on estimation of parameters relevant to population dynamics and management. However, estimation should not be viewed as a stand–alone activity. Absent the context provided by the processes of science or management, estimates are not very useful and are of little intrinsic value. Two other broad classes of methods are useful in the conduct of science and management, those associated with dynamic process modeling and decision analysis (Williams et al., 2002). Here, I note that David Anderson has made seminal contributions to these other methodological components of the processes of science and management as well as to the estimation component. Finally, I argue that the emphasis of Burnham & Anderson (1992, 1998, 2002) on model selection has resulted in renewed interest in the multiple model approach to the conduct of science (e.g., Chamberlin, 1897; Hilborn & Mangel, 1997).

Modeling biological processes

The most common use of mathematical models in the conduct of science is to deduce consequences of associated hypotheses (e.g., Nichols, 2001; Williams et al., 2002).

We have one or multiple hypotheses about a system of interest and develop models for each hypothesis of interest. Each model is used to make a prediction about system response to an observed perturbation or experimental treatment. These predictions are then compared to the estimate of system response (an important role of estimation), and the distance between estimate and predictions is used to either reject a single hypothesis or not, or to modify relative degrees of faith in the different models in a multiple hypothesis context.

During his early work on mallard population dynamics, David Anderson was asked to address questions about the effects of hunting on mallard survival and populations dynamics. In another landmark monograph, Anderson & Burnham (1976) provided a conceptual framework and developed a model structure for addressing these questions in a formal manner. Define S_i as the annual survival rate (probability of surviving all mortality sources) for year i, S_0 as the probability of surviving nonhunting mortality sources in the absence of hunting, and K_i as the probability of dying in year i as a result of hunting in the absence of nonhunting mortality. Then various hypotheses about the effects of hunting on survival can be expressed in the following model:

$$S_i = S_0(1 - bK_i) \qquad (1)$$

If $b = 1$, then the model in (1) corresponds to the completely additive mortality hypothesis. Instantaneous risks associated with hunting and nonhunting are additive, and annual survival decreases in a linear manner with increases in hunting mortality. If $b = 0$, then (1) corresponds to the completely compensatory mortality hypothesis, such that for a range of hunting mortality rates less than some threshold c, $K < c$, changes in hunting mortality rate bring about no corresponding change in total survival. Intermediate values of b, $0 < b < 1$, correspond to intermediate models exhibiting partial compensation (Conroy & Krementz, 1990). As simple as this construction now seems, it represented an important step in the scientific process, the articulation of a model from which testable predictions could be clearly deduced.

In their development of methods for estimating survival rates, Anderson and Burnham explored ways of incorporating this process model into the statistical models used for parameter estimation. For example, the model ($S_.$, f_i) was closely associated with the compensatory mortality hypothesis (Burnham & Anderson, 1984), as annual survival is constant in the face of time–varying hunting mortality (recall that recovery rates, f_i, index hunting mortality). When the appropriate numerical methods became available (White, 1983), they also developed ultrastructural models in which annual survival was modeled as a function of scaled recovery rate, permitting direct estimation of b and related parameters (Burnham et al., 1984).

Anderson used process models in other aspects of his work on mallard population dynamics. Pospahala et al. (1974) developed autoregressive models of pond numbers in prairie Canada (an important environmental covariate) as a function of rainfall. In a monograph on mallard population dynamics, Anderson (1975a) used a number of models. He modeled mallard reproductive rate as a nonlinear function of mallard breeding density and environmental conditions (pond numbers). He developed a 2–sex deterministic matrix model for the purpose of investigating asymptotic population growth rate and sex ratio. He then developed a stochastic analog that incorporated covariances among the age– and sex–specific survival rates (Anderson, 1975a).

In summary, Anderson was well aware of the role of models in the conduct of science and developed and used them as needed. The use of mathematical modeling was not widespread in animal population research in the late 1960s and early 1970s, and I believe that Anderson can be viewed as one of our field's pioneers with respect to model use. With respect to the question of effects of hunting, we are now exploring models (e.g., Johnson et al., 1993; Williams et al., 2002) that are less phenomenological and more mechanistic than the original models of Anderson & Burnham (1976). Nevertheless, as noted by Lebreton (in press) in a recent review of effects of exploitation on animal populations, we have made surprisingly little progress in modeling the exploitation process since the important work of Anderson & Burnham (1976; also Burnham & Anderson, 1984; Burnham et al., 1984).

Decision analysis

When the process of interest is management or conservation, the class of methods associated with decision analysis is needed. Management problems involve five key elements (Kendall, 2001; Williams et al., 2002): 1. Management requires a clear articulation of objectives, in the form of an objective function; 2. Management requires a set of possible actions that can be taken; 3. Management requires models (or at least a single model) that reflect our understanding of the system and that permit prediction of system response to management actions; 4. In the case of multiple models (structural uncertainty about system dynamics), we require measures of our relative faith in the different models (sometimes referred to as "model weights"); 5. Finally, informed management requires a monitoring program providing estimates of system state for the purpose of making state–dependent decisions. Armed with these elements, at each decision point in the time frame, the manager would like to select the management action that is "best" with respect to achieving objectives.

The step in the management process of deciding the best management action is a problem in dynamic optimization. Each decision carries a specified consequence for the objectives and drives the system to a new state. Our decisions must be state–specific and must account for system dynamics. To make the problem more difficult, because of environmental variation and other forms of uncertainty, our system model will typically be stochastic, permitting only probabilistic predictions about system state in the subsequent time step. We thus require a method that will yield optimal decisions for dynamic systems that permit only stochastic predictions (Williams et al., 2002).

While working on mallard harvest problems, Anderson recognized the potential utility of stochastic dynamic programming (Bellman, 1957) for solving problems in optimal stochastic control. For his Ph. D. research at the University of Maryland, Anderson used dynamic programming to explore optimal decision policies for mallard hunting regulations under two contrasting models, completely compensatory mortality and totally additive mortality. The state of the system was characterized by the number of breeding mallards each spring and the number of ponds (environmental state), the decision involved the total mallard harvest (management action), and the objective was to maximize total harvest over a long time horizon. The computing difficulties associated with dynamic programming were substantial in the early 1970s, yet Anderson (1975b) was able to obtain optimal state–specific policies for the two models reflecting different hypotheses about hunting effects. The demonstration of very different optimal policies for these two competing models was important in demonstrating the importance to management of distinguishing between these two alternatives.

I view Anderson's recognition that duck harvest management is a problem in optimal stochastic control as an extremely important development in wildlife management. Most decisions in wildlife management and conservation are made very subjectively in the absence of some of the important components of a management process (e.g., no clear statement of objectives, no specific model(s) predicting system responses to management actions). Anderson not only identified the necessary components of an objective process, but he also found an optimization approach to compute optimal management decisions. Anderson's (1975b) use of stochastic dynamic programming is one of the earliest uses in natural resource management and the first use, to my knowledge, in wildlife management. Duck hunting regulations for mallards in North America are now established using a formal program of adaptive management (Walters, 1986; Williams et al., 2002), and the process represents a model for this approach. I believe that the articulation of competing hypotheses and models for the effects of hunting on survival (e.g., Anderson & Burnham, 1976), the recognition that the establishment of hunting regulations was a classic problem in decision analysis, and the use of stochastic dynamic programming as a means of obtaining optimal policies (Anderson, 1975b) represent key points in the evolution of the North American program of adaptive harvest management for ducks (Nichols, 2000). Without these contributions, I very much doubt that we would be using adaptive management today.

Model selection, science and management

Here, I no longer consider the separate methodological components of science and management and move to the overall processes, themselves. Although much of the original motivation of Burnham and Anderson for studying model selection appeared to be to choose estimators with good properties, their work has had substantial influence in the conduct of science. The multiple hypothesis approach to science articulated by Chamberlin (1897) saw little use for nearly a century, but has now become fairly popular (e.g., Hilborn & Mangel, 1997; Williams et al., 2002). We admit that truth is unknowable and, even if it were not, that it would be incomprehensible to us and too complex to use for prediction. The task of the scientist is then to develop simplifying hypotheses, together with their corresponding models, and to use them to deduce predictions that are then confronted with data. This confrontation leads to changes in the relative degrees of faith held in the different hypotheses and in the predictions of their associated models. Science then becomes a task of selecting among competing hypotheses and models.

A current trend in parameter estimation is to develop model–averaged estimators (e.g., Buckland et al., 1997; Burnham & Anderson, 1998, 2002). The scientific analog occurs when we need to make predictions, as when the scientific process is embedded in a management program. In such cases, we turn to something akin to weighted model averaged predictions (Williams et al., 2002), where the model weights reflect the relative degrees of faith in the different hypotheses. These model weights are themselves a result of the scientific process, and are based on the past predictive abilities of the models as judged against estimates of true system state. The point of this brief development is simply that the model selection philosophy popularized by Burnham and Anderson has extended well beyond estimation to the conduct of science and management.

On individual contributions

The EURING meetings are very important and contribute substantially to defining the state of the art with respect to methods for studying animal populations. The strength of the meetings is the attendees, who represent the most important contributors to this field. Here, I would like to consider the metrics by which individual contributions can be judged, using David Anderson as an example. First, I consider a metric that is best viewed as an abstraction, hopefully useful in defining what constitutes an important contributor, though probably not useful in actual measurement. Then I consider metrics that can be actually measured and that are hopefully correlated with real contributions.

Fisher's (1930) reproductive value is a metric that has proven useful in the study of demography. It is a function of age–specific rates of survival and fecundity and essentially quantifies the relative contributions of different individuals (in this case differing by age or stage) to future population growth (e.g., see Stearns, 1976). One way to view reproductive value is to consider removal of an individual from the population and to consider the population size at some time period in the distant future relative to the case where a different individual (different age or stage) is removed. The ratio of the future population sizes should reflect the ratio of reproductive values of the two individuals.

Although very much an abstraction in the case of individual contributions, this is the sort of question we would like to ask in order to judge the relative contribution of a single individual to the growth of knowledge. We would like to summon Clarence Odbody, angel second class, from the movie "It's A Wonderful Life". Just as Clarence showed George Bailey what Bedford Falls, N.Y. would have looked like had George never been born, we could ask Clarence to show us the current state of knowledge in our field had any individual of interest "never been born" or otherwise never contributed. In the case of David Anderson, I would argue that the difference (current knowledge with and without his contributions) would be substantial.

With respect to estimation, I would guess that the modeling of band recovery data, capture–recapture data, and distance sampling data would not be nearly as advanced as they now are. The landmark synthetic monographs (Brownie et al., 1978, 1985; Buckland et al., 1993, 2002; Burnham et al., 1980, 1987; Lebreton et al., 1992; Otis et al., 1978; White et al., 1982) have simply been too important in providing a base for further development. I believe it is nearly impossible to overstate the importance of such synthetic points of departure for new work in a field.

It is also unlikely that comprehensive software development would be nearly as advanced as it now is. Although there were computer programs available to compute capture–recapture estimators before Anderson's work, these were stripped down computational programs with little effort devoted to either flexibility or user friendliness. Except perhaps for the software developed by Arnason (e.g., Arnason & Baniuk, 1980), the user–friendly and comprehensive programs developed as part of Anderson's early work (e.g., BROWNIE, ESTIMATE, TRANSECT, CAPTURE) were unique. These programs can be viewed as the early ancestors of such current software as MARK (White & Burnham, 1999), MSURGE (Cloquet et al., 2003) and POPAN (Arnason & Schwarz, 1999). I doubt that software evolution would have produced anything resembling the current state of development, in the absence of this work during the 1970's.

Certainly, I believe that the number of biologists and managers possessing a working knowledge of modern estimation methods would be much smaller in the absence of Anderson's contributions. With respect to specific innovations, I suspect that eventually we would have developed joint band recovery and capture–recapture models even in the absence of the suggestions of Anderson & Sterling (1974), but I doubt that the trapping web would be with us had it not been for Anderson et al. (1983).

With respect to the larger issues involving the conduct of science and management, I have argued above and elsewhere (Nichols, 2000) that there would probably be no formal program for adaptive waterfowl harvest management had it not been for Anderson's early work on mallard populations. Specifically, his key contributions were:

1. Development of competing hypotheses and associated models for responses of survival rates to hunting mortality; 2. Incorporation of these survival models into larger population–dynamic models; and 3. Identification and use of stochastic dynamic programming for computing optimal harvest policies. With respect to the conduct of science, I believe that the recent emphasis on model selection by Burnham and Anderson has popularized the multiple–hypothesis approach to science and focused needed attention on the manner in which hypotheses are evaluated (e.g., Johnson, 1999; Franklin et al., 2001).

Of course all of the above speculation represents an exercise in *a posteriori* story–telling, as I have no ability to test any of these stories about what our state of knowledge might be like in the absence of Anderson's varied contributions. When we search for more tangible metrics that might be correlated with the reproductive value abstraction, we might focus on publications and citations of his work. David Anderson has published about 150 journal articles and book chapters and 15 books and research monographs, and there are approximately 6,500 citations of his work in the scientific literature. Another approach would be to quantifying contributions using empirical data would be to investigate the scientific collaboration network (Newman, 2001) in the field of animal population parameter estimation. We would select a group of interest; for example all scientists who have authored at least one EURING proceedings article during the last five EURING meetings. For each member of this set, or for a randomly selected subset of these individuals, we would compute the path length (e.g., Watts & Strogatz, 1998), or the number of steps required to link each individual, via collaboration and coauthorship, with David Anderson. For example, only one step is required to link me with David as we have written papers together. Juan–Carlos Senar, to my knowledge, has not coauthored a paper with Anderson. Senar has authored papers with Mike Conroy, who has coauthored papers with Anderson, so the path length linking Senar to Anderson would be 2. I speculate that average path length required to link scientists with Anderson would be substantially less than required to link scientists with most other focal individuals. If this speculation is correct, then it would provide yet another metric reflecting the disproportionate influence and contribution of David Anderson to our field.

In closing this section on individual contributions, I believe it is wise to examine the characteristics and habits of important contributors, as such knowledge may make better contributors of the rest of us. One attribute of Anderson is his ability to discriminate between important and mediocre topics and to devote his valuable time to the important ones. The ability to discriminate may involve not only knowledge but also intuition, and I am guessing that this is something that cannot necessarily be learned. However, given that the investigator has decided that some topics are more important than others, he/she certainly has the ability to focus energy on the important questions. Too frequently, research topics are selected based on such factors as funding sources, interests of collaborators, and projected ease of study. While these factors are of some relevance, they should be viewed as minor relative to our judgments about the potential importance of the contributions. Human life spans are finite, and we should be extremely jealous and protective of our time.

Another important characteristic of Anderson, in my opinion, is the premium placed by him on disseminating his completed work to potential users. In most areas of endeavor, the value of a contribution is defined not so much by intrinsic characteristics such as novelty and potential utility, as by the degree to which the work is actually used. As emphasized in the sections on estimation, Anderson's approach of writing monographs for a biological readership, providing accompanying user–oriented software, and conducting workshops to explain the methods to users has provided our discipline with an immensely successful model for methodological dissemination. Anderson is an excellent verbal communicator with a knack for explaining complex issues in a simple and straightforward manner, and this ability has no doubt proven useful in explaining new methods to biologists and managers.

Another idea that comes to mind regarding Anderson's success is his tendency to surround himself with other good scientists with similar interests and distinct, yet broadly overlapping, skills and abilities. The resulting synergies have proven to be extremely productive and useful to all participants. Many of the best scientists in our field, including many EURING participants, have been collaborators and students of Anderson.

Finally, I believe that Anderson has been very innovative with respect to both specific methods (e.g., distance sampling, trapping web) and broader visions of the future (e.g., comprehensive methodological software packages, institutional adoption of decision–theoretic approaches to animal population management). Although I do not claim that innovation can be learned, I do suspect that some of us do not spend adequate time thinking beyond well–defined problems and at least attempting to be more visionary.

Estimation methods, present and future

The preceding discussion on the evolution of methods has been historical in nature. Such discussions are only useful if past failures and, in this case, successes are informative of promising paths for future work. Here I comment on some of the aspects of our current state that seem especially promising, exciting, and likely to provide bases for useful future work.

The preceding text included a short section dealing with models for multiple data sources on marked animals. Such combination models tend to exhibit the advantages of increased precision, increased flexibility and ability to obtain separate estimates of parameters that are confounded with single data sources. In addition to some of the combinations discussed in the historical review, work is either in progress or has been recently completed on new combinations. For example, Skvarla et al. (in press) have implemented a robust design in a multistate framework, permitting estimation of temporary emigration from the study system as well as survival and movement among study sites. Bailey et al. (in press) have used a special kind of open robust design based on amphibians captured while entering and leaving breeding ponds to estimate parameters of interest, including probability of temporary emigration, which is equivalent to probability of nonbreeding in this system. Kendall et al. (in review) have extended this modeling to multiple breeding ponds. Barker (in review) and Kendall (pers. comm.) have developed robust design models that also include band recoveries and incidental observations. I continue to believe that there remain many opportunities for combining radio telemetry and capture–recapture data in useful ways (e.g., Powell et al., 2000). Powell (in press) has recently developed multistate models to use the extra information from isotope or genetic signatures that identify the location of a captured animal the previous time period, regardless of whether or not the animal was caught that period.

An issue of special concern in studies of marked animals is the appropriate treatment of uncertainty. Lukacs & Burnham (in review) have considered the sampling of low quality sources of DNA (e.g., hair samples, fecal samples) for the purpose of identifying individual animals using microsatellite molecular data. Different kinds of error in identification can result from such data and constitute a source of uncertainty that should be incorporated into the modeling and estimation. Kendall et al. (2003) use the robust design to permit estimation under multistate models in cases where errors can be made in state assignment. Pradel (in review) and Nichols et al. (in press) consider the problem of uncertainty in assignment of sex to individuals. In cases where it is possible to observe at least some behaviors that are definitive of sex, and even some cases where this is not true, estimation is possible within an open population framework. Such modeling is preferred to a typical *ad hoc* approach, which yields sex–specific survival estimates that are positively biased.

Individual heterogeneity is an important topic that was discussed at the previous EURING conference (Link et al., 2002; Cam et al., 2002). This previous work was based on a sampling situation in which capture probability was effectively 1, permitting hierarchical modeling and direct estimation. Link (2003) has incorporated heterogeneous capture probabilities into a standard open model framework using a Bayesian approach, and Pledger et al. (2003) have developed finite mixture models for dealing with heterogeneity under the robust design. Link's (2003) demonstration of the nonidentifiability of abundance in the presence of heterogeneous capture probabilities in closed population models is both important and sobering. It would be valuable to be able to identify characteristics of distributions that are most likely to cause serious problems. In the absence of such a classification, this result should place a premium on studies of known populations or subpopulations, as this will become our only means of gaining confidence in particular estimators and models.

As the EURING conferences are becoming increasingly broad in subject matter, I note several interesting developments in the analysis of data from observational studies. One involves the decomposition of detection probability estimates (Pollock, pers. comm.) into components associated with: 1. Detection conditional on both presence in the study area and on the organism not being invisible (e.g., submerged manatee, silent songbird); 2. Visibility given presence in the study area; and 3. Presence in the study area. The detection probabilities associated with some estimation methods (e.g., Royle & Nichols, 2003) include all three components, others (e.g., Farnsworth et al., 2002) include components 1 and 2, and still others (Buckland et al., 2001) deal only with component 1. This hierarchy permits estimation of the individual components in situations where this might be useful. The consideration of detectability in observation–based studies brings up a recurring design issue for large–scale monitoring programs. How much effort should be allocated to the estimation of detection probability within sample units, versus better dealing with geographic variation by surveying more sample units (Pollock et al., 2002)? Can double sampling approaches be used such that detection probability is estimated on only a subset of sample units? Large–scale monitoring programs may also benefit from consideration of state variables other than abundance, and the recent work on estimation of occupancy may be useful in this regard (Mackenzie et al., 2002, 2003, 2004; Mackenzie & Bailey, in press; Royle & Nichols, 2003; Royle, 2004; Royle & Link, in review).

Royle (pers. comm.) has noted that the large majority of modeling effort in distance sampling has involved detection probabilities, whereas the densities themselves are the quantities of real interest. Royle (pers. comm.) has noted the potential to embed models for both spatial and temporal variation in densities in joint likelihoods for distance sampling data. Link et al. (2003) have recently modeled observational data on whooping cranes, in which observed birds are categorized by state (e.g., young and adult). The deterministic nature of state transitions (knowledge of the number of years spent as young) permits inference about survival. Finally, J. M. Nichols et al. (in press) are exploring the possibility of using attractor–based methods (e.g., Pecora et al., 1995, 1997; Schiff et al., 1996) developed for the analysis of nonlinear time series data to detect coupling (dynamical interdependence) based on time series of abundance estimates from potentially coupled systems. The methods should be preferable to the linear cross–correlation typically used in ecology (e.g., Bjornstad et al., 1999; Koenig, 1999) because the attractor–based approaches do not rely on the assumption of linearity and because they can detect asymmetry in the coupling.

One of the most exciting areas of research is the combination of data from both observations and marked animals. Observation–based data provide information on abundance, density and rate of change in abundance, whereas marked animal data provide information on vital rates, abundance, and rate of change in abundance. Various combinations of such data permit direct estimation of all important components of population dynamics in a synthetic and consistent manner. Variations on this general idea have been provided by Trenkel et al. (2000), Besbeas et al. (2002), White & Lubow (2002), Gove et al. (2002), as well as in EURING–03 presentations by Brooks, Caswell, King, Lebreton, Morgan, and Otto. Estimation approaches range from least squares approaches to use of the Kalman filter and hierarchical modeling within a Bayesian framework. Finally, Fonnesbeck & Conroy (in review) have presented a synthetic view of decision theory combining modeling, estimation and optimization in a single Bayesian framework for use in management programs.

Summary

As noted in the introduction, the EURING meetings and their participants have played an important role in the field of parameter estimation for animal populations. David Anderson is certainly one of the outstanding contributors in this field of endeavor, with seminal publications not only in the EURING specialty area of estimation, but also in the methodological areas of modeling and decision theory, and even in overall approaches to the conduct of science and management. It would be wise for all of us to examine the characteristics of Anderson and his work in an effort to try to insure that our research efforts are maximally useful. Our field is relatively mature now, yet there are many exciting topics worthy of our efforts. Some of the more important of these topics involve efforts to integrate different data sources, methods, and general approaches in an effort to create a synthetic view and treatment of estimation, modeling and decision theory. I fully expect the participants in this and other EURING conferences to be among the leading contributors to these promising developments.

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