

Lecture Notes in Statistics

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Statistics in Ornithology

Edited by B. J.T. Morgan and P.M. North



Springer-Verlag
Berlin Heidelberg New York Tokyo

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Mathematics Subject Classification (1980): 62D05, 62P99, 62HXX

ISBN- 978-0-387-96189-7

e-ISBN-13:978-1-4612-5138-5

DOI:10.1007/978-1-4612-5138-5

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2147/3140-54321

STATISTICS IN ORNITHOLOGY

PREFACE

The genesis of this volume was in a one-day meeting arranged under the auspices of the Mathematical Ecology Group, jointly of the British Region of the Biometric Society and the British Ecological Society, and held in the Natural History Museum in London on the 4th May 1982.

The object of the meeting was to bring together individuals from different disciplines but with a common interest in ornithology. In this volume we have tried to preserve the flavour of the meeting so that all but two of the papers read or presented as posters can be found here. The two papers that have not been included have since been published elsewhere: see Birkhead and Nettleship (1983) and Cavé (1983). Further papers have been added to the volume from contributors who were unable to attend the London meeting, or were unable to present a paper there. All of the papers were refereed by ourselves.

A volume which contains papers by both statisticians and non-statisticians is inevitably going to be variable with regard to the depth and range of statistical techniques used. Thus non-statisticians are likely to find some of the papers written by statisticians difficult at times, and conversely statisticians may find that they would have treated some problems differently from non-statisticians. It is hoped, however, that this volume will increase awareness of the interests and problems (including solutions), in the general area of ornithology, and stimulate cross-fertilisation of ideas.

Byron J.T. Morgan
Philip M. North

Canterbury, Kent, England
January 1985

ACKNOWLEDGEMENTS

In addition to the authors of the papers in this volume, a number of other people have made valuable contributions, and we would like to express our gratitude for their assistance. Our thanks are due to Ian Jolliffe, for refereeing assistance with one of the papers, to Keith Darby for help with proof-reading, to Duncan Forrester for assistance with the production of diagrams, to Jonathan Hart and Simon Bishop for the construction and setting of the Bibliography, to Janet Morgan for help with the construction of the Subject Index, to Pat Allen for following up queries relating to references and last, but by no means least, to Di Mayes for her very patient and efficient typing of the papers.

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DETAILS OF THE AUTHORS

ALAN J.B. ANDERSON (MA., M.Sc.), worked at Rothamsted from 1966 to 1970 on clustering methods and multivariate analysis in botany and ecology. From 1970 to 1974 he was with the Medical Research Council in Edinburgh developing data base techniques for use in genetic research and since then has lectured at Aberdeen University in the Department of Statistics.

HUGH BOYD is a senior scientist, Canadian Wildlife Service, Ottawa. He began his ornithological career as Warden of Lundy Bird Observatory (1948-1949), then studied geese and other waterfowl for the Wildfowl Trust (1949-1965) and the Nature Conservancy (1965-1967). He joined the Canadian Wildlife Service as Research Supervisor, Migratory Birds, Eastern Region (1967-1975), later becoming Director, Migratory Birds Branch (1975-1980) and Senior Policy Advisor (1980-1982), before reverting to a research position.

STEPHEN T. BUCKLAND (B.Sc., M.Sc., Ph.D.) took up a lectureship in the Department of Statistics, University of Aberdeen, in 1977, upon completion of a one year post-graduate course at Edinburgh University. He has since specialised in developing methodology for estimating animal abundance, and is organiser of the North-East Scotland bird atlas.

ROBERT A. CHEKE began his biological career as a field and research assistant at The British Trust for Ornithology before going to the University of St. Andrews to read Zoology. As an undergraduate he participated in ornithological expeditions to the Mole game reserve in Ghana and the Cherangani Mountains of Kenya, where he studied the physiology and ecology of sympatric sunbirds. After graduating he continued studies of the ecology of sympatric species but switched to insects for his Ph.D. thesis on the population dynamics of two *Psocopteran* species and their shared parasitoids, at the University of Leeds. In 1973 he went to teach quantitative ecology and other biological courses at Plymouth Polytechnic, followed by a spell at Sheffield University. He took up his present post in 1976, which has provided opportunities to return to Africa where he has studied grasshoppers, locusts and other pests of subsistence agriculture but since 1979 has been working on the taxonomy, biology and control of the *Simulium damnosum* species complex which transmits human onchocerciasis. He went to Mauritius and Réunion in 1974 to assist the British Ornithologists' Union expedition to the Mascarene Islands and maintains an active interest in birds at home and abroad.

JEAN CLOBERT graduated in zoology at the catholic university of Louvain (Belgium) in 1975. He obtained his Ph.D. there in 1981, on Starling population biology. He is still working on Starling populations, with his main interests in population dynamics and control.

MICHELINE CLOBERT-GILLET graduated in zoology at the catholic university of Louvain (Belgium) in 1976. After some work in population ecology, she now works in the medical field.

MICHAEL J. CONROY received his Bachelor of Science (1974) and Master of Science (1976) degrees in Wildlife Ecology from Michigan State University. His research emphasis was quantitative analysis of wild-life populations and habitat relationships.

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His masters research was a study of habitat factors related to the distribution of snowshoe hares (*Lepus americanus*) in clear-cut areas of Michigan. He received the Doctor of Philosophy degree in Forest Biometrics from Virginia Polytechnic Institute and State University in 1979 for research on plant species succession and forage production following thinning of loblolly pine (*Pinus taeda*) plantations. Since 1979, he has been a research biologist/statistician with U.S. Department of Interior, Fish and Wildlife Service, at Patuxent Wildlife Research Center. His main research interests are the analysis of population statistics of migratory waterfowl, population modelling, methods for analysis of band (ring) recovery and recapture data, and field research into quantifying time- and source-specific mortality of wintering waterfowl.

HERVÉ COQUILLART graduated in zoology at the University of Lyon (France) in 1978. In 1981 he obtained a Master's Degree also at Lyon, on Swallow population biology. and is still working on this subject. He also has worked on fish populations.

RICHARD M. CORMACK did his schooling in Glasgow and took a mathematics degree at Cambridge after abandoning his intention to become a theoretical astronomer and turning instead to statistics. The inspiration of having Anscombe, Daniels, Lindley and Wishart as teachers for the Cambridge Diploma confirmed him on this course. Failing to get an industrial post with Shell Research he went to Aberdeen to be interviewed for a job at Torry Research Station. Professor Finney greeted him by saying "My Assistant Lecturer has left me for a post at Shell Research. Would you consider yourself a candidate for that post?"

His first lectures were to Honours and postgraduate students in Botany and Zoology. They came for help with their projects, followed by their lecturers, Charles Gimingham and George Dunnet, with respectively the first paper on Association Analysis and capture-recapture data on quokkas.

Thus, nearly thirty years ago, were his major interests formed. They were strengthened by an eye-opening sabbatical year with Doug Chapman in Seattle, and encouraged throughout his sixteen years with David Finney in Aberdeen and Edinburgh. Marriage to a plant ecologist has kept his statistical feet firmly anchored to the ecologist's needs, while trying to develop some new methodology for the ecologist to use. In the current jargon he believes that the applied statistician should do strategic as well as applied research.

JOCELYN R. DALE is a scientist with the Applied Mathematics Division, DSIR, Auckland, New Zealand, where her work involves applications of statistics to horticulture, entomology and plant diseases. On study leave recently at the Department of Mathematics, Imperial College, London she completed a Ph.D. thesis on statistical methods for ordered categorical data and sparse contingency tables.

KEITH V. DARBY graduated from the City University, London, with an honours degree in Actuarial Science, in 1978. He obtained his M.Sc. in Statistics at the University of Kent at Canterbury in 1979, writing dissertations on species diversity and spatial analysis of ringing data, both using data from the British Trust for Ornithology.

After this, in collaboration with the British Trust for Ornithology, he prepared a Ph.D. thesis entitled "A Statistical Examination of British Bird Observatories Data" and from this work arose the paper presented in this edition. After working as a Research Associate and as a Lecturer in Statistics at the University of Kent, he moved to industry as Senior Statistician at Imperial Tobacco Ltd., Bristol.

Details of the Authors

ANDREW DOBSON obtained his first degree in the Department of Zoology at Imperial College, London University, and prepared his D.Phil. thesis on "The Mortality Rates of British Birds" at the Edward Grey Institute, Zoology Department, Oxford University. This thesis was based on an analysis of data collected by the British Trust for Ornithology. Since then he has been working on a number of mathematical problems concerned with the population dynamics, genetics and coevolution of parasites, pathogens and their hosts, initially at Imperial College, London and now at the Department of Biology, Princeton University.

PETER W. GREIG-SMITH went to Sussex University in 1976 to begin his Ph.D.-project, after taking a B.Sc. degree in Zoology at the University of Aberdeen, and spending several periods studying tropical birds (in New Guinea, Ghana, Nigeria and the Seychelles). The thesis was concerned with field studies of the behaviour and ecology of a population of Stonechats on lowland heath at Ashdown Forest. Working for the Ministry of Agriculture since 1980, he is currently occupied with research into mechanisms of food selection by Bullfinches, in order to help the development of new methods of preventing damage to crops, using chemical deterrents.

GARY L. HENSLER received a B.S. degree in Mathematics from the University of Oklahoma and M.S. and Ph.D. degrees in Mathematics and Statistics from the University of Illinois. He has taught Statistics at Syracuse University and at the University of Maryland. Having become interested in birding and ornithology while in graduate school, he started working for the United States Fish and Wildlife Service at the Patuxent Wildlife Research Center in 1976. He has published research on environmental contamination and endangered species as well as on the Mayfield Method.

COLLEEN HYSLOP is a research biologist with the Canadian Wildlife Service, Ottawa. She began working with the Migratory Birds Branch in 1980 and heads the Canadian Bird Banding Program.

ROBERT F. JANZ was born in Indonesia in 1953. After spending nine years of his childhood in Brisbane, Australia, he moved with his parents to The Netherlands and attended High School in Amsterdam. He enrolled at the Free University, Amsterdam, and chose to study Biology because of his love for nature. At about the same time (1970) he became involved in an investigation into the population dynamics of the Grey Heron (*Ardea cinerea*) first as a ringer, and later also as a thinker. The biology study and the practical side of an investigation of migratory birds initiated an interest in the analysis of ringing data and birdwatching data. This interest took him to Groningen to study Theoretical Biology with Dr. J. Reddingins, the ornithological side of the study being covered by Dr. R. Drent. After finishing his studies (in 1978) Robert first worked as a biology teacher in a school for adults. In 1980, he received a grant to investigate methods of analysing ringing data with the emphasis on subjective inference. This investigation was cut short by the acceptance of a job at the Computer Centre of the State University of Groningen. His main activity there is the development of courses in the use of computers.

At first he hoped to continue with his study of subjective inference in his own time, but his present occupation has proved to be too time-consuming to allow him to keep up with "the state of the art". He has therefore abandoned the study.

PETER C. LACK obtained his Ph.D. from Oxford University conducting fieldwork in Kenya (November 1974 to January 1977). Following a variety of short-term jobs, he joined the British Trust for Ornithology in September 1980, to be National

Details of the Authors

Organiser of the Winter Atlas Project.

KEN H. LAKHANI was born in 1934 in Uganda. He came to England in 1957 to study law, and became a Barrister (Lincoln's Inn) in 1960. He decided to settle here, and changed careers by joining The Nature Conservancy, London, in 1961. The Nature Conservancy (NC) became a part of The Natural Environment Research Council in 1965, and in 1973 the research wing of NC became the Institute of Terrestrial Ecology (ITE).

Ken became a member of the Institute of Statisticians in 1965, and was awarded a B.Sc. (Special) degree in Statistics by the University of London in 1968. Since 1968, Ken has been the biometrical consultant for some thirty senior scientists at one of ITE's major research stations - Monks Wood Experimental Station, Abbots Ripton, Huntingdon.

Monks Wood staff generate a wide variety of quantitative-ecology problems which vary from the botanical, zoological, ornithological and computational. Ken enjoys working in all areas of statistical ecology but his primary interest is in the field of population dynamics. He has published a number of papers, most of them jointly with biologists, and these include studies on earthworms, mosquitoes, shrimps, juniper fauna, swallowtail butterfly, cinnabar moth, grassland invertebrates, and bird survival. Ken is a firm believer that in most areas of ecology it is necessary for the biologist and the biometrician to act collectively and collaboratively as 'one organism'.

JEAN-DOMINIQUE LEBRETON graduated in Applied Mathematics at the University of Grenoble (France) in 1971. He obtained a Master's degree (1974) and a Ph.D. (1981) at the University of Lyon, France. His research work is devoted to population dynamics models, bird population biology (Black-Headed Gull), and statistical ecology.

BRYAN F. J. MANLY was born in London in 1944. He took a B.Sc. (Hons) in Applied Mathematics at the City University, London (1966). Following eighteen months working as a statistician for Fisons Ltd., he then took up an Assistant Lectureship in Mathematics at the University of Salford, Lancashire in 1967. This was followed by teaching posts at the University of Papua and New Guinea (1970-73), and the University of Otago, New Zealand (1973 to the present). In 1981 he was a Visiting Associate Professor in the Department of Experimental Statistics at Louisiana State University in Baton Rouge, U.S.A.. His present position is Associate Professor in Mathematics at the University of Otago.

From 1980-83 he was a Council Member of the International Biometrics Society. For 1984-85 he is the Secretary of the Australasian Region of this society. He is a Fellow of the Royal Statistical Society, and a member of the Society for Population Ecology, the New Zealand Statistical Association, the Royal Society of New Zealand and the Statistical Society of Australia.

His research interests are mainly in statistical applications in the area of animal ecology, particularly the analysis of mark-recapture data, the construction and analysis of life tables, and detection and measurement of natural selection. Lately he has also been working on the analysis of archaeological data.

BYRON J. T. MORGAN obtained his B.Sc. from Imperial College and his Ph.D. from Cambridge University. His work as a statistician has included a short stay at the World Health Organisation Cancer Research Centre at Lyons, France, three years at the Applied Psychology Unit, Cambridge, England, and one year with the Division of

Details of the Authors

of Mathematics and Statistics of CSIRO, in Melbourne, Australia. He joined the University of Kent in 1972, where he is currently Reader in Statistics. He obtained the 1982 George Snedecor Award for the best publication in Biometry.

MALCOLM D. MOUNTFORD obtained his B.A.(Oxon) in Mathematics (1952), followed by a Diploma in Statistics (1953). From 1953-1973 he was biometrical consultant with the Nature Conservancy and subsequently with its offshoot, the Institute of Terrestrial Ecology. His interests include: the role of variation in the functioning of biological processes; population growth and regulation; statistical aspects of territoriality; estimation of the abundance of animal populations; numerical classification.

PHILIP M. NORTH, for many years a keen birdwatcher, obtained his B.Sc. (in Mathematics) and his M.Sc. (in Statistics) at the University of Sussex, after which he taught Mathematics and Statistics in schools in both England and Holland. He returned to England in 1975 to take up studies at the University of Kent for his Ph.D. on "Statistical Methods in Ornithology". This research was carried out in collaboration with the British Trust for Ornithology. His research interests have remained in this area, as well as broadening to include other ecological, biological and medical applications of Statistics. He is a member of the Committee of the British Region of the Biometric Society, within which he is also Secretary of the Mathematical Ecology Group. After two years as a Lecturer in statistics at the University of Kent he moved into its Applied Statistics Research Unit in 1980, and is now its Director.

DAVID T. PARKIN obtained his B.Sc. in Zoology from Durham University and his Ph.D. in Zoology from Manchester University. He was a Demonstrator in Zoology in Edinburgh University (1967-71), and a Lecturer in Genetics in Nottingham University (1971-79) where he is now Senior Lecturer. His research interests are: evolutionary and population genetics, especially of birds. He is currently analysing the genetic structure of House Sparrow populations within Britain and around the world. He is also interested in the genetics of Snow Geese, and the relationships between population structure and genetic variation.

ALLAN REESE went to university with the intention of reading Zoology but became more interested in analysing data than in memorising facts. After transferring to Computer Science, he graduated and worked with mini-computers in industry for a year before taking an M.Sc. in Computational and Statistical Methodology.

Since 1976 he has worked in university computing services, first at Sheffield then at Hull, with responsibility for making statistical methods available to the university community, and educating potential users to make sensible choices.

He is particularly concerned that the computer is viewed as a tool and a means to an end, so that writing a computer program does not become the end in itself. He is also concerned about standards of programming and documentation of programs made available for general use.

He is a member of the British Ornithologists' Union, the British Trust for Ornithology and the Institute of Statisticians.

BRIAN RIPLEY became Professor of Statistics at Strathclyde University in 1983 after seven years as Lecturer and Reader at Imperial College, London. His best-

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known work is in spatial patterns and simulation. Natural History is a hobby which has motivated applications in ecology. He represents the Royal Society on the International Council for Bird Preservation.

PETER ROTHERY obtained a B.Sc. in Mathematics in 1968 (Dunelm) and a Diploma in Mathematical Statistics (Cantab) in 1969. He was biometrical consultant with the Nature Conservancy (1969-73) and then with the Institute of Terrestrial Ecology. His interests include: statistical problems in point-quadrant sampling; the non-parametric measurement of intra-class correlation; the analysis of spatial patterns; population growth and regulation; estimating survival rates of birds; Monte Carlo methods.

He is a member of the editorial board of the Journal of Ecology and a regular statistical referee for the journal.

GEORGE A.F. SEBER took a B.Sc. degree in Mathematics and Physics and an M.Sc. degree in Mathematics (1960) at Auckland University, New Zealand, and a Ph.D. degree in Statistics from the University of Manchester, England (1963). He taught Mathematics and Statistics at the London School of Economics for two years before returning to Auckland as a lecturer. In 1971 he was Director of the Biometrics Unit at Otago University, and became a Professor of Mathematics and Head of the Statistics Unit within the Mathematics Department at Auckland in 1973. Since then he has had a spell of six years as Head of the Mathematics Department.

His research and writing interests are in estimating animal abundance, human blood genetics and paternity testing, linear and non-linear models, and multivariate statistical analysis.

GRAHAM UPTON was born in 1944 in Edinburgh. He is an enthusiastic compiler of lists of birds. He was formerly a lecturer in Statistics at the University of Newcastle-upon-Tyne and now lectures at the University of Essex. His most recent foray into ornithological statistics involved the development of a model of territory reoccupancy (*Biometrics*, 37, 113-128). He is currently engaged in writing a book on the analysis of spatial data.

MICHAEL B. USHER studied forestry as an undergraduate at the University of Edinburgh, specialising in Silviculture and Forest Zoology, though his background was Mathematics, with no Biology at all. Having graduated, he returned to studying Mathematics with the aid of a Nuffield Foundation Bursary. His Ph.D. work was on the population ecology of soil Collembola in the Black Wood of Rannoch.

Since 1967 he has been a lecturer, then senior lecturer, in the Department of Biology, University of York, largely responsible for developing and organising the M.Sc. course in 'Biological Computation'. His research interests are in both population/community ecology of soil arthropods and in wildlife conservation. Two sabbatical periods were as follows: one for two years in Ghana, West Africa, as adviser on termite research, and the other for three and a half months in the Antarctic working on terrestrial ecology.

RICHARD WHITE-ROBINSON obtained a B.Sc. in Ecology from Edinburgh University. He is currently completing a Ph.D. thesis on the applied ecology of Canada Geese in lowland England. He has worked on Barnacle and Brent Geese with Dr. Mynfyn Owen of the Wildlife Trust, who is his joint supervisor with Dr. D. T. Parkin.

Details of the Authors

MARK WILLIAMSON has spent almost all his life in and near Universities, being brought up at Oxford and Yale. His first degree and his doctorate are both from Oxford, in Zoology, where, as a departmental demonstrator, he worked on the theory and practice of population ecology and population genetics, mostly studying snails and slugs. In 1958 he moved to Edinburgh to take charge of the Herring section of the Scottish Marine Biological Association Oceanographic Laboratory, a job primarily concerned with plankton ecology. In 1962 he moved to the Department of Zoology in Edinburgh University as a lecturer.

The University of York started in 1961, and Mark Williamson was the first biologist appointed, in 1963, moving to York in 1965 as Professor and Head of Department, which he has been ever since. He has been a visiting professor at the University of California (Scripps Institution of Oceanography) and the University of Victoria, in British Columbia (Department of Biology). He is the author of *The Analysis of Biological Populations* (1972) and *Island Populations* (1981,1983).

THE GENERAL CONTEXT OF STATISTICS IN ORNITHOLOGY

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SUMMARY

This paper sets the scene for those that follow. Particular attention is paid to analyses of ring recovery, census and migration data. Ornithological data are being collected on a wide scale, and they are seen to pose challenging problems of interpretation and modelling.

Keywords: ORNITHOLOGY; RING RECOVERY; CENSUS DATA; MIGRATION DATA; STATISTICAL ANALYSIS; MODELLING

1. INTRODUCTION

The aim of this paper is to provide a general setting for those that follow. It is not possible in this one paper to provide a comprehensive review of Statistics in Ornithology. Studies in ornithology are inherently statistical, ranging from the collection and management of large sets of national census data, to much smaller experimental investigations. Both large- and small-scale studies are represented in the papers of this volume.

In Britain the British Trust for Ornithology (B.T.O.) co-ordinates most of the major studies of British birds. These include the Common Birds Census, discussed later by Mountford (1985), the national ringing scheme (resulting in data of the kind analysed in papers of Section C and in information on bird movements) and the bird observatories network, discussed later by Darby (1985). In Britain, ornithological studies are also carried out by, amongst others, the Institute of Terrestrial Ecology, the Royal Society for the Protection of Birds and the Edward Grey Institute of Field Ornithology, the last being notable especially for the long-running study of the Great Tit (*Parus major*) population in Wytham Wood, Oxford. Many of the available data sets contain counts, from censuses or surveys, while others, such as ringing data, include much additional biometric information. A study such as the Nest Record Scheme (organised by the B.T.O.) provides detailed information on breeding habits.

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Similar studies take place throughout the world, as in, for example, the North American Breeding Bird Survey and the Christmas Bird Count, which respectively provide counts of breeding and wintering birds in North America. The practice of hunting birds in North America can result in data of a kind that one does not encounter in the United Kingdom (see the papers by Boyd and Hyslop, 1985, and Conroy, 1985, which follow). In addition to large-scale surveys, attempts have been made to record the observations made by ordinary bird-watchers (see Darby, 1985, and Reese, 1985, later). While the data resulting from such attempts would inevitably be treated with caution, serious deficiencies may exist in any data set due to observer variability. Kepler and Scott (1981) point out the alarming 'window species' found with even trained observers. These are species which they consistently fail to record even though conspicuously present. Ramsey and Scott (1981) recommend testing observers for hearing ability, but it is clear that such ground rules cannot be generally followed. In some cases (see Darby, 1985, and North and Morgan, 1979) factors such as weather may be directly included in data analysis, but more typically the influence of weather conditions is ignored, as is also the effect of sampling terrain. Ripley (1985) later develops methodology for dealing with the difficult edge-effects problems which inevitably arise in census studies.

Digests of data can be found in popular books such as Fisher and Flegg (1978) and Perrins (1974), but here too caution is needed in interpretation. For example, in Perrins (1974, p.129), adult mortality rates and longevities of some common birds are presented which mask the uncertainties and statistical problems which accompany the computation of mortality (survival) rates (see Lakhani, 1985, later).

Historically, the first main impact of statistics in ornithology was in the analysis of ring recovery data, and it is no coincidence that Section C of this volume is the largest. The background here is provided in the next section. We continue with a discussion of the analysis of census and migration data before concluding with general remarks about the future.

2. ANALYSIS OF RING RECOVERY DATA

2.1 Survival Studies

For many years now birds have been ringed (or banded in American terminology) and recoveries of rings some time later used to provide information on the birds' movements and survival. Indeed, it is through such information that much of what is currently known about birds' journeys on migration was discovered. Such knowledge

The general context

was perhaps, primarily what was being sought in the early days of ringing, and is still of immense interest today. Of course, ring recoveries also provide information on birds' survival and it is here that the statistical analysis of ring recoveries has been most extensively developed. However, even now there still remain difficulties, which can perhaps be overcome only by supplementing the ringing of young with further ringing of other age classes (see, for example, Brownie *et al.*, 1978) or by some further field information (Lakhani and Newton, 1983; Janz, 1985).

The pioneering work in the estimation of bird survival rates from ring recoveries was done by Lack (1951). His approach is only applicable to 'complete' ring recovery data, in the sense that no more rings are expected to be recovered in the study in question. This work was extended later by Haldane (1955), to be applicable also to 'incomplete' data sets, where some rings, on birds still alive, remain to be recovered at some time in the future. However, both models are only suitable for adult birds and deal only with ring recoveries from dead birds, which are the most common recoveries. Some biologists still use these methods, despite the fact that there has been considerable development of relevant statistical methodology over the past fifteen years.

Cormack, in the statistical appendix to Fordham and Cormack (1970), concerning a study of the Dominican Gull, allowed in his model for age-specific survival rates, as opposed to the constant annual adult survival assumed by Lack (1951) and Haldane (1955). Cormack also considered a full maximum likelihood approach incorporating the information on the number of birds ringed, as well as numbers recovered. Seber (1971) developed a computationally attractive approach to the age-specific survival analysis (but see North and Cormack, 1981, for a critical appraisal of the method) and considered a calendar-year-specific case elsewhere (Seber, 1970a). Much of the further development of the methodology was carried out in the U.S.A., and age-specific and year-specific effects for the survival and/or the recovery rates were built into the various models developed by Brownie and Robson (1976) and by Brownie *et al.* (1978). The paper in this volume by Dobson (1985) considers age-specific survival rates.

We may note again here the point made in the introduction that most of the work from North America relates to hunted wildfowl, in contrast to studies in Britain, for example, where most ring recovery data arise from birds found dead, rather than shot. Recently, statisticians have expressed concern about the validity of the assumptions underlying the models used to analyse ring recovery data. In particular the assumption of a constant recovery probability has been questioned by Burnham and Anderson (1979) and Anderson *et al.* (1981) address this problem, while Lakhani (1985)

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(see also Lakhani and Newton, 1983) considers the non-identifiability of the survival estimates, even if all the other model assumptions hold, and warns about the possibly misleading effect of the generally used constraint, *viz.* that the annual survival probabilities for the two or more oldest year groups are equal. The problem considered by Lakhani illustrates the benefit of having additional information available, in this case in the form of a likely range of values for the ring recovery probability. Discussion with ornithologists suggests that in practice it might be possible to obtain information about the likely range of values for the ring recovery probability, so that an approach like that described later by Janz (1985) could then be useful. More research is needed into deciding which kind of further information is most profitable and how best to incorporate it to derive reliable estimates.

The ring recovery analyses that have been discussed so far in this section relate to situations where there is at most one recovery for each bird, usually when the bird is dead. However, in the wider area of animal ecology, the need to assess the abundance of animal populations has led to the development of capture-recapture methods when multiple recapture data can be collected. This has not in the past often been the case in ornithological applications. However, recently there have been published analyses of multiple recaptures of birds, and this volume contains further examples (See Section C.)

Boyd (1956) applied capture-recapture methods to data on Pink-footed Geese (*Anser brachyrhynchus*), and Orians and Leslie (1958) did so in a study of Manx Shearwaters (*Puffinus puffinus*) (see also North, 1981, for further modelling of multiple recapture data for this species). Long (1975) applied a capture-recapture approach to Reed Warbler (*Acrocephalus scirpaceus*) data. More recently, Buckland (1982a) described an approach that can combine both multiple recapture and ring recovery data. Its use is illustrated with data on Fulmars (*Fulmarus glacialis*) and Galahs (*Cacatua roseicapilla*). In this volume, Seber (1985) and Seber and Manly (1985) provide further useful extensions to the capture-recapture methodology.

'Recaptures' of birds may sometimes only be resightings as, for example, in the study of colour-ringed Fulmars, reported by Dunnett, Anderson and Cormack (1983) and by Cormack (1973). Buckland, Rowley and Williams (1983) discuss the use of resighting data for Galahs, while Brownie and Robson (1983) have generalised the Jolly-Seber (Jolly, 1965; Seber, 1965) model to estimate time-specific survival rates from resightings, and illustrate their approach with data on the Semi-palmated Sandpiper (*Calidris pusillus*).

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In this volume Clobert, Lebreton, Clobert-Gillett and Coquillart (1985) also consider the use of sightings as well as recaptures. Pollock (1981a) has earlier developed capture-recapture models allowing for age-dependent survival and capture rates, and illustrated them with an application to Giant Canada Geese (*Branta canadensis maxima*). In the present volume Parkin and White-Robinson (1985) report on a study of Canada Geese (*Branta canadensis*). Age-dependent survival is also considered here by Rothery (1985) in his study of Hen Harriers (*Circus c. cayneus*).

Other recent work by Pollock (1974, 1975) and Buckland (1982a) has concentrated on the problems of unequal survival and catchability. The latter is likely to be a problem in some ornithological applications. For example, MacArthur and MacArthur (1974) and Manly (1977a) have pointed out that standard capture-recapture methods should not be used with data resulting from birds being trapped in mist nets. This is because birds which have been captured and released tend to avoid mist nets from then on, and because birds caught in the nets may come from a mixed population of resident and migrant birds. For example, Buckland and Hereward (1982) estimated that immature Yellow Wagtails (*Motacilla flava flavissima*) at a pre-migratory roost, which had not been captured before, were probably six or seven times more likely to be netted than previously captured birds.

Cormack (1985) later describes how GLIM can be used to fit log-linear models to capture-recapture data, and illustrates the approach with a number of ornithological examples, including an application to data described by Cheke (1985) in this volume.

2.2 Movement Studies

Ring recoveries have provided much valuable information on birds' movements but statisticians have not developed methodology here to anything like the extent that they have for survival studies. This is partly because many problems exist with the data. For a start, recovery rates are typically very low, and may vary over a bird's range. Many of the possible problems involved are met in a study of Razorbills (*Alca torda*), reported by North (1980a), following a study of the same species by Lloyd (1974). For a discussion of ring recovery data for various auks see Mead (1974). Other quantitative studies of seabird movements from ring recoveries are by Coulson and Brazendale (1968) for the Cormorant (*Phalacrocorax carbo*) and by Birkhead (1974) for the Guillemot (*Uria aalge*). Later North (1985) discusses random-walk models which might be used qualitatively to describe bird movements, based on the evidence of ring recoveries.

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The problem of the distinction between migration and dispersal is likely to prove difficult to resolve in many cases. However for some species the situation is quite clear-cut, and Kendall (1974) has elegantly shown how simple migration strategies can result in successful migration passages.

3. ANALYSIS OF CENSUS DATA

Ornithological censuses provide another rich area for the involvement of statisticians, as can be seen from the Symposium on Estimating numbers of Terrestrial Birds, held at Asilomar, California in 1980. (See Ralph and Scott, 1981.)

The British Common Birds Census has attracted the attention of a number of statisticians in recent years. The basis of the census is a mapping technique which is used to estimate the numbers of territory-holding males of the commoner species on the census plots, using results accumulated over a number of visits to each plot during the breeding season by voluntary observers (one observer per plot). The estimation of territory numbers and relative positions can be viewed as a problem in cluster analysis, and is currently carried out by hand. Attempts to produce an automated objective approach to this estimation problem have been reported in a series of recent papers by North (1979, 1980b, e.g.). Although it is primarily the numbers of territories that are of interest here, it is also useful to have information on the relative positions of territories. At a simple level these can be shown to correlate well with habitat features, as would be expected - see Morgan and North (1980). However, spatial analysis is also of interest. The paper later by Ripley (1985), giving an analysis of nest spacings, is a current example. Others are by Bartlett (1974), who considered Swallows (*Hirundo rustica*), perching on a telegraph wire, and the distribution of nests of two species of gull. Besag and Diggle (1977) present an application of a Monte Carlo test to data relating to Blackbird (*Turdus merula*) migration, and also use Monte Carlo testing to investigate the possible interaction between nest locations and laying dates in a colony of Kittiwakes (*Rissa tridactyla*). Ripley (1977) presented an application of his methods to data on nest sites of birds of prey, though Cormack (1977) pointed out the care that needs to be exercised here, since spacing between nests may simply be imposed by the availability of suitable nest sites.

The aim of the Common Birds Census is to monitor the fluctuations in population levels of the commoner species in Britain, and the census is carried out in a number of different types of habitat, but most commonly on farmland or in woodland. Each year, a summary of between-year comparisons for just two consecutive years, for each

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of the species monitored, has been presented in Bird Study (this is being continued from 1984 in B.T.O. News). Upton and Lampitt (1981) describe a model for investigating such between-year comparisons, while in the present volume Mountford (1985) discusses an index of population change, illustrated with applications to Common Birds Census data (see also Mountford, 1982). Simple models to describe annual numbers of territories, for single species, over a period of successive years, are discussed by North (1983). Applications of Taylor's power law (Taylor, 1961) to Common Bird Census data, for individual species, have recently been described by Taylor, Woiwod and Perry (1978, 1980); see also Taylor and Woiwod (1980). Bulmer (1975) provides a test for density-dependent effects.

Most of the work that has been done in this area to date has concentrated on single species at a time. But the communities being studied on the census plots are made up of many species, and multi-species approaches to analysing the data seem desirable and overdue. A simple multi-species comparison between a pair of consecutive years is described by North (1982). Later, Buckland and Anderson (1985) present a multivariate analysis of atlas data.

For many years ecologists have been interested in species-area relationships for many-species communities and in the measurements of species diversity. The papers in this volume by Usher (1985) and by Williamson (1985) examine species area relationships, which provide a summary approach to the analysis of data from many-species communities. Related material is to be found in Reese (1985).

Another type of survey much used by ecologists for counting animals, birds or plants is the line transect survey. Although this type of survey is not represented amongst the papers in the present volume, it is a topic which has interested statisticians considerably in recent years. The monograph by Burnham *et al.* (1980) provides a useful review of the topic. Recently, the circular plot technique has been increasingly used by ornithologists. Here, the observer remains stationary and counts birds around him/her, for a number of selected positions. Statistical development is provided by Buckland (1984).

4. VISIBLE MIGRATION

The discussion on movement in the preceding section covers the evidence provided by ring recoveries. However, information on migration can also be obtained by direct observation. At one extreme, in Europe, this can take the form of the spectacular

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visible migration of birds of prey at Falsterbo and over the Bosphorus, for example. In the 1960's considerable use was made of radar to study the pattern of bird movements, across such passages as the North Sea (see Lack and Eastwood, 1962; Eastwood 1967).

In Britain data have been collected for many years on visible migration past or through the British bird observatories, all situated on the coast. These data are collected both from sea watches and from observations on the land surrounding the observatories. Darby (1985) describes the use of linear discriminant analysis to investigate the relationship between migration counts and weather conditions.

With the observatory migration work, there is a link with the census work described earlier. The Common Birds Census aims to produce a population index for each of the species monitored, and one can also consider constructing a population index from migration data. If this can be shown to be useful, it might enable species which are unsuitable for monitoring by the census mapping method to be monitored by the migration index. Recently, similar work has also been done in North America (see Hussell, 1981).

Part of the data collection procedure at the observatories consists of sea watching. Sometimes it can be difficult to count birds passing by at sea, and it can be especially difficult, in situations where movements are taking place in both directions, to assess the net number of birds involved. Upton (1985) considers this problem later.

5. DISCUSSION

The papers by Cheke (1985), Dale (1985) and Greig-Smith (1985) of Section A all deal with particular small-scale investigations, as do those by Lack (1985) in Section B, and by Hensler (1985) in Section C. The data set considered by Dale presents particular problems of analysis on account of the paucity of the available data. Many other studies can also suffer from lack of data, for example due to the small recovery rates of dead ringed birds. To some extent these problems will be alleviated as the studies progress through time.

On a different point, Buckland (1982b) and Burnham (1981) have emphasised the deficiencies that exist in current statistical methods and analysis in ornithology, with new methodology quite often taking many years after it is established, before

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it is used in the field. Again, this is a situation which will improve with time, but clearly there needs to be better communication between statisticians and ornithologists. It is hoped that this volume will help in this respect.

ACKNOWLEDGMENTS

We are grateful to Stephen Buckland and Ken Lakhani for their very helpful comments on an earlier draft of this paper.

SECTION A

GENERAL: COLOUR, FEEDING, MOVEMENT AND MIGRATION

WINTER FEEDING ASSEMBLIES, WING LENGTHS
AND WEIGHTS OF BRITISH DUNNOCKS

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SUMMARY

1. Analyses of capture-recapture data from a winter feeding assembly of Dunnocks showed that, on any one day, between 40 and 80 birds were involved but that during the course of the winter there was a substantial turnover amongst the individuals comprising the population.
2. Analyses, according to season and region, of data on wing lengths and weights of British Dunnocks showed that:
 - (a) Dunnocks gain weight in winter. On average they were about 1 g heavier in winter than in autumn;
 - (b) There was a south to north trend of decreasing wing length; and
 - (c) Weight was related to wing length. Autumn and winter data from all regions studied could be fitted to a linear regression with a common slope. However, because of the increases in weights in winter the intercept of the regression for this season was significantly higher.

Keywords: DUNNOCK, CAPTURE-RECAPTURE, FEEDING ASSEMBLIES, WING LENGTH, WEIGHT, ANALYSIS OF VARIANCE, LINEAR REGRESSION, ENGLAND, SCOTLAND, REGIONAL AND TEMPORAL VARIATION.

1. INTRODUCTION

The Dunnock (*Prunella modularis*) is usually thought of as an unobtrusive, often solitary species rather than as a bird with a complex social organisation. However, Campbell (1952, p.88) remarked that Dunnocks "chase about in parties of three" and Snow (1965) saw that they often consorted in trios during their breeding seasons. Furthermore, it is now known that they are sometimes co-operative breeders with more

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than two birds tending a brood and that the territories of males may overlap (Birkhead, 1981; Snow and Snow, 1982). Indeed, two males' territories may sometimes overlap almost completely with one male dominant over the other (Davies, 1983; Snow and Snow, 1983). Also, groups of up to four Dunnocks defend feeding sites in winter (Birkhead, 1981) and in this report I describe a much larger community which formed a winter feeding assembly.

A capture-recapture bird-ringing programme was conducted in order to estimate the size of the population forming the assembly. The data obtained have been analysed using a novel method (Cormack, 1981) by Professor Cormack (1985, pp.243 to 273) who has explained the computational procedures and presented the ensuing estimates. It is the purpose of this contribution to provide the biological background to Cormack's calculations.

During the course of the capture-recapture study, biometric data on the trapped birds were recorded and, to see if this population was representative of British Dunnocks as a whole or if there were regional differences, the data were compared with samples from a variety of sites. In addition to investigating regional differences, seasonal changes, the weight changes of individual birds and relations between wing length and weight were also examined. These subjects are of interest since recent authors have separated the sexes of Dunnocks according to weight (Birkhead, 1981), have argued behavioural points such as the dominance in social interactions of heavier (Birkhead, 1981) or longer-winged birds (Davies, 1983) and have claimed that males are longer-winged than females (Snow and Snow, 1982; Davies, 1983).

2. METHODS

Birds were trapped in mist-nets, ringed, measured, weighed and released. Wing lengths were recorded to the nearest 1.0 mm using the maximum chord method (B.T.O., 1972) and the birds were weighed to the nearest 0.1 g in plastic containers suspended from 30 g Pesola spring balances. The birds were trapped between 1966 and 1982 at various sites in the following three regions: (1) Scotland (St. Andrews, Fife; Dundee and Brechin, Angus; Arisaig, Invernesshire), (2) North England (Bramham, Leeds, Ripon and Sheffield, Yorkshire; Nantwich, Cheshire; Lincoln, Lincolnshire) and (3) South England (Bramley, Hampshire; Dorking, Surrey; Weymouth, Dorset; Norwich, Norfolk; Aldbury, Hertfordshire; Newick, Sussex). Most of the birds in regions 1 to 3 were caught at St. Andrews, Bramham and Bramley respectively. A brief description of the two last sites, and details of parasites recorded from birds caught

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at them, have appeared elsewhere (Cheke *et al.*, 1976), and the characteristics of the Bramham site are described in the next section.

Juvenile birds still in their first plumage were noted but no attempts were made to estimate the ages of Dunnocks in post-juvenile plumages since the usual method, differences in eye-colour (*cf.* Dale, 1985) is unreliable after November (Spencer and Mead, 1978) and the degree of skull ossification can only be used as a guide (Svensson, 1975, p.73). No attempt was made to record systematically the sex of birds since sexing of Dunnocks is only reliable during the breeding season when incubation patches or cloacal protuberances may be observed (Svensson, 1975, p.73).

3. WINTER FEEDING ASSEMBLIES

Here we concentrate solely on the birds caught at the Bramham site. During the winter of 1972-73 a loose group of twenty or more Dunnocks was regularly seen feeding on a mound of rotting potatoes at Black Fen ($53^{\circ}51'N$, $01^{\circ}22'W$) in Bramham Park near Wetherby in Yorkshire. Since such large assemblies of Dunnocks are unusual (Witherby *et al.*, 1943, p.210, state that the species is not really gregarious at any time) a capture-recapture sampling programme was conducted to assess the size of the population involved.

The potatoes had been tipped down the side of a steep bank about 6 m high and 40 m long beneath a track running between two stretches of mixed woodland. At the base of the mound the trees were predominantly birch (*Betula pendula*), which were separated from a young conifer plantation, some open ground and mature deciduous woodland by a small stream.

The Dunnocks were not feeding in cohesive flocks but they spread out to feed all over the surface of the mound. The assemblies were restricted to the potato mound and were never seen elsewhere. No obvious signs of aggression or territoriality were noted but detailed behavioural studies were not conducted, partly because the birds were alert and hurriedly dispersed when an observer came within their view. Dunnocks are predominantly insectivorous in summer but switch to a largely vegetarian diet, mostly seeds, in winter (Witherby *et al.*, 1943, p.216) so the potatoes themselves may have represented a superabundance of food, but the birds were probably taking many of the insects which had also been attracted to the mound or had been reared in it.

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The Dunnocks were caught in mist-nets totalling approximately 200 m² in area, some of which were positioned in a line along the base of the potato mound. The nets were erected in the same places on each sampling occasion but the times during which they were in operation varied (Table 1). Table 1 also gives the numbers of birds trapped on each sample date which were not caught again during the 1972-73 winter and the capture histories of those individual birds which were re-trapped. These data can easily be re-arranged into the form presented and analysed by Cormack (1985, pp.253 to 259) but they are given in more detail here since he has stressed the usefulness of his method in the context of individual birds and this point will be illustrated later.

Eighty different individual birds were caught (Table 1) but it is probable that more visited the site during the course of the winter since it is most unlikely that all the birds involved were trapped. However, Cormack's analysis clearly showed that fewer than 80 birds were present on any one day (Table 1). Cormack also stressed that although the population estimates were similar for each date there was evidence for a substantial turnover amongst the birds. Certainly there was immigration into the locality during the autumn, as few Dunnocks were present at the site during the preceding summer and the site became much less populated the following summer, but the conclusion that changeovers of birds were occurring throughout the winter was unexpected. However, although there was no evidence to suggest that the weather was an important factor in the present case, it is possible that the samples discussed coincided with periods of flux as Witherby *et al.* (1943, p.211) state that there are indications that the species makes weather-related movements in winter, but most long-distance displacements take place in autumn (see in particular Williamson, 1962) and spring. Birkhead (1981) found that his birds established winter territories by late October and then became sedentary from October to February.

If the assumption of constant trapping effort is accepted for the four later sampling dates, which is not unreasonable in view of the similar times expended netting on these days and Cormack's finding that changes in the capture probability estimates do not correspond with variations in the sampling efforts, then it can be concluded that the assemblies consisted of between 47 and 70 Dunnocks. However, if the assumption of constant sampling effort is abandoned, the estimates range from a population of 40 to one of 80 with a 100% increase occurring within a week during February. The timing of the effects of immigrations, emigrations and death on the population size differ in the two cases but the population estimates are surprisingly similar in range which, intuitively, gives grounds for confidence in their accuracy in addition to Professor Cormack's objective tests of acceptability. So it seems

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Table 1

Details of the numbers of Dunnocks caught and re-trapped on five sampling dates at the winter feeding assembly in Bramham Park and the calculated population estimates

Date	7 October 1972	18 February 1973	25 February 1973	17 March 1973	14 April 1973
Trapping Times	1500-1815	1130-1800	1230-1830	1000-1900	1200-2000
Total Times (Hrs.)	3.25	6.5	6	9	8
Number of Birds Ringed Which Were Not Caught Again	10	13	11	16	14
Ring Numbers and Capture Histories of Birds Ringed (+) and Later Re-Trapped (*)					
JK40396	+			*	
JK40399	+	*			
JK63301	+	*	*		*
JK63307	+	*			
JJ40370	+	*		*	
JK63364		+	*		
JK63365		+	*		
JK63366		+		*	
JK63367		+		*	*
JK63372		+		*	
JK63375		+	*	*	*
JK63387		+	*	*	
JP93702			+	*	
JP93707			+		*
JP93721			+	*	
JP93732				+	*
Cormack's Population Estimates (see pages 256 and 259)					
Constant Trapping Effort	-	61.0	53.4	69.8	47.4
Varying Trapping Effort	-	40.0	79.17	51.30	-

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that about 60 Dunnocks were regularly coming to one place to feed together and that some of these birds remained throughout the winter while others came and went.

Cormack (1981) explained the *a priori* assumptions about the populations under investigation which constrain the capture-recapture method. One of these is that there can be no temporary emigration from the study population i.e. the animals must not leave the area and then return during the sampling programme. Although there is no proof that this assumption was not violated in the present study, neither is there any clear evidence for any temporary emigrations and the suggestion by Cormack (1985) of substantial movements by the birds only became apparent *a posteriori* in the wake of his calculations. As far as some of the other assumptions were concerned, Cormack's analyses suggested that trap dependence was unimportant but drew attention to possible heterogeneity in the catchabilities. Of the four birds which he singled out as being caught more frequently than expected two (JK63301 and JK63387) were also involved in instances of being caught more than once on the same dates (Table 2). Although these may just have been birds returning repeatedly to the site they could also have been the possessors of territories, which either included parts of the feeding site or abutted onto it, which they were unable to defend successfully against an influx of opportunistic conspecifics. Snow and Snow (1982) mentioned that territory-holding Dunnocks can dominate intruders when they are near them, but not drive them out. Some of the birds may have been temporary residents while in transit from one area to another or else have been local birds congregating at the site from a limited catchment area in the vicinity. Subsequent recoveries of the ringed birds might have helped to resolve this question but unfortunately there was only one: JK63372 was killed by a van on a road nearby on 29 March 1974. Other members of the 1972-73 assembly were present in the 1973-74 winter also, when a similar feeding assembly was gathered again at the same site, since six of the 1972-73 birds were re-trapped during further netting sessions on 10 March and 10 April 1974. In addition two others were present on 6 September 1974.

It seems likely that the feeding site, perhaps on account of its scale, became a communal resource to be used freely by Dunnocks which had either temporarily abandoned their own neighbouring, but less profitable, feeding territories or else were taking part in dispersive movements through the region. The possibility that the assemblies had some unknown social function or were epideictic displays (Wynne-Edwards, 1962, p.16) cannot be excluded.

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Table 2

Weight changes (g) of individual Dunnocks caught twice on the same day at Bramham Park (BH) and Leeds (L)

Ring Number	Site	Date	FIRST CATCH Time	Wt.	SECOND CATCH Time	Wt.	WEIGHT CHANGE
BP03625	L	23.04.72	0730	23.0	1500	25.0	+2.0
JK63301	BH	18.02.73	1245	21.7	1630	21.5	-0.2
JK63301	BH	17.03.73	1230	22.0	1720	21.8	-0.2
JP93739	BH	17.03.73	1330	21.0	1545	20.0	-1.0
JJ40370	BH	17.03.73	1130	21.0	1700	22.0	+1.0
JP93721	BH	17.03.73	1000	21.7	1400	21.0	-0.7
JK63387	BH	17.03.73	1030	20.7	1720	21.1	+0.4
JR99714	BH	10.03.74	1155	22.1	1315	21.7	-0.4
JR99724	BH	10.03.74	1415	20.9	1545	19.8	-1.1
JR99732	BH	10.03.74	1515	21.0	1715	22.0	+1.0
JR99725	BH	10.03.74	1415	20.5	1715	19.9	-0.6
JR99723	BH	10.04.74	1600	20.8	1845	19.9	-0.9
JP93763	BH	10.04.74	1720	22.0	1845	21.3	-0.7
JR99734	BH	06.09.74	1500	24.8	1845	25.5	+0.7

4. WING LENGTHS AND WEIGHTS OF BRITISH DUNNOCKS

The frequency distribution of the wing lengths of the Dunnocks at Bramham Park, where the birds described in the previous section were caught, was not significantly different from a normal distribution ($\chi^2 = 4.36$ on 6 d.f., $P > 0.05$) so there was no indirect evidence, such as a bi-modal or markedly-skewed distribution, for, respectively, any sexual dimorphism in size nor for any biases in the population sampled. Given this result, biometric data on the Bramham Park birds and on other samples of British Dunnocks from a variety of sites were analysed and compared by region and the results are discussed in this section. Although the samples were taken over 17 years it is unlikely that any major changes in the ecology or genetics of the species occurred during this brief period and none have been documented, so this possible source of variation was ignored. Before the regional comparisons, the weights of individual Dunnocks will be considered, followed by variations in both weight and wing lengths according to season and region and, finally, the relations between weight and wing length.

Most diurnal birds lose much weight overnight and tend to feed voraciously soon after dawn in order to make good their overnight losses. Thereafter during the day their weights fluctuate, but not as markedly as the changes between dusk and dawn. The Dunnock is no exception and the extent of some variations in weight of individual

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birds caught twice on the same day are presented in Table 2.. In the breeding season while carrying developing eggs adult females are likely to be heavier than males and the weight of juveniles may increase by 2.0 g as they progress from post-natal plumage to mid-moult and then drop by 1.0 g as they complete feather growth (Boddy, 1983). Boddy stated that these changes were independent of season and his data were for the period July-October. The weight changes during the course of a bird's life can be more extreme, as illustrated by the examples in Table 3. Clearly weight is not stable enough to be used as a sex determinant in the way described by Birkhead (1981), who ignored variation due to time of day, season or individual bird size, and supported his statement with data on only ten birds.

In order to examine weight variation according to season and region the available data from the three regions (Scotland, North England and South England) were grouped into birds caught in Spring (March, April and May), Summer (June, July and August), Autumn (September, October and November), and Winter (December, January and February). For this and all following analyses only one data-set for each individual bird was used and this was that obtained on its first capture in post-juvenile plumage, all data on juvenile birds being omitted. Also excluded were any data obtained before 1000 hrs., to allow for recovery from overnight weight losses. Birds were caught throughout the rest of the day at all sites, so it is assumed that any within-day variations after 1000 hrs. were random.

Table 3

Examples of individual Dunnocks caught and re-trapped at Leeds (L), Bramham (BH) and Bramley (BL) whose weights changed by at least 2.2 g.

Ring Number	Site	Minimum Date	Weight Time	Wt.	Maximum Date	Weight Time	Wt.	Range (g) of Wt. Change
BP03623	L	12.02.72	0845	20.4	23.04.72	1500	25.0	4.6
BP03611	BL	13.05.72	1200	22.0	14.11.71	1415	26.0	4.0
JP93851	BL	25.05.75	0900	20.4	25.03.75	1915	24.0	3.6
JP93745	BH	17.03.73	1545	23.1	06.09.74	1215	26.5	3.4
JV06958	BL	03.09.75	0845	21.1	14.08.76	1945	24.1	3.0
BP03627	L	18.03.72	1210	26.0	26.02.72	1600	29.0	3.0
JJ40370	BH	02.09.72	1715	20.5	18.02.73	1630	23.4	2.9
JS14092	BL	03.09.75	0800	19.2	29.12.75	1540	22.0	2.8
KC85819	BL	06.06.76	1215	20.0	11.03.78	1000	22.4	2.4
JP93707	BH	14.04.73	1200	21.3	25.02.73	1530	23.5	2.2

An unbalanced two-way least squares analysis of variance (Snedecor and Cochran, 1967, pp.488-492) revealed significant differences in weights according to season

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($F_1 = 4.44$ on 3,273 d.f., $P < 0.01$) but not according to the regions (Table 4). The

Table 4

Mean weights of Dunnocks in different regions and seasons. There were significant differences between seasons (see text): for these data column means adjusted to allow for different sample sizes and so that they average to the overall mean are also provided

Region	Season				Total	Regional Mean (all seasons)	S.E. of Regional Mean
	Spring	Summer	Autumn	Winter			
Scotland	22.73	20.75	22.02	23.33	51	22.06	0.19
N. England	22.45	22.88	21.95	23.05	172	22.57	0.12
S. England	22.17	21.38	21.77	22.63	62	22.11	0.20
Total	128	30	65	62			
Seasonal mean (all regions)	22.32	22.29	21.96	22.99			
S.E. of seasonal mean	0.11	0.30	0.21	0.20			
Adjusted seasonal mean	22.30	22.29	22.01	22.96			
S.E. of adjusted seasonal mean	0.13	0.27	0.18	0.19			

birds were heaviest in winter and this finding, that Dunnocks put on weight in winter, is not surprising since such increases also occur in other temperate birds (e.g. tits, Perrins, 1979, pp.128-130) and are explicable in terms of the physiological requirements for surviving longer nights in winter and for coping with periods when food is scarce or difficult to obtain.

In order to see how the wing lengths varied with season and region the data were subjected to the same unbalanced analysis of variance which was used for the

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weights. There was no significant difference between seasons but there were significant regional differences ($F = 4.28$ on 2,272 d.f., $P < 0.05$). Furthermore, the mean values (Table 5) show that the birds were smaller the further north they were caught. This south to north trend suggests the existence of a cline rather than different subspecies but further investigations are indicated. *P.m.occidentalis* is the common mainland race in Britain, *P.m.hebridium* occurs in the Hebrides and parts of western Scotland but its geographical limits are unknown and *P.m.modularis* occurs on the European continent (Witherby *et al.*, 1943, p.208).

If the Scottish populations were a different race from the English birds then they would be expected to be bigger rather than smaller, according to Bergmann's rule. This states that, among the forms of a polytypic species, body-size tends to be larger in cooler parts of the total range and smaller in the warmer parts (Thomson, 1964, p.90). Nevertheless, although the Scottish birds were significantly smaller according to wing length and so would be expected to be lighter since weight is related to wing length (see below), they were not significantly lighter (Table 4).

For examining the relationship between weight and wing length only the autumn and winter data sets were used since, as already mentioned, when birds are carrying eggs they are likely to be much heavier than at other times. For instance, Blue Tits (*Parus caeruleus*) may be as much as 50% heavier when laying than in winter (Perrins, 1979, p.128). Dunnocks commence breeding in April (occasionally as early as March) and have two, sometimes three, broods (Harrison, 1975, p.236). Visual inspection of the data, when plotted, suggested a straight line relationship between weight and wing length, with considerable variation distributed evenly about it, so linear regressions without any transformations were compared, as follows, by the methods described by Snedecor and Cochran (1967, Section 14.6, Chapter 14 "Comparison of Regression Lines").

Since it has already been shown that winter weights are significantly different from weights at other seasons, the data sets for autumn were investigated separately from the winter weights. There were no significant differences between the slopes or intercepts for the regressions for the data obtained in each of the three regions in autumn so the autumn data were combined into a single linear regression in which variations in wing length could account for a significant ($F = 11.98$ on 1,62 d.f., $P < 0.001$) amount of the variability in weight. This was also the case ($F = 25.30$ on 1,60 d.f., $P < 0.001$) for the regional sets for winter. With x = wing length and y = weight the two regressions were:

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Autumn $y = 0.356 x - 2.594$ (estimated standard error
of the slope = 0.103)
Winter $y = 0.491 x - 11.201$ (estimated standard error
of the slope = 0.098)

The slopes of these two regression lines are not significantly different and can be fitted to a common slope of 0.416 but significantly more of the variability in weight ($P < 0.01$) can be accounted for by the variability in wing length if different intercepts are used. With the common slope the autumn intercept is -6.758 and the intercept for winter becomes -5.990.

Table 5

Mean wing lengths of Dunnocks in different regions and seasons. There were significant differences between regions (see text) and for these data means adjusted to allow for different sample sizes are also provided

Region	Season				Total	a	b	c	d
	Spring	Summer	Autumn	Winter					
Scotland	68.18	69.50	68.74	69.66	50	68.76	0.26	68.91	0.27
N.England	69.72	69.95	69.33	69.49	172	69.63	0.14	69.61	0.14
S.England	70.07	71.00	69.33	70.00	62	70.08	0.24	70.04	0.24
Total	128	30	64	62					
Seasonal Mean (all regions)	69.66	70.23	69.05	69.63					
S.E. of Seasonal Mean	0.17	0.33	0.24	0.22					

^aRegional Mean (all seasons)

^bS.E. of Regional Mean

^cAdjusted Regional Mean

^dS.E. of Adjusted Regional Mean

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ACKNOWLEDGEMENTS

For statistical contributions, discussion and comments on an earlier draft I am indebted to S.M. Green. For assistance in the field I am very grateful to M. Hassall and C.I. Hughson. I thank A.S. Cheke and J.A. Coles who commented on the manuscript and also helped in the field. I also thank G.F. Lane Fox and G.P. Priestley for permission to ring birds in Bramham Park and Professor R.M. Cormack for his thought-provoking analyses of the capture-recapture data.

Footnote: For a recent description of a winter feeding group of Dunnocks see du Feu, Hounsome and Spence (1983)

A BIVARIATE DISCRETE MODEL OF CHANGING COLOUR IN BLACKBIRDS

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SUMMARY

As first-winter male Blackbirds (*Turdus merula*) mature, the eye ring and bill colours change from black to yellow. Interest is in the change over time of both colours and their interrelationship. Mantel's score statistic is used to test for association between eye ring and bill colour, measured on a discrete scale. A constant global cross-ratio model is developed which incorporates changes in each feature and the association between orbital ring and upper mandible colours. Marginal changes are fitted as logistic models of cumulative probabilities, linear over time. Association is measured by dichotomizing both responses, taking the cross-ratio of the resulting 2 x 2 table of probabilities, and constraining this expression to be equal for all times and possible dichotomies. Evidence from the data under study suggests that the colour of orbital rings changed faster than that of upper mandibles.

Keywords: ASSOCIATION; BIVARIATE DISCRETE ORDERED RESPONSE; CONTINGENCY TABLE;
GLOBAL CROSS-RATIO; LINEAR LOGISTIC REGRESSION; MANTEL'S SCORE STATISTIC;
PRODUCT MULTINOMIAL

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1. INTRODUCTION

Adult and immature male Blackbirds (*Turdus merula*) can be differentiated by plumage characteristics. As a first-winter male Blackbird matures, the bill and eye ring colours change from black to yellow. In a preliminary field study by Dougall (in Dougall and Dale, 1982) which dealt principally with total yellowness, two interesting questions arose: whether changes in bill and eye ring colour were associated, and whether these changes occurred at the same rate. Using data collected by Dougall (Table 1), we firstly test for no association using a one-sided version of Mantel's

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score statistic. Then a global cross-ratio (GCR) model (Dale, 1983, Chapter 3) is defined and fitted. It describes association between upper bill and eye ring colour in terms of global cross-ratios, constant over all cutpoints and times, and expresses the change in colour of both features as logistic regressions. Our statistical analysis of the data indicates positive association between bill and eye ring colour and a rate of change of colour greater for eye rings than for bills.

2. THE DATASET

The colour of the orbital ring (OR) around the eye and of the upper and lower mandible for each Blackbird handled was recorded throughout the study by one person. For mandible colours the scores assigned were 0 (totally black), 1 (less than 1/3 mandible yellow), ..., 4 (totally yellow), and for orbital rings 0 / 1 / 2 corresponding to black / transitional / yellow. The observer was satisfied that the scores were assigned objectively and without error. Birds were caught in mist nets and ringed and released as they entered two winter roosts in Fife, Scotland. Colours were recorded during eighteen ten-day periods from October 1, 1980 to the last week in March, 1981: data were not collected in period 9. There were occasional recaptures of the same bird in different time periods: the total of 70 birds includes nine birds which were handled twice and one three times. Since the upper and lower mandible scores appear highly correlated, we use only upper mandibles (UM) in the ensuing discussion.

To ensure the validity of statistical analyses which follow, it was necessary to assume

- (a) that all captures in a given ten-day period were independent and identically distributed;
- (b) that repeated sightings of the same bird in different periods were equivalent to sightings of different birds;
- (c) that there was a constant relationship throughout the study between orbital ring and upper mandible colourings.

Assumptions (a) and (c) were acceptable, whereas (b) may not strictly hold, since colourings are very unlikely to become blacker with time.

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Table 1
Number of Blackbirds, classified by colour score

Period	Orbital Ring Score	Upper				Score	Period	Orbital Ring Score	Upper			
		0*	1	2	3				0*	1	2	3
1**	0	1	-	-	-	-	10**	0	-	-	-	-
	1	-	-	-	-	-		1	-	2	-	1
	2	-	-	-	-	-		2	-	-	-	-
2**	0	2	-	-	-	-	11	0	-	-	-	-
	1	-	-	-	-	-		1	3	-	-	-
	2	-	-	-	-	-		2	-	-	1	-
3**	0	5	-	-	-	-	12	0	-	-	-	-
	1	-	-	-	-	-		1	1	2	-	-
	2	-	-	-	-	-		2	-	-	-	1
4	0	9	2	1	-	-	14	0	1	-	-	-
	1	3	1	-	-	-		1	1	2	1	2
	2	-	-	-	-	-		2	-	-	1	2
5	0	7	2	-	-	-	15**	0	-	-	-	-
	1	-	-	-	1	-		1	1	1	-	-
	2	-	-	-	-	-		2	-	-	-	-
6	0	4	-	-	-	-	17**	0	-	-	-	-
	1	1	2	-	-	-		1	-	-	-	1
	2	-	-	-	-	-		2	-	-	-	-
7**	0	2	-	-	-	-	18**	0	-	-	-	-
	1	3	-	-	-	-		1	-	-	-	1
	2	-	-	-	-	-		2	-	-	-	-
8	0	6	1	-	-	-		0	-	-	-	-
	1	2	2	2	2	-		1	-	-	-	-
	2	-	-	-	-	-		2	-	-	-	-

*Black

* Yellow

**Omitted from analyses

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3. MANTEL'S SCORE STATISTIC

As a preliminary investigation of the relationship between orbital ring and upper mandible colours, we apply Mantel's score statistic (Mantel, 1963, equation 13). A score a_{ik} , $i = 0, 1, 2$ is assigned to the i^{th} orbital ring category for time period t_k , and a score b_{jk} , $j = 0, \dots, 4$ to the j^{th} upper mandible category. Let y_{ijk} be the number of first-winter Blackbirds recorded at time t_k as having orbital ring category i and upper mandible category j , $k = 1, \dots, K$. Then the one-sided version of Mantel's score statistic, for testing for no association against the alternative of positive association in all tables is

$$R_M = \frac{\sum_{k=1}^K \sum_{i=0}^2 \sum_{j=0}^4 y_{ijk} (a_{ij} - \bar{a}_k) (b_{jk} - \bar{b}_k)}{\left\{ \sum_{k=1}^K (n_k - 1)^{-1} \sum_{i=0}^2 y_{i+k} (a_{ik} - \bar{a}_k)^2 \sum_{j=0}^4 y_{+jk} (b_{jk} - \bar{b}_k)^2 \right\}^{1/2}} \quad (1)$$

where replacement of a subscript by "+" denotes summation over the subscript, $n_k = y_{++k}$, and $\bar{a}_k = n_k^{-1} \sum_{i=0}^2 y_{i+k} a_{ik}$, with \bar{b}_k defined in the same manner.

For $K = 1$, (1) is similar to the statistic given by Yates (1948), and is the product-moment correlation between the colours with respect to the scores. R_M has good power against alternatives in which the association is the same in each of the K response tables. Asymptotically as K becomes large, under no association and conditional on the original marginal totals, R_M has a standard normal distribution. For the k^{th} table to give a non-zero contribution to the denominator of R_M , at least two distinct colour categories of both OR and UM must be observed in that time period. In the analyses which follow, only the times which satisfy this requirement are included: periods 4, 5, 6, 8, 11, 12, 14.

Two score types are considered: integers $a_{ik} = 0, 1, 2$; $b_{jk} = 0, \dots, 4$; $k = 1, \dots, K$, and the average within-period relative ranks for the margins:

$$a_{ik} = n_k^{-1} \left\{ \sum_{q=1}^{i-1} y_{q+k} + \frac{1}{2}(y_{i+k} + 1) \right\} \quad ,$$

and a similar definition for b_{jk} , yielding:

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Score Type	Sample R_M Value	Asymptotic Probability * Under No Association
Integer	7.84	3×10^{-7}
Within-period relative ranks	4.51	10^{-5}

* of exceedance of observed value

Now R_M is large and positive. Despite having only seven tables in the analysis, this suggests a strong association between OR and UM colour, whether measured on the objective integer scale or in terms of relative ranks. We now incorporate the association in a statistical model.

4. CONSTANT GLOBAL CROSS-RATIO MODELS

The model which we use in this section describes several aspects of the data at once: the marginal dependence of OR and UM colouring on time as a linear logistic model for cumulative probabilities, and association between OR and UM colour in terms of a global cross-ratio which takes the same value at all time-points. A product multinomial sampling distribution is assumed, i.e. the analysis is conditional on the number of observations at each time-point. The model itself is for the cumulative probabilities of the response contingency table underlying the multinomial model.

Let $\tilde{Z}(t) = (Z_1(t), Z_2(t))$ be a discrete random vector dependent on t , such that $Z_1(t)$ takes the values $1, \dots, r$ according to the cumulative probabilities

$$\eta_{it} = \Pr[Z_1(t) \leq i]$$

and similarly $Z_2(t)$ satisfies

$$\xi_{jt} = \Pr[Z_2(t) \leq j], \quad j = 1, \dots, c,$$

with

$$\eta_{ot} = \xi_{ot} = 0,$$

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$$\eta_{rt} = \xi_{ct} = 1 ,$$

$$\eta_t = (\eta_{1t}, \dots, \eta_{r-1,t})^T$$

and

$$\xi_t = (\xi_{1t}, \dots, \xi_{c-1,t})^T .$$

The cumulative probability function of $\tilde{Z}(t)$ is $F_{ij}(t; \Delta, \eta_t, \xi_t) = \Pr[Z_1(t) \leq i, Z_2(t) \leq j]$, where $\psi = e^\Delta$ is the global cross-ratio to be defined. Divide the space of possible values of Z into four quadrants $\{Z_1 \leq i, Z_2 \leq j\}$, $\{Z_1 \leq i, Z_2 > j\}$, $\{Z_1 > i, Z_2 \leq j\}$, $\{Z_1 > i, Z_2 > j\}$. Such a division is said to occur at cutpoint (i,j) . Then the global cross-ratio (GCR) at cutpoint (i,j) is required to be the same for all i,j so that

$$\begin{aligned} e^\Delta &= \frac{\Pr[Z_1(t) \leq i, Z_2(t) \leq j] \Pr[Z_1(t) > i, Z_2(t) > j]}{\Pr[Z_1(t) > i, Z_2(t) \leq j] \Pr[Z_1(t) \leq i, Z_2(t) > j]} \\ &= \frac{F_{ij}(t; \theta_t) \{1 - \eta_{it} - \xi_{jt} + F_{ij}(t; \theta_t)\}}{\{\xi_{jt} - F_{ij}(t; \theta_t)\} \{\eta_{it} - F_{ij}(t; \theta_t)\}} \end{aligned} \quad (2)$$

where $\theta_t = (\Delta, \eta_t, \xi_t)$. The solution of (2) for $F_{ij}(t; \theta_t)$ yields

$$F_{ij}(t; \Delta, \eta_t, \xi_t) = \begin{cases} \frac{1}{2}(e^\Delta - 1)^{-1} \{1 + (\eta_{it} + \xi_{jt})(e^\Delta - 1) - S(\eta_{it}, \xi_{jt}, \Delta)\} & \text{if } \Delta \neq 0 ; \\ \eta_{it} \xi_{jt} & \text{if } \Delta = 0 ; \end{cases} \quad (3)$$

where

$$S(\eta, \xi, \Delta) = [(1 + (\eta + \xi)(e^\Delta - 1))^2 + 4e^\Delta(1 - e^\Delta)\eta\xi]^{\frac{1}{2}} .$$

Expression (3) may be shown to be a *bona fide* cumulative distribution function provided that the η_t and ξ_t are cumulative probabilities, i.e. $0 < \eta_{1t} < \dots < \eta_{r-1,t} < 1$ and $0 < \xi_{1t} < \dots < \xi_{c-1,t} < 1$. Such a distribution is called a constant global cross-ratio distribution, since the GCR takes the same value, for all cutpoints and for all values of t . A further restriction is placed on the

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marginal cumulative probabilities. They are specified in terms of linear logistic models in t for the cumulative probabilities, as in McCullagh (1980,§2):

$$\begin{aligned} \ln\{\eta_{it} / (1 - \eta_{it})\} &= \alpha_{1i} - \beta_1 t \quad , \quad i = 1, \dots, r - 1 ; \\ \ln\{\xi_{jt} / (1 - \xi_{jt})\} &= \alpha_{2j} - \beta_2 t \quad , \quad j = 1, \dots, c - 1 ; \end{aligned} \quad (4)$$

which leads to

$$\eta_{it} = \Pr[Z_1(t) < i] = \exp(\alpha_{1i} - \beta_1 t) / \{1 + \exp(\alpha_{1i} - \beta_1 t)\} \quad ,$$

$$i = 1, \dots, r - 1 \quad ,$$

and a similar expression for the ξ_{jt} , where $\alpha_1 = (\alpha_{11}, \dots, \alpha_{1,r-1})$ and $\alpha_2 = (\alpha_{21}, \dots, \alpha_{2,c-1})$. The GCR family of models are extensions for discrete, bivariate responses of those proposed by Pearson and Heron (1913), and Plackett (1965) for a single $r \times c$ table, and of Mantel and Brown (1973) for a sequence of 2×2 response tables. Other more general formulations are possible - see Dale (1983, Chapter 3). An important property of GCR models is their dependence on marginal responses only through the marginal cumulative probabilities. Thus a GCR model is invariant under any order-preserving transformation of the marginal variables. Further, combination of adjacent row categories i and $i + 1$ results in the loss of cutpoint parameter $\alpha_{1,i+1}$, but leaves the rest of the model essentially unchanged.

The data of Table 1 have many zero entries, making an application of standard goodness-of-fit tests inappropriate. Thus in addition to restricting the analysis to periods 4, 5, 6, 8, 11, 12 and 14, we combine UM categories 1 and 2, and 3 and 4. It was considered unwise to merge adjacent time periods. The marginal distributions depend strongly on time, and thus in a table collapsed over time, what appears to be association may be the effect of contributions from different times. GCR models defined by (3) and (4) were fitted to the data derived from Table 1 as described above, with t being time in ten-day periods. Two models were considered:

- (a) allowing the marginal slopes β_1 and β_2 for orbital rings and upper mandibles to differ;
- (b) constraining the slopes to be equal.

Parameter estimates and goodness-of-fit statistics under a maximum likelihood fit are presented in Table 2. Model (a) appears to fit the data very well: the goodness-of-fit statistics are both significant at the lower 5% level, under the asymptotic

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Table 2
GCR model fit to Blackbird colouring dataset

Model (a)

Parameter*	Symbol	Estimate	Standard error
log ψ	Δ	2.25	0.57
OR 0/1	α_{11}	3.75	0.76
OR 1/2	α_{12}	7.48	1.30
UM B/M	α_{21}	2.44	0.61
UM M/Y	α_{22}	4.26	0.77
OR slope	β_1	0.522	0.099
UM slope	β_2	0.288	0.068

Likelihood ratio G^2 = 33.9 with 49 degrees of freedom**Pearson χ^2 = 32.3 with 49 degrees of freedom**

Model (b)

Parameter*	Symbol	Estimate	Standard error
log ψ	Δ	1.96	0.54
OR 0/1	α_{11}	2.78	0.56
OR 1/2	α_{12}	5.69	0.78
UM B/M	α_{21}	3.19	0.60
UM M/Y	α_{22}	5.30	0.76
common slope	β	0.381	0.063

Likelihood ratio G^2 = 40.2 with 50 degrees of freedom**Pearson χ^2 = 40.8 with 50 degrees of freedom**

Likelihood ratio statistic for common slope = 6.3 with 1 degree of freedom

*OR = orbital ring; UM = upper mandible; a/b is the cutpoint between categories a and b.

Upper mandible category: B = 0; M = 1,2; Y = 3,4.

** too good a fit under the asymptotic χ^2 distribution, probably because of the large number of zero entries in the table of data.

χ^2 distribution. Presumably, this is partly because many cells have low or zero counts. The multinomial distribution may be incorrect. Examination of the Poisson standardized residuals (Table 3) suggests an adequate fit, with all residuals no

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larger in modulus than 2.23.

Table 3
Fitted cell probabilities and residuals under model (a)

Period	Orbital Ring Score	Upper mandible score		
		0	1 or 2	3 or 4
4	0	0.721 (-0.75)	0.103 (1.06)	0.017 (-0.52)
	1	0.061 (2.06)	0.070 (-0.11)	0.025 (-0.63)
	2	0.001 (-0.14)	0.002 (-0.18)	0.001 (-0.15)
5	0	0.641 (0.23)	0.101 (0.99)	0.016 (-0.40)
	1	0.087 (-0.93)	0.110 (-1.05)	0.038 (1.01)
	2	0.002 (-0.13)	0.003 (-0.18)	0.003 (-0.16)
6	0	0.545 (0.09)	0.090 (-0.80)	0.014 (-0.31)
	1	0.122 (0.16)	0.161 (0.82)	0.055 (-0.62)
	2	0.002 (-0.13)	0.005 (-0.19)	0.005 (-0.19)
8	0	0.327 (0.49)	0.058 (0.14)	0.010 (-0.38)
	1	0.201 (-0.59)	0.273 (-0.05)	0.096 (0.47)
	2	0.004 (-0.25)	0.012 (-0.43)	0.019 (-0.54)
11	0	0.092 (0.61)	0.022 (-0.30)	0.005 (-0.14)
	1	0.223 (2.23)	0.360 (-1.20)	0.146 (-0.76)
	2	0.009 (-0.19)	0.040 (2.08)	0.101 (-0.64)
12	0	0.055 (-0.47)	0.016 (-0.25)	0.004 (-0.12)
	1	0.199 (0.23)	0.351 (0.50)	0.146 (-0.76)
	2	0.011 (-0.21)	0.058 (-0.48)	0.160 (0.45)
14	0	0.018 (1.52)	0.008 (-0.33)	0.002 (-0.18)
	1	0.133 (-0.63)	0.268 (-0.39)	0.112 (0.34)
	2	0.018 (-0.50)	0.111 (-0.45)	0.330 (0.64)

Note: Residuals are in parentheses

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There is statistical evidence to suggest a difference between orbital rings and upper mandibles in rate of change of colour with respect to time. In model (a) the standard error of the difference in marginal slopes is 0.099, and the likelihood ratio statistic for comparing models (a) and (b) is statistically significant ($p \approx 0.012$). Hence model (a) is preferred. The expected rate of change of colour under model (a) is for orbital rings approximately 1.8 times that of upper mandibles, on the logit scale. We describe the fitted orbital ring slope, represented in Figure 1, as follows.

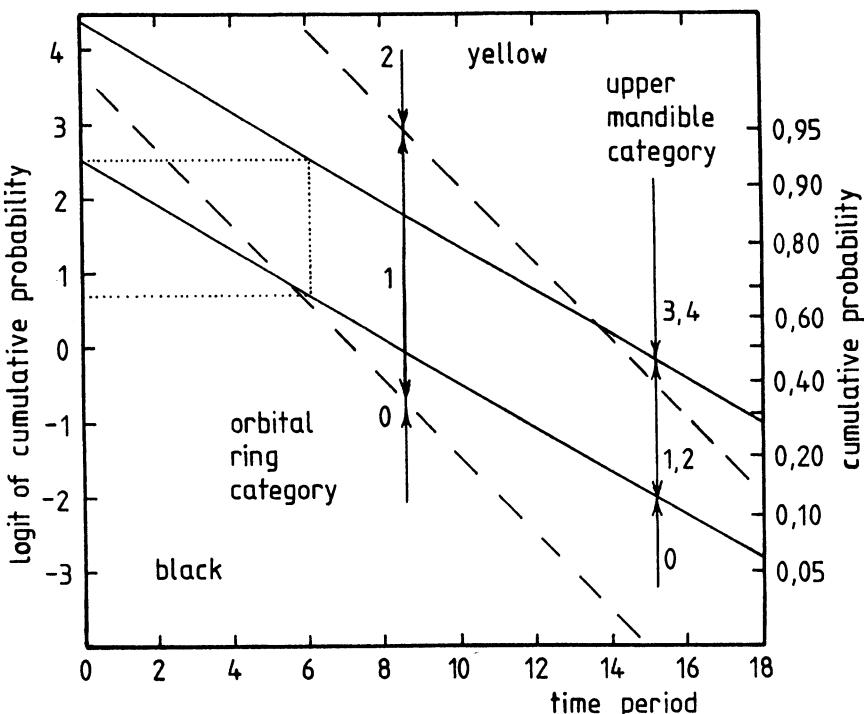


Figure 1 Fitted cutpoint position versus time period, for orbital ring colourings (—) and upper mandible colourings (---): model (a)

For any orbital ring colouring i , and any time period t ,

$$\frac{\Pr[\text{OR} \leq i \text{ at period } t]}{\Pr[\text{OR} > i \text{ at period } t]} = e^{-0.522} \times \frac{\Pr[\text{OR} \leq i \text{ at period } t-1]}{\Pr[\text{OR} > i \text{ at period } t-1]} .$$

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Now $\exp(-0.522) = 0.59$, so the odds on the orbital ring being 'as black as or blacker than i' reduces by 0.59 each period. For upper mandible colour, the expected reduction of odds is $\exp(-0.288) = 0.75$. The fitted probability of being in a particular marginal category in a given period can be read from Figure 1. For example, following the dotted line ('.....') for period 6: $\text{Pr}[\text{UM} = 1 \text{ or } 2] = \text{logit}^{-1}(2.53) - \text{logit}^{-1}(0.71) = 0.93 - 0.67 = 0.26$, where $\text{logit}^{-1}(x) = e^x / (1 + e^x)$. The expected probability of having a given orbital ring and upper mandible colour simultaneously in a given period is obtained by differencing the fitted bivariate cumulative probabilities. For any orbital ring score i and any upper mandible category j , given that $\text{UM} \leq j$, the odds on $\text{OR} \leq i$ are expected to be $\exp(2.25) \approx 9.5$ times higher than the odds on $\text{OR} \leq i$ given $\text{UM} > j$. This odds ratio $\psi = e^\Delta$ has approximate 95% confidence interval (3.0, 30.1).

In summary, this statistical analysis suggests that observed orbital ring and upper mandible colours were associated, in the first-winter Blackbirds under study, with GCR estimated to be 9.5. The change in colour over several months was about 1.8 times faster (on the logit scale) for orbital rings than for upper mandibles. With only 70 observations, these conclusions are only tentative, but it is hoped that the approach of this paper will be useful in related studies on larger sets of data.

ACKNOWLEDGEMENTS

The data were collected by T. W. Dougall, formerly of the Department of Geography, University of St. Andrews, with whom a helpful correspondence is acknowledged. Useful comments were also received from P. J. Brown, R. M. Cormack, D. R. Cox, and P. McCullagh. This work was supported by a New Zealand NRAC Fellowship and an ORS Fees Support Scheme Award.

MIGRATION COUNTS AND LOCAL WEATHER AT
BRITISH BIRD OBSERVATORIES - AN EXAMINATION
BY LINEAR DISCRIMINANT ANALYSIS

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SUMMARY

Linear discriminant analysis is presented as an alternative to multiple regression analysis for the study of relationships between migration counts and local weather conditions. Discriminant analysis is seen to be a useful tool for this purpose since it offers straightforward interpretations of results, and it is based on assumptions that appear to be upheld by the data.

The particular type of migration data that are considered in this paper are counts of grounded migrants at Bird Observatories, and the differences between these and the more commonly used radar counts are discussed.

The main conclusions from the work are brought together and presented in a summary section (Section 4.3).

Keywords: BIRD OBSERVATORIES, MIGRATION, WEATHER, DISCRIMINANT ANALYSIS.

1. INTRODUCTION

This work formed part of a large scale study of British Bird Observatories' data, undertaken in collaboration with the British Trust for Ornithology. A major aspect of this study was the construction of an annual migration index, for each migrant species, which can be used for monitoring fluctuations in the breeding population sizes. For species that are territorial in behaviour and that breed in large numbers throughout the British Isles the Common Bird Census (CBC) indices allow population fluctuations to be quantified (see, e.g., Mountford, 1985). However, many

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migrant species are not territorial species and therefore little is known about population trends. The idea behind the use of observatories' data is that the birds are censused as they enter or leave the British Isles rather than at their breeding grounds. Williamson (1963) first suggested using migration data in this way. But up to now only two small-scale isolated studies have been made using British observatories data. Sharrock (1969) investigated annual totals of Grey Wagtails (*Motacilla cinerea*) seen migrating through observatories, and he proposed a simple migration index which was found to correspond with population fluctuations estimated from Nest Record Scheme data. Cowley (1979) briefly describes how annual totals of migration counts of Sand Martins (*Riparia riparia*) correspond approximately to other forms of population indices based on counts from individual colonies.

The use of observatories data for population monitoring has been investigated in other countries. Hussell (1981) has used migration data from Long Point Bird Observatory, Ontario, for estimating population fluctuations of some North American migrants and he found that in order for his results to correspond to alternative results from breeding bird censuses, allowance had to be made for weather conditions at observatories. Svensson (1978) examined daily ringing totals and migration counts from three Swedish observatories (Falsterbo, Torhamn and Ottenby) and found that for some species, correlations between observatory-based indices and breeding bird indices from the interior of Sweden were encouraging.

From the studies mentioned above, it is clear that observatory-indices based on annual totals of migration counts, for example, will reflect major fluctuations in population size, but the work of Hussell (1981) has suggested that it may be possible to achieve greater sensitivity by incorporating weather information in the indices. There is little doubt among ornithologists that the occurrence of migrants at observatories is, to some extent, related to weather conditions. Ornithologists are familiar with the basic rules, such as: wet and cloudy nights generally produce large numbers of grounded migrants on the following day whereas clear, calm nights enable the migrants to continue their journeys without interruption. However, for British data no attempt has so far been made to examine this connection objectively, and this we attempt to do in the present paper.

The weather data used in this paper consist of daily means of seven variables (see Section 2.2). We also consider the same variables, lagged by one day, giving a total of fourteen variables for inclusion in our analysis. The use of lagged variables seems sensible for two reasons: Firstly, the weather that determines whether or not a bird will land at an observatory may be the weather experienced

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prior to arrival. This may be the case in both the spring and autumn since in the spring it is possible that if the weather is particularly bad over northern France then the birds may not set off until an improvement occurs. Also, if the birds do set off and fly sufficiently high, they may fly over any localised mist or fog on the south coast of Britain. Thus we see that the weather situation prior to the day of arrival may be important in our study. In autumn the same applies, since if Britain is experiencing extremely unfavourable weather, then the birds may not leave their breeding areas until conditions improve. In both the cases described above, we notice that ideally we would like weather data from sites away from the observatories. We are relying on the assumption that, to a greater or lesser extent, the weather data obtained from observatories are indicative of the general synoptic situation. For some variables such as temperature and atmospheric pressure this will be the case, but for variables such as wind direction and low cloud cover local variations are bound to occur, particularly as most British observatories are situated on peninsulas or offshore islands, which are geographically distinct from the surrounding coastline.

The second justification for introducing lagged variables is that we allow for the influence of changes in the recorded values. In other words, a value for pressure may not be important, but a sudden drop from one day to the next may be.

A closely related area of research that has received much attention in the biological literature in both Great Britain and North America is that of radar studies of migration. With the advent of radar equipment during the Second World War, ornithologists were able to assess the volume of migration as it was actually in progress. Many studies have been made of the influence of weather on radar counts but these studies involve very different problems from those that face observatory workers. At observatories, birds are recorded when, for whatever reason, they are forced to land, while radar equipment records birds in flight. The influential weather variables, if any, will clearly be very different. Further, it is very difficult to distinguish between species by using radar echoes, which means that inferences can only be made on groups of species.

Unlike radar counts, counts of grounded migrants from observatories are not necessarily correlated with the numbers of birds actually migrating. A zero count may indicate that no migration has taken place, or that all the migrants flew over the observatory without landing. Similarly, when birds are recorded on the ground, the size of the count is not necessarily indicative of the number of birds migrating - the count may represent a sample of the available migrants, or perhaps on some

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nights the count may comprise most of the migrants which were forced down due to adverse weather conditions. Another difficulty with correlating counts of grounded birds with migration density is that the observatories are in fixed locations, while the 'front' of migrants may be of varying width and covering various areas of coastline.

The statistical analyses that have been carried out in radar studies have mostly been multiple regression analyses; see Lack (1960, 1963a,b), Nisbet and Drury (1968), Able (1973), Alerstam *et al.* (1973), Richardson (1974). In the present paper we use linear discriminant analysis in order to find those weather variables that best discriminate between high and low counts of migrants. If it is possible to discriminate successfully between categories of migration counts in this way, then we have a means of weighting annual totals of migrants according to weather conditions, thus achieving more sensitive population indices.

The basic problem of discriminant analysis is to assign an observation, in this case a multivariate weather observation for a particular day, of unknown origin, to one of a number of distinct groups on the basis of the value of the observation. A simple measure of the success of the analysis is provided by the proportion of observations that are assigned to the correct group - we assume that the data consist of correctly assigned observations which can be re-assigned using results from the analysis. Assignments are made using discriminant functions and the derivation of these, with other statistical details of discriminant analysis can be found in Morrison (1973) and Lachenbruch (1975).

Note that discriminant analysis has been used successfully with weather data in the past, though in a different context - see Glahn (1965).

2. THE DATA

2.1 The Bird Data

The response variable used in the discriminant analyses described in this paper is the number of grounded migrants seen on the observatory recording area in one day. These daily observations are taken over the whole of the migration seasons; a typical spring season extends from April to June and an autumn season from July to October.

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Each count is an estimate of the maximum number of birds present at any one time during each day, and is made by a variable number of observers. The observatory warden is present each day to censure and collate the records before arriving at the final figure for each species. It is this aspect of observatories' activities that gives some uniformity to their data which would otherwise be heavily dependent on the experience and number of people present at the observatory each day.

Further details of activities and birds seen at observatories can be found in Durman (1975), and a statistical examination of the recording techniques can be found in Darby (1984).

The observatories that we are concerned with in the present paper are both situated on the south coast of England; Dungeness in Kent and Portland Bill in Dorset. These were chosen because south coast observatories are less likely to receive migrants heading for or returning from Scandinavia than, for example, east coast observatories. Also, weather data were readily available only from these two locations. There are usually about a dozen other observatories operating at other coastal locations around Britain; see Durman (1975).

The time period chosen for this study was also determined by the availability of weather data: at Dungeness from 1961 to 1972 and 1967 to 1970 for spring and autumn respectively, and from 1968 to 1970 at Portland for both spring and autumn.

The species that we consider are the Redstart (*Phoenicurus phoenicurus*), Whitethroat (*Sylvia communis*), Willow Warbler (*Phylloscopus trochilus*) and Sedge Warbler (*Acrocephalus schoenobaenus*). These were chosen since they are among the commonest of migrants occurring at both observatories, thus providing suitable sample sizes with which to work. For a guide to species that are regularly seen in substantial numbers at other observatories, Riddiford and Findley (1982) present over three hundred histograms of daily counts of migrant birds recorded at nine British observatories, including Dungeness and Portland.

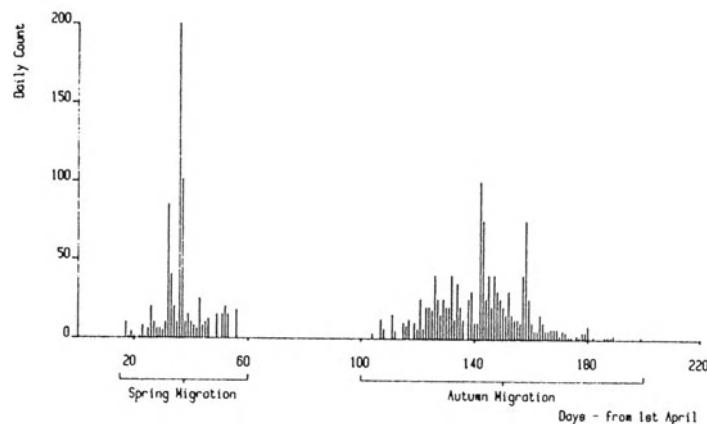
The daily counts of grounded migrants are clearly only estimates of the numbers of birds present on the recording area each day since some birds will be overlooked amongst undergrowth for example. Also, some birds may be recorded by more than one observer.

Despite these fundamental shortcomings of the data, the patterns of migration seasons, as reflected by the data, are much as one would expect, i.e., a build up

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to a peak period followed by a decline as the migration draws to a close. Figure 1 shows two examples of the seasonal patterns. One can easily make out the two seasons in each diagram as well as the overall 'shape' of the migration. Notice also the large variability in the daily observations, and the different timing and lengths of the migration seasons.

Whitethroat - Dungeness 1964



Redstart - Portland 1967

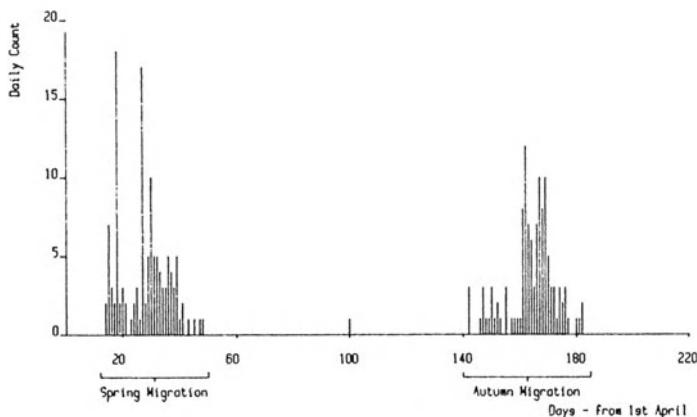


Figure 1 Examples of daily counts of grounded migrants

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Both diagrams show some noticeably large and small counts and it is these on which we focus our attention in this paper. Precisely how we define 'large' and 'small' is considered in Section 3.

2.2 The Weather Data

Daily means of seven weather variables are available from meteorological stations adjacent to Portland and Dungeness observatories. An observation on each variable was made at three-hourly intervals on each day throughout the spring and autumn migration seasons in each year.

The variables are:

- (i) Wind direction: a continuous variable with a maximum value of +1 when the wind is from the south-east, and a minimum value of -1 when the wind is from the north-west. This axis was chosen because of the favoured SE/NW direction of migrants' flight to and from Britain as determined by radar studies.
Thus the variable measures the extent to which the wind is favourable (tailwind) or unfavourable (headwind);
- (ii) Wind speed: a continuous variable measured in knots;
- (iii) Low cloud cover: a continuous variable measured in oktas. Zero represents no low cloud, not necessarily a clear sky. 9 oktas represents an obscured sky, possibly by mist or fog;
- (iv) Visibility: a discrete variable where the distances are measured to known landmarks that are visible. The units are metres;
- (v) Air-temperature: a continuous variable measured in tenths of a $^{\circ}\text{C}$;
- (vi) Humidity: a continuous variable measuring relative humidity, i.e., a percentage; and
- (vii) Atmospheric pressure: a continuous variable measured in millibars.

These variables were chosen from a larger set of eleven on the basis of their correlation structure. The seven variables tend to exhibit low correlations between one another, which is a desirable property when using multivariate analyses such as discriminant analysis. If two or more variables are highly correlated, numerical problems may arise when the covariance matrix is inverted (a part of discriminant analysis). Also, if we use a set of independent variables we minimise the amount

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of work involved, i.e., we do not use two variables that are highly correlated where one will do satisfactorily.

Table 1 shows the correlation matrix of the seven variables for a sample of the data used in this paper. The matrix was constructed from 122 observations over the spring of 1968 at Dungeness. This matrix is typical of those formed from spring and autumn data from both Portland and Dungeness observatories.

Table 1
*Example of correlation matrix of weather variables, Spring 1968,
Dungeness, based on 122 observations*

Wind Direction	1.00						
Wind Speed	.05	1.00					
Low Cloud	.09	.27*	1.00				
Visibility	.15	.23	-.22	1.00			
Air Temperature	-.07	-.05	-.18	-.15	1.00		
Humidity	.00	.16	.44*	-.46*	.23	1.00	
Pressure	.01	-.35*	-.28*	-.01	.04	-.38*	1.00
	Wind Direction	Wind Speed	Low Cloud	Visibility	Air Temperature	Humidity	Pres- sure

*significant at 1% level

Although some high correlations are seen among the variables, each variable appears to be uncorrelated with at least two of the remaining six.

3. PREPARATION OF THE DATA FOR ANALYSIS

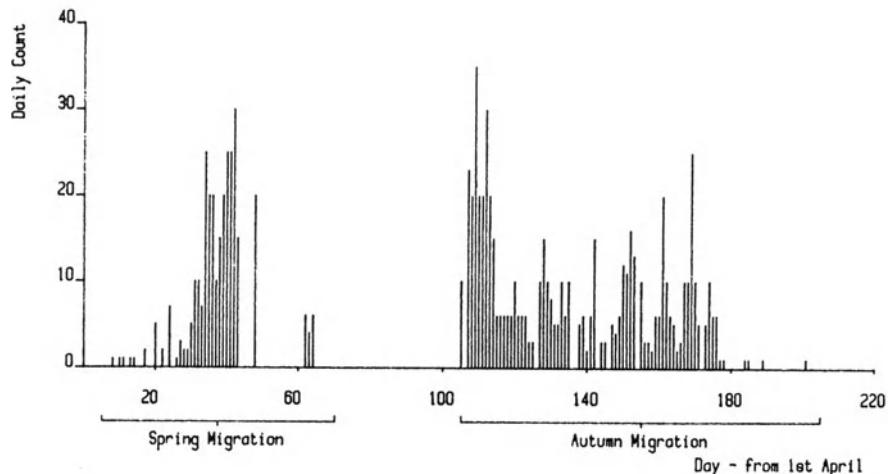
3.1 Time Dependency of Bird Counts

As the examples of Figure 1 show, the number of birds recorded each day varies according to the time of the season. Since we are looking for the influence of weather on a day-to-day basis we must first remove the underlying trend from the data.

The pattern observed in each series of counts is by no means consistent and Figure 2 shows two examples which are very different in character. The spring counts at

Migration counts and local weather conditions

Sedge Warbler - Dungeness 1967



Sedge Warbler - Portland 1967

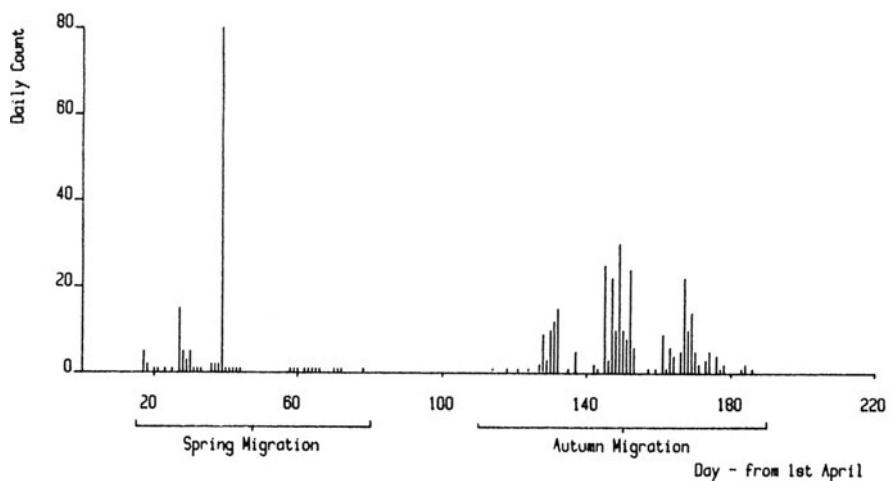


Figure 2 Examples of daily counts of grounded migrants

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Dungeness in Figure 2 appear to be abruptly interrupted, and the part of the season with most activity is at the start. The example from Portland shows for the spring, a series of low counts with one extremely high count and in the autumn one can see three 'waves' of migration. Waves of migration have been noticed in similar diagrams for other species and at other observatories. Possible explanations for this feature are discussed in Darby (1984).

There are two approaches that we could take in order to deal with the time dependency:

- (i) We could fit a time-series model, for instance, a Box-Jenkins type model, to each series and then base the discriminant analysis on the estimated residuals.

Drawbacks to this method are that we only have short series, sometimes as short as fifteen days, and also this method would involve a considerable amount of work in finding the optimum model for each series; and

- (ii) A simple approach related to the fitting of time-series models is to use the deviations of the observed counts from a moving average. This approach is easily applied, and if the length of the moving average is suitably chosen, the pattern of each individual season should be removed. Several means were tried, and a seven-day mean was eventually selected. A mean of this length was found to produce a suitably smoothed series of counts (see Figure 3 for an example) from which to obtain the deviations and also, a seven-day mean guards against any biases entering the data from weekend effects (which may arise if more people are present at weekends than at other times; see Sharrock, 1966).

A useful feature of this method of detrending the data is that all series of counts can be treated in the same manner. In other words, a series that initially shows no trend may be 'detrended' without distorting this fact. Thus the detrending process can be performed automatically without examining each series.

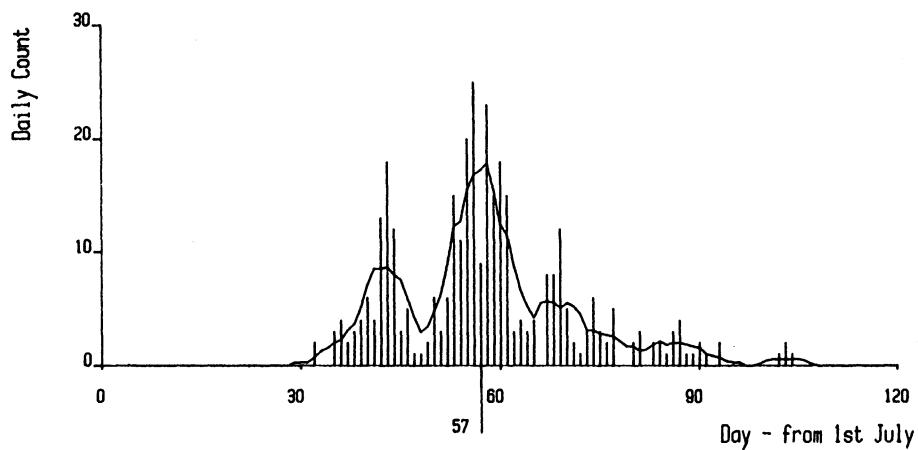
This method is also independent of the timing of the migration season as a whole, which may vary from year to year - according to climatic factors in the birds' wintering areas for example.

Figure 3 shows an example of the detrending process. The original counts and

Migration counts and local weather conditions

Portland Bill (1970) - Whitethroat

(a) Daily counts and 7 - day Moving Average



(b) Detrended data

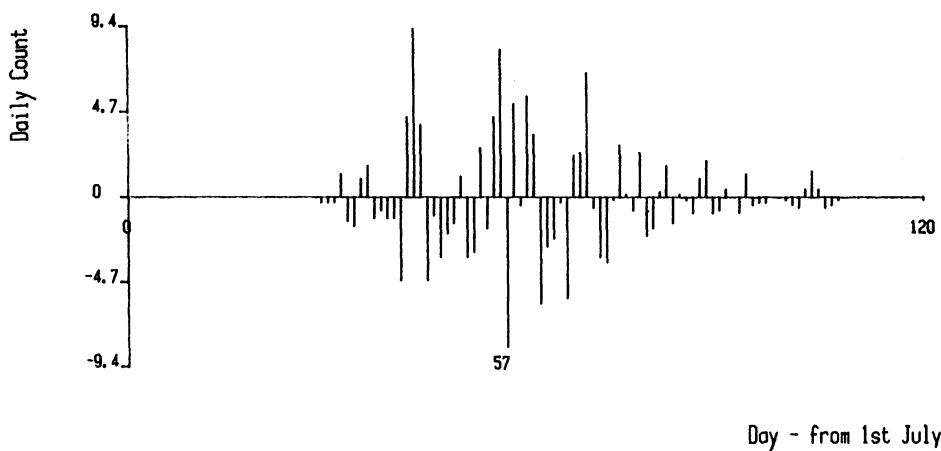


Figure 3 Example of detrending a series of daily counts

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a curve representing the seven-day moving average are shown in Figure 3(a) and the deviations from this curve are shown in Figure 3(b). In the next sections we divide these deviations into 'low count' and 'high count' categories in order to see whether there is an association with the weather variables.

The detrending operation has enabled exceptionally low counts amidst a run of large counts to be readily identified - see for example, the count of day 57 in Figure 3. Also, the exceptionally large counts are identified by this approach. There will obviously be a group of counts in the middle that can neither be described as large nor small; in particular the extremes of each season will consist of a high proportion of such 'medium' counts - see Figure 3(b). We choose to ignore a large proportion of the available data, and we shall only consider the very large or very small counts, and attempt to discriminate between these two groups on the basis of the weather data. As mentioned in the introduction, an assumption of discriminant analysis is that the data are correctly classified into groups. This assumption is more likely to be met if we restrict our attention to extreme counts. Also, it is desirable to have group sizes roughly equal. Owing to the frequency distribution of the deviations (approximately normal in shape), in order to achieve three groups of approximately equal size one needs the central group to be so narrow in range that it consists of deviations of less than, say, one quarter of a standard deviation from the mean. Thus the two outer groups could then hardly be described as representing high and low counts.

Finally, it is unreasonable to expect to be able to discriminate successfully between three groups of counts when each count is only a rough estimate of the two figures.

To sum up, if x_i is the observed count for day i in a given season, then the detrended count y_i is given by

$$y_i = x_i - \frac{1}{7} \sum_{t=i-3}^{t=i+3} x_{i+t}, \quad 3 < i < n-3$$

where n is the number of counts made during the season.

Migration counts and local weather conditions

3.2 Subdividing Counts into Groups

The object of our analysis is to divide the counts of migrants into groups representing high and low counts, and then to attempt to discriminate between the groups using weather data. Recall that each count has been corrected for seasonal effects.

A discriminant function is derived for each group which enables us to calculate, for each day's observation, the probability of that observation belonging to each of the two groups. Each observation may then be allocated to the group corresponding to the highest probability. If the analysis has been successful, then we will find that small counts are allocated to the group representing small counts, and high counts are allocated to the group representing high counts. If the analysis has not been successful, then many counts will have been wrongly classified.

We would like the initial groups to be of similar size since the allocation of observations is carried out partly on the basis of prior probabilities which, in the absence of a suitable alternative, are usually taken to be the relative group sizes. If we had one group much larger than the other, this group may receive an unduly large number of allocations.

Many criteria may be used for defining the groups, but our method which helps to ensure that the two groups contain only noteworthy deviations is to define 'noteworthy' as meaning greater than one standard deviation from the mean. This is purely an *ad hoc* method, but it does produce 'low' and 'high' groups of approximately equal size.

Figure 4 shows two examples of histograms of the two groups, together with the group sizes. These data are the amalgamation of three years' counts in each case. In all future analyses, the counts are pooled over a number of years, the precise numbers having been given in Section 2.1.

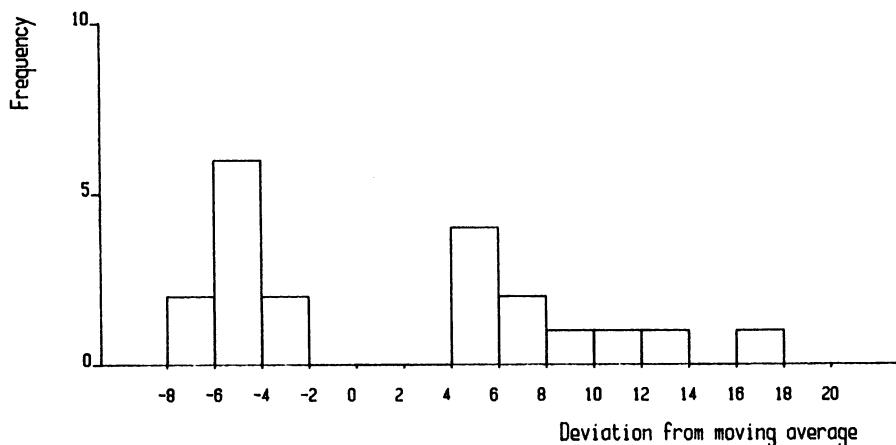
4. DISCRIMINANT ANALYSIS

4.1 Preliminary Tests

Before we examine the results of the analyses, we first consider the underlying assumptions of linear discriminant analysis, namely multivariate normality of the discriminating variables and equal covariance matrices of the two groups of observations. These assumptions are needed for the significance tests of this section, and

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(a) Redstart Data, Portland, Spring



(b) Redstart Data, Portland, Autumn

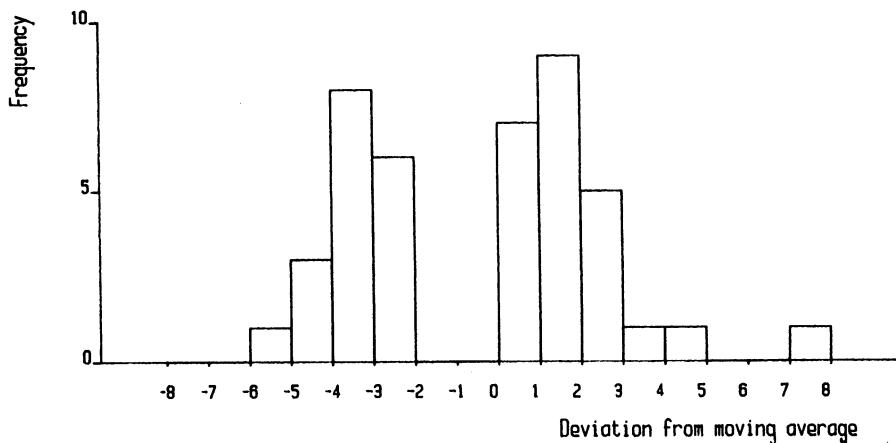


Figure 4 Histograms of detrended daily counts

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also for the stepwise procedures of the following section.

In order to test the equality of two covariance matrices we must assume multivariate normality among the discriminating variables. Mardia (1974) reports that testing covariance matrices is seriously influenced by multivariate kurtosis, but not multivariate skewness. Also, Mardia (1974) states that tests of sample mean vectors such as Hotelling's T^2 are sensitive to skewness rather than kurtosis. In the light of these remarks, the form of multivariate-normality testing that we adopt here is that based on the coefficients of skewness and kurtosis. There are other forms of testing such as those based on the univariate Shapiro-Wilk test (see Royston, 1983), but in the absence of a suitable algorithm, this method involves a formidable amount of computing. A recent review of other forms of testing is given in Mardia (1981). See also Gnanadesikan (1977) and Cox and Small (1978) for reviews.

The coefficient of skewness for a set of data consisting of n observations on p variables is estimated by

$$b_{1,p} = \frac{1}{n^2} \sum_{i,j=1}^n r_{ij}^3$$

where

$$r_{ij} = (\underline{x}_i - \bar{\underline{x}})' \underline{S}^{-1} (\underline{x}_i - \bar{\underline{x}}) ,$$

\underline{x}_i is the vector of observations for the i^{th} case and $\bar{\underline{x}}$ is the vector of means of the discriminating variables. r_{ij} , therefore, is the Mahalanobis angle between the vectors $(\underline{x}_i - \bar{\underline{x}})$ and $(\underline{x}_j - \bar{\underline{x}})$ where \underline{S} is the sample covariance matrix. Mardia (1974) shows that, asymptotically, $n b_{1,p}/6$ has a chi-square distribution with $p(p+1)(p+2)/6$ degrees of freedom for a multivariate-normal population. The coefficient of kurtosis is estimated by

$$b_{2,p} = \frac{1}{n} \sum_{i=1}^n r_{ii}^2$$

which, asymptotically, has a normal distribution with mean $p(p+2)$ and variance $8p(p+2)/n$ for a multivariate-normal population.

Table 2 shows the best statistics for the 16 species/observatory/season combinations. For most of the data sets, the coefficient of skewness is non-significant, suggesting that T^2 tests on the mean vectors associated with these data are feasible

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- these tests form the basis of two-group discriminant analysis. On the other hand for all but 5 data sets, the coefficient of kurtosis is highly significant. This means that tests of equality of covariance matrices will be approximate, and little importance should be attached to the significance levels obtained. Unlike the univariate case, it is difficult to overcome the non-normality by choosing a suitable

Table 2

Test statistics for assessing multivariate normality of the discriminating variables. In each case, p = 14, k represents the standardised statistic for b_2 , i.e., $k \sim N(0, 1)$

Species	Spring		Autumn	
	$nb_{1,p}/6$	k	$nb_{1,p}/6$	k
Sedge W. (D)*	742.7**	0.50	632.4*	-1.55
Willow W. (D)	571.1	-2.55**	587.9	-2.74**
Whitethroat (D)	556.4	-2.43**	762.7**	0.50
Redstart (D)	623.4*	-0.61	550.7	-2.74**
Sedge W. (P)**	369.9	-4.88**	433.4	-4.08**
Willow W. (P)	393.1	-4.61**	422.8	-4.27**
Whitethroat (P)	403.5	-4.47**	454.2	-3.75**
Redstart (P)	389.9	-4.67**	596.2	-1.84*

*significant at the 5% level
**significant at the 1% level

* Dungeness

** Portland

transformation of the data since there are numerous combinations of variables that may need to be transformed. There is little that one can do other than proceed with caution under the assumption of normality.

The test statistic for comparing two covariance matrices is given by the formula

$$\chi^2 = n \log_e |\underline{S}| - n_1 \log_e |\underline{S}_1| - n_2 \log_e |\underline{S}_2| ,$$

where $\underline{S}_1, \underline{S}_2$ and \underline{S} are the sample covariance matrices for the two groups and the pooled estimate of the covariance matrix respectively. (\underline{S}_1 refers to the low count group and \underline{S}_2 to the high count group). This test is a likelihood ratio test and under the null hypothesis χ^2 is asymptotically distributed as a chi-square variate with $\frac{1}{2}p(p+1)$ degrees of freedom, where p is the number of variables, in this case 7.

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We do not use lagged variables here since in several cases there are insufficient data to estimate both S_1 and S_2 . Even with 7 variables, in two cases one group was too small to allow us to estimate its covariance matrix.

Table 3 shows the observed test statistics for each data set. The critical value for the chi-square distribution at the 1% level of significance with $\frac{1}{2}(p+1)p = 28$ degrees of freedom is 48.3. Three of the fourteen observed statistics exceed this value, while none of the other statistics is significant at the 5% level. There is little that one can do about the three significant cases since the implication of the test results is that one should use quadratic discriminant analysis which is known to be unsuitable on small data sets (Lachenbruch and Goldstein, 1979). We

Table 3

Testing the equality of within group covariance matrices. Statistic shown is χ^2 - see text

	Spring	Autumn
Sedge W. (D)	25.8	35.6
Willow W. (D)	36.5	28.6
Whitethroat (D)	28.8	54.6**
Redstart (D)	27.9	31.8
Sedge W. (P)	-	69.1**
Willow W. (P)	36.5	34.4
Whitethroat (P)	-	51.2**
Redstart (P)	40.5	31.5

**significant at the 1% level (5% level critical value = 41.3)

should, however, treat further results pertaining to these data sets with a certain amount of caution. Recall, however, that the significance levels shown in Table 3 are only approximate.

4.2 Results

There is little point in trying to discriminate between two groups of observations if the group means are approximately equal. Before examining results from discriminant analyses it is as well to check the separation of group means. The

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appropriate measure to use is the Mahalanobis squared distance between the two groups of observations which is given by

$$D^2 = (\bar{x}_1 - \bar{x}_2)' S^{-1} (\bar{x}_1 - \bar{x}_2)$$

The significance of D^2 can be tested by calculating the F-ratio

$$F = \frac{n_1 n_2 (n_1 + n_2 - p - 1)}{(n_1 + n_2)(n_1 + n_2 - 2)p} D^2$$

which, under the null hypothesis, has an F-distribution on p and $n_1 + n_2 - p - 1$ degrees of freedom, where p is the number of variables. We first examine the separation of group means using the full set of seven variables, and we introduce lagged variables later on. Table 4 shows the values of D^2 and the associated P-values for the set of 16 data sets, i.e., all combinations of species, observatory and season.

Table 4
Mahalanobis distances between group means using 7 weather variables

Species	D^2	Spring		D^2	Autumn
		P			
Sedge W. (D) ^a	0.35	0.223		1.30	0.002**
Willow W. (D)	2.09	0.000 **		1.63	0.001**
Whitethroat (D)	0.70	0.036 *		1.63	0.000**
Redstart (D)	0.56	0.131		0.51	0.389
Sedge W. (P) ^b	3.11	0.494		4.40	0.077
Willow W. (P)	5.89	0.138		1.93	0.294
Whitethroat (P)	2.23	0.571		3.89	0.004**
Redstart (P)	3.28	0.237		1.34	0.149

^aDungeness

^bPortland

*significant at 5% level

**1% level

It appears that discriminant analysis is likely to be more successful for autumn data than spring, particularly on Dungeness data, and Table 5 shows the classification success rates evaluated using the jackknife method. This method entails classifying each observation using discriminant functions derived from the data set with

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that particular observation omitted. This estimate of the success rate is known to be less biased than certain other estimates; see Lachenbruch and Mickey (1968).

Table 5
Success rates for discriminant analyses using 7 variables

Species	Spring (%)	Autumn (%)
Sedge W. (D) ^a	56.0	67.9
Willow W. (D)	73.6	66.7
Whitethroat (D)	59.8	72.7
Redstart (D)	62.2	52.3
Sedge W. (P) ^b	50.0	59.1
Willow W. (P)	61.1	59.3
Whitethroat (P)	57.9	14.3
Redstart (P)	55.0	57.1

^aDungeness

^bPortland

Table 5 shows that only five of the success rates exceed 65%. These correspond to data sets with a significant D^2 - see Table 4. Success rates of the order of 75% or above are generally considered to be high, but for one data set, the Sedge Warbler data from Portland (spring), a success rate of only 50% was obtained. This means that the allocation of observations would be just as successful if we used a random procedure.

With seven variables in each analysis, it is difficult to spot any patterns among the results, and so we now move to a stepwise analysis where the aim is to include only the important discriminating variables. We also introduce lagged variables (each of the seven variables is repeated, with a lag of one day) in order to try to achieve more successful discrimination for all the data sets. In the interests of simplicity we use the BMDP stepwise procedure where variables are entered or deleted from the analysis on the basis of F-tests. One can set the critical values for the tests and thus control the number of variables that are permitted in the analysis: see Dixon (1981, p.533). In theory, one can set the critical F-value so that a conventional significance level is used, e.g., 5%, but this entails using a different value for each data set since the sample sizes vary from data set to data

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set. In the light of this feature an *ad hoc* approach was adopted *viz.* the choice of an F-value that allows a 'small' number of variables in the analysis, while also considering the results with other F-values to see whether a marked improvement in the success rate was obtainable or not. 'Small' in this context usually meant four or five variables out of fourteen, although the minimum and maximum numbers used turned out to be one and seven respectively.

Table 6 shows the success rates for the stepwise analyses starting from fourteen variables. The figures in parentheses are the success rates obtained in the initial analyses.

Table 6
Success rates for stepwise analyses

Species	Spring (%)	Autumn (%)
Sedge W. (D) ^a	62.1 (56.0)	69.0 (67.9)
Willow W. (D)	75.8 (73.6)	76.9 (66.7)
Whitethroat (D)	68.0 (59.8)	73.7 (72.7)
Redstart (D)	65.6 (62.2)	61.5 (52.3)
Sedge W. (P) ^b	81.2 (50.0)	90.9 (59.1)
Willow W. (P)	88.9 (61.1)	70.4 (59.3)
Whitethroat (P)	68.4 (57.9)	71.4 (74.3)
Redstart (P)	90.0 (55.0)	76.2 (57.1)

^a(D) = Dungeness

^b(P) = Portland

In fifteen of the sixteen cases either the reduction in the number of variables or the inclusion of lagged variables has led to an improved success rate, and in some cases a considerable improvement: see, e.g., the Redstart data from Portland in both spring and autumn. Table 7 shows the corresponding values of D^2 , together with an indication of the significance of each value.

Table 7 shows that we are able to form linear functions of the variables that discriminate between groups. The separation of group means is significant at least at the 5% level in every case.

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Table 7

Mahalanobis distances between group means: stepwise analyses with lagged variables

Species	Spring	Autumn
Sedge W. (D) ^a	0.29*	1.18**
Willow W. (D)	1.99**	3.04**
Whitethroat (D)	1.03**	1.47**
Redstart (D)	0.27*	0.34*
Sedge W. (P) ^b	10.25*	11.27**
Willow W. (P)	5.30**	1.75*
Whitethroat (P)	6.38*	2.81**
Redstart (P)	11.25**	1.60*

^a(D) = Dungeness

^b(P) = Portland

*significant at 5% level

**1% level

One method of investigating which variables are important in the discrimination is to form, for each data set, a single linear combination that best discriminates between groups. This linear combination is referred to as a canonical variate, and since we are discriminating between only two groups, only one such canonical variate exists for each data set. The variate is such that the between group variability in canonical scores is maximised while the variability of within group scores is minimised.

Table 8 shows the coefficients of the weather variables that form the canonical variates. We can see from this table which variables are important discriminators, and, of those that are important, we can see how each variable is weighted. For example, the coefficients for the variate for the spring Sedge Warbler data from Portland include the following components: 0.92 (wind direction, no lag) + 0.42 (wind direction, lag 1) and 0.85 (wind speed, no lag) - 0.76 (wind speed, lag 1). The wind direction component appears to be an average taken over two days with extra weighting on the first day, while the wind speed component appears to represent a sudden increase in mean wind speed over the two-day period. This feature is repeated

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Table 8

Canonical variate coefficients. For each data set, left and right hand columns represent variables lagged by 0 and 1 day respectively

Spring

Variable	Sedge W. (D) ^a	Willow W. (D)	Whitethroat (D)	Restart (D)
Wind Direction			.42	
Wind Speed	.14	.64	.63	
Low Cloud	-.70	-1.07		-1.00
Visibility				
Temperature		-.83		
Humidity			-.85	
Pressure			-.50	
	Sedge W. (P) ^b	Willow W. (P)	Whitethroat (P)	Restart (P)
Wind Direction	.92	.42		
Wind Speed	.85	-.76	1.34	-.83
Low Cloud		1.56	-1.66	1.33
Visibility			-1.85	1.34
Temperature	-.84	1.29	-.68	
Humidity				1.17
Pressure				1.42

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Table 8 (Cont'd.)

Autumn					
Variable	Sedge W. (D)	Willow W. (D)	Whitethroat (D)	Restart (D)	
Wind Direction		-.56 .44	-.42		
Wind Speed	.95		.76	1.00	
Low Cloud					
Visibility		-.68 .56	-.42		
Temperature	.41	.48			
Humidity			-.32		
Pressure		-.85	-.54		
	Sedge W. (P)	Willow W. (P)	Whitethroat (P)	Restart (P)	
Wind Direction	-1.38	-.64	-.65		
Wind Speed	1.58 .68	.87	.75	.62	
Low Cloud		.65		.54	
Visibility				.93	
Temperature	1.54		-.55	1.05	
Humidity					
Pressure					

^a(D) = Dungeness

^b(P) = Portland

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in several cases, as Table 8 shows, and emphasises the usefulness of including lagged variables. One could, of course, include variables with a lag of, say, two days, enabling local maxima or minima to be detected - for example a rise in pressure after several days' decrease may indicate the passing of a low pressure system which in turn brings a wave of migrants.

It is difficult to pick out any interesting patterns from Table 8, save for the fact that there is such a wide variety of weather variables included. There appears to be great variability between species, and there seems to be no noticeable similarities or differences between observatories or seasons. Also, several cases involve no lagged variables at all, while one case, the Whitethroat (spring) at Dungeness consists entirely of lagged variables.

The variable that occurs in most cases in Table 8 is wind speed (fourteen out of sixteen cases), whether lagged by one day or not. This is followed by temperature (eight cases), wind direction (seven cases) and low cloud cover (seven cases). The fact that these variables appear in approximately half the cases might suggest that this subset of the seven variables may be able to discriminate between groups satisfactorily for all cases, although not being the optimal subset in each case. If this was the case, then this would greatly simplify any applications of this work, such as the construction of migration indices using totals of migration counts weighted according to the number of 'bird days' in each season for example - see Section 1.

Table 9 shows the results of attempting to discriminate between groups using the same set of four variables (and associated lagged variables) in every case. In all but one case the jackknife success rate has fallen with the use of a common subset of variables and indeed, the Mahalanobis squared distance between groups is not significant in over half of the cases. There may possibly exist a subset of the fourteen variables that is suitable for discrimination in each case, although sub-optimal, but the question is how do we find it? In the above example we have taken an educated guess and found that the subset is not suitable for the whole set of cases. Ideally one would examine every subset but, even for seven variables, there are 127 possible subsets to examine over sixteen sets of data. It would appear that in order to achieve good discrimination in each case, the cases need to be treated individually.

We now briefly return to Table 8 and attempt to give simple ornithological interpretations to some of the variables that occur in the canonical variates. The

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Table 9

Mahalanobis distances and jackknife error-rates for analyses using a common subset of four variables

Species	D ²	Spring Success Rate	D ²	Autumn Success Rate
Sedge W. (D) ^a	0.56	57.8%	1.38**	60.7%
Willow W. (D)	2.17**	73.6%	1.25**	66.7%
Whitethroat (D)	0.78*	57.7%	1.59**	70.7%
Redstart (D)	0.57	57.8%	0.57	52.3%
Sedge W. (P) ^b	10.99	62.5%	13.35**	90.9%
Willow W. (P)	7.15	66.7%	3.03	55.6%
Whitethroat (P)	2.10	47.4%	3.28*	68.6%
Redstart (P)	5.09	65.0%	0.80	57.1%

^a(D) = Dungeness

^b(P) = Portland

*significant at the 5% level

**1% level

most frequently occurring variable is wind speed (variable 2). From the data it is clear that high wind speeds are associated with low counts of migrants. This is contrary to what we may have expected since calm weather is usually regarded by ornithologists as being associated with low counts, but if we look further we find that for those datasets where wind direction is found to be an important discriminator, the high winds associated with the low counts are in fact favourable winds, i.e., blowing in the direction of the birds' flight. It is not surprising that such conditions encourage birds to fly straight over the coastal observatories. An important variable in spring, and to a lesser extent in autumn, is low cloud cover. In all five cases featuring this variable in spring, low amounts of low cloud cover are associated with low counts of migrants. This again confirms the opinions of observatory workers and visitors which were hitherto based largely on practical experience as opposed to scientific investigation.

Taking the data sets as a whole, it is difficult to determine any other consistent features as regards variables.

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There are no obvious differences between the results for spring and autumn apart from a suggestion that lagged variables are slightly more important in spring than autumn. The success rates for individual species are much the same for both seasons, although the power of discrimination differs between Portland and Dungeness observatories for the Sedge Warbler and Redstart. In both cases the success rates are considerably higher for the Portland data. The average success rate is also higher for Portland: 80% compared with 69% for Dungeness. This may be due to the geographical differences between the two sites. The distance travelled over sea by those spring arrivals passing through Dorset is considerably larger than the distance from France to Kent. If bad weather is met by birds heading for Dorset then by the time they arrive at the coast one would expect them to be more exhausted and disorientated than those birds taking a shorter crossing. Similarly, birds that are about to depart in the autumn may be more reluctant to do so from Dorset in poor weather since the sea crossing is that much longer.

4.3 Summary of the Main Results of the Discriminant Analysis

In this section the main conclusions that may be drawn from the discriminant analyses are summarised. Eleven conclusions are listed, but of course many more details are available in the tables of results that are presented in Section 4.2.

- (i) There is some evidence to suggest that discriminant analyses are more successful when using autumn data rather than spring data;
- (ii) Discrimination was, in general, improved by using lagged weather variables;
- (iii) Subsets of lagged weather variables were found to be adequate for successful discrimination. Most subsets contained approximately four or five variables;
- (iv) High discrimination success rates were obtained for the following data sets (see Table 6):
 - (a) Sedge Warbler, Portland - autumn
 - (b) Willow Warbler, Portland - spring
 - (c) Redstart, Portland - spring and autumn;
- (v) Low success rates were obtained for the following data sets (see Table 6):
 - (a) Sedge Warbler, Dungeness - spring
 - (b) Redstart, Dungeness - autumn;

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- (vi) Successful discrimination - as measured by the statistical significance of D^2 between groups - was achieved for every data set;
- (vii) Different variables appear to be important for different data sets, although wind (direction and/or velocity) appear to be an important feature for most data sets;
- (viii) Lagged variables are not predominant in the optimal subsets of discriminating variables, but several occurrences of the difference between a weather observation on one day and the previous day are seen;
- (ix) No common subset of variables suitable for discrimination is readily available, but no suitable method of finding such a subset is known;
- (x) High winds in the direction of birds' flight appear to give rise to low counts at observatories; and
- (xi) Low amounts of cloud cover appear to give rise to low counts of birds at observatories.

5. DISCUSSION

Many examples of regression analyses using weather and migration data are to be found in ornithological or biological journals. The results from these studies are generally difficult to interpret since large numbers of variables are used and in many different forms (transformations, differences, etc.). Furthermore, it is doubtful that the data stand up to the rigorous demands made by multiple regression - for example, normality, linearity and independence. This paper offers not only an alternative to multiple regression, but a study of the relationships between weather and migration data which is kept on a very simple level.

This work is not the first attempt at using discriminant analysis in this area, although the two previous attempts (Able, 1973, and Richardson, 1974), used radar data. Able (1973) divided his observations into eight groups according to the direction of flight of the migrant passerines, and obtained a significant canonical variate for discriminating between groups. He used seven weather variables selected on the basis of univariate F-tests, but employed no further variable selection techniques so it is not clear whether the subset is optimal in any sense. Although Able's work is not comparable with the results of the present paper - he used autumn

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radar counts of passerine migrants - it is encouraging to see that wind direction was found to be an influential variable. Richardson (1974) also used autumn radar counts, and reported overall classification success rates of less than 60%. However, he used three groups for his analysis, and so one would expect lower success rates than those reported in the present paper. Note that Richardson does not make clear whether or not his success rates are apparent or jackknife estimates, and so the true success rates may well be lower.

One of the objectives of the work reported in the present paper was to construct a migration index for monitoring population levels of common summer migrants. The above has shown that simple general rules using weather information, for all species, are not likely to be forthcoming. The success with some species is, however, worth following up when more data become available - for example, data from more observatories and for longer time periods. Certainly the weather variables included in the relevant discriminant functions can be explained in simple terms.

ACKNOWLEDGEMENTS

I would like to thank Drs. B.J.T. Morgan and P.M. North for their supervision of this work, as well as their comments on an earlier draft of this paper.

I would also like to thank the British Trust for Ornithology for allowing me access to their archives of observatories data.

This research was supported by a Science and Engineering Research Council Studentship and a Studentship from the University of Kent, Canterbury, England.

STATISTICAL PROBLEMS IN THE STUDY OF SEED-EATING BIRDS

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SUMMARY

The 'profitability' of different sizes of seeds can be assessed as: kernel weight divided by the time taken to eat (handling time). Experiments with bullfinches eating sunflower seeds showed that handling times for larger seeds may be greater or smaller, depending on experimental context, and on which dimension of seed size is measured. There was very little variability of kernel weight among seeds of a given size, but handling times were highly variable, and bullfinches apparently judged the ease of handling by brief manipulation of seeds before choosing one to eat. Many periods of handling ended without the seed being eaten, owing to deliberate or accidental dropping, and cause difficulties in calculating average handling times that reflect birds' likely feeding costs. Field observations of bullfinches feeding on ash seeds implied that wild birds may forage similarly to those in laboratory experiments.

Keywords: BULLFINCHES; SUNFLOWER SEED; FORAGING BEHAVIOUR; HANDLING TIME;
SEED SIZE; PROFITABILITY

1. INTRODUCTION

In the recent upsurge of quantitative studies concerned with the adaptive aspects of animals' tactics, both birds and statistical techniques have played a prominent part. A large number of experimental tests have employed birds as subjects (see Cúrio, 1976; Krebs, 1978; Kamil and Sargent, 1981), and it is convenient to accommodate the natural variations of behaviour by the use of routine descriptive statistics. However, potential problems arise because of the ways in which foraging behaviour can be measured and summarised. In this paper I wish to illustrate how

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the biological interpretation of foraging experiments may suffer through over-reliance on certain statistical measures of behaviour. Examples will be drawn from results obtained in a continuing series of experiments concerned with the tactics used by Bullfinches (*Pyrrhula pyrrhula*) feeding on a variety of plant seeds. This work is directed at understanding the reasons for Bullfinches' dietary preferences, in order to improve the prospects for diverting their foraging from the buds of commercial fruit-trees onto alternative wild foods.

2. COSTS AND BENEFITS OF FEEDING

For animals that eat discrete items of food, it has become accepted practice to calculate the 'profitability' of individual items, by balancing food content (benefit) with the time taken to eat (cost), on the assumption that animals are limited in the time available for feeding (Schoener, 1971). The way in which observational data are taken to support this view can be illustrated by an early study (Hespenheide, 1966) of the North American White-throated Sparrow (*Zonotrichia albicollis*) feeding on sunflower seeds (*Helianthus annuus*) (Figure 1). Average kernel weights, and the birds' handling times (i.e. the time between picking up a seed, and finishing eating it) were computed for a range of seed size classes, and both showed a progressive increase with seed size. Their ratio, however, declined with increasing seed size, and corresponded closely to the numbers eaten by the birds in a choice experiment, apparently demonstrating an adaptive preference for the smaller, more profitable seeds. To explore why a more detailed approach is required for this kind of investigation, I will examine the behaviour of Bullfinches eating the same kind of seed.

3. HANDLING TIME AND SEED SIZE

Positive relationships between handling times and the size of food items, such as that illustrated in Figure 1, are so widespread as to be considered almost universal in birds (e.g. Willson, 1971; Goss-Custard, 1977; Draulans, 1982; Sutherland, 1982; Sherry and McDade, 1982). Measurements of Bullfinches' handling times in two experiments with sunflower seeds reveal how fragile that assumption is. In Experiment I, eight birds were individually offered dishes containing seeds of a single size class. Seed size classes were defined by three weight categories and four length categories, and each bird received a one-hour trial with each of the twelve classes, in random sequence, separated by periods of deprivation. In Experiment II,

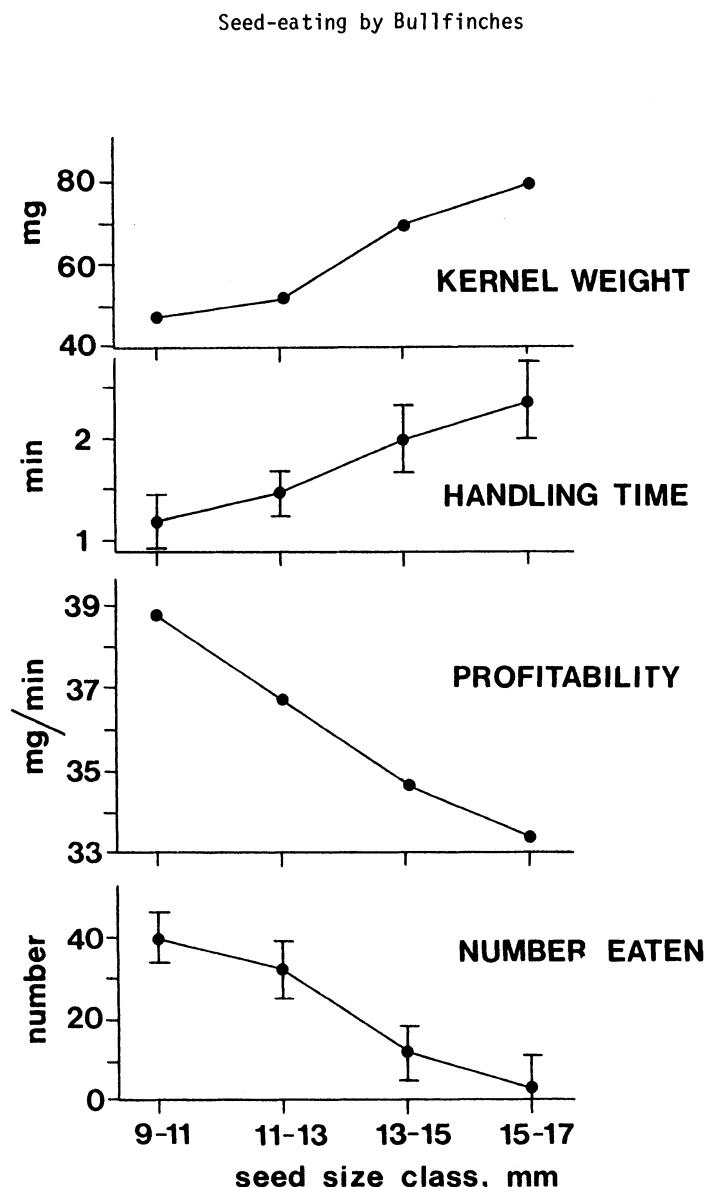


Figure 1 Average measurements, profitability (kernel weight/handling time) and numbers of sunflower seeds eaten by three White-throated Sparrows (data from Hespenheide, 1966).

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nine birds experienced three-hour trials in which they were presented with a sequence of randomly-chosen pairs of seeds, and allowed to eat one seed from each pair before the other seed was removed, and the next pair introduced. Seed weights, lengths, widths, and thicknesses were measured exactly, but for the present purpose seeds are grouped into a series of size classes based on weight and length, as in Experiment I. The only difference affecting the physical process of husk removal was that birds in Experiment I handled seeds above a solid floor from which they could retrieve seeds that fell, whereas in Experiment II, seeds that dropped were lost through a barred floor.

Figure 2 shows average handling times in the two conditions, with data for all birds combined. The results are presented separately in relation to seed weight and seed length classes. In both cases, handling times increased with increasing seed weight, but whereas in Experiment II the relationship with seed length was also positive, in Experiment I it was strongly negative. The cause of this unexpected difference is difficult to identify, because there were many changes between experiments in the procedure, and pattern of presenting seeds. A further series of observations showed that in otherwise identical conditions, Bullfinches took longer to eat seeds of a given size, and were less likely to drop them above a barred floor than above a solid floor (Greig-Smith, 1984). Thus the difference may have been connected with an adjustment of handling technique in the face of the added risk of losing dropped seeds. However, the important feature of Figure 2 for the present discussion lies in the fact that if the size of seeds had been measured only by weight (as in Willson's (1971) study of N. American finches), very different conclusions would have been drawn from Experiment I, and by comparing the two experiments than if length alone had been measured (*cf.* Hespenheide, 1966). Thus an experimenter's choice of which aspect of prey size to measure may be critical, and for food items which vary greatly in shape as well as in size, a multivariate analysis of several dimensions may be necessary.

4. VARIABILITY OF COSTS AND BENEFITS

Although a bird's natural foods are generally available in a continuous range of sizes, items used in experimental studies are commonly classified into a relatively small number of categories, often merely 'large' and 'small' (e.g. Krebs *et al.*, 1977). The variability of behaviour in relation to size can then be expressed by computing averages for each category, as in Figure 2. This has certain advantages, in simplifying analyses and reducing numbers of experimental trials, but

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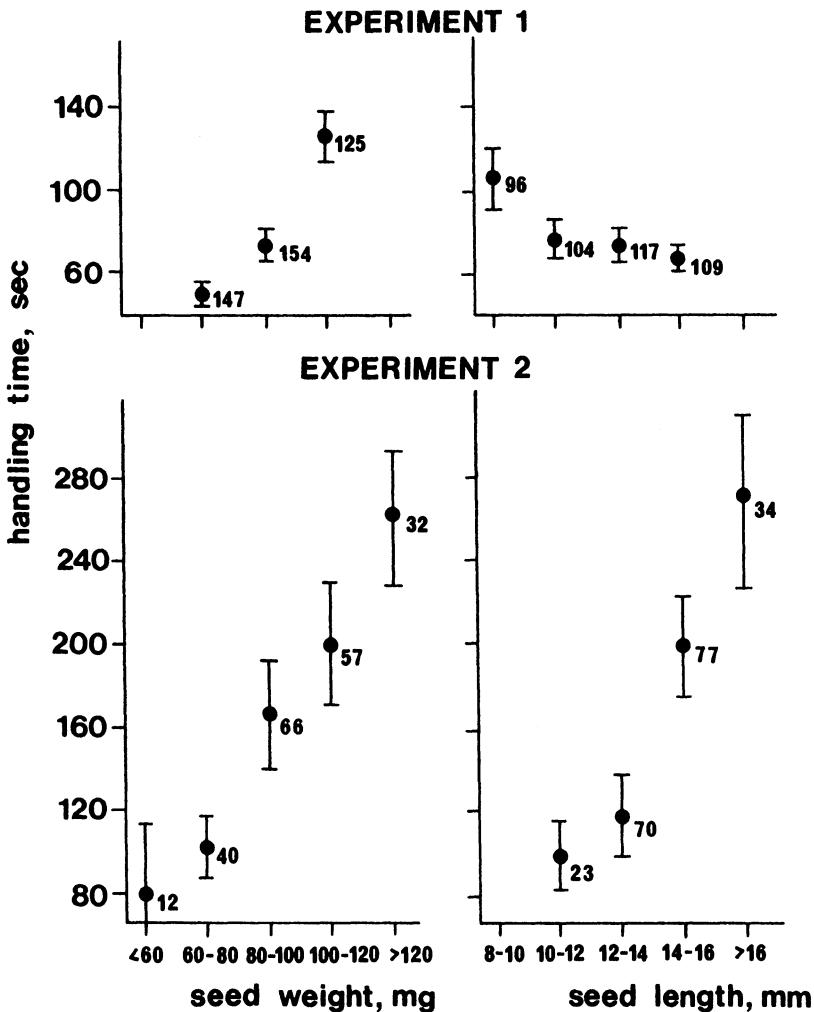


Figure 2 Average handling times (mean \pm s.e.) for Bullfinches feeding on sunflower seeds in two experiments, in relation to seed length and seed weight.

Sample sizes are beside the points. In all four cases, linear trends were highly significant ($P < 0.002$).

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may encourage mis-interpretation when the food concerned does in fact vary over a continuous range. The behaviour of Bullfinches eating sunflower seeds again provides an example of the problem.

Figure 3 shows the average kernel weights and handling times obtained for sunflower seeds of five size classes. Both show obvious positive correlations with seed size, and regression analyses using logarithmic transformation of handling times provided statistical confirmation of highly significant trends ($P<0.001$). From these data, it is easy to conclude that it would be adaptive for the birds to base their feeding preferences on a trade-off between the slopes of these two relationships, and Figure 3 shows that the smallest seeds were the most profitable. However, 'exact' measurement of seed sizes (to the nearest 1 mg) revealed a more complicated situation. Kernel weight still showed an obvious, close relationship with seed size, and indeed, linear regression accounted for 88% of the variance in the sample of 200 seeds. In contrast, there was a huge scatter in the plot of handling times against seed size, and although some of the largest seeds were very slow to handle, others were dealt with as rapidly as were the smallest seeds (Figure 4). This pattern of variability presents rather different opportunities to the birds than the picture implied by relying on the trends of means shown in Figure 3. In this case, and perhaps generally, it is more informative to measure prey sizes 'exactly' than to group items into a few broad size categories.

Variability in the costs of eating a particular size of seed may be an important determinant of birds' feeding preferences. Recent theoretical models and experimental tests (Real, 1980; Caraco, 1980, 1981; Stephens and Charnov, 1982) have shown that birds may respond to both the mean and the variance of alternative feeding opportunities, and the relative weight given to each aspect may depend on factors such as whether they are able to meet their daily energy requirements. Thus although the preferences shown by Bullfinches in a series of choice experiments, in which they selected light sunflower seeds (Greig-Smith and Crocker, in preparation), is consistent with a simple model of profitability based on average values of kernel weight and handling time (Figure 3), it would be equally possible to interpret this result as a preference for low variance in the rate of food intake.

5. POWERS OF ESTIMATION

The patterns of variability described above mean that it should be easy for a bird to estimate the likely food content of a seed by visually judging its size, before starting to handle it. It could hardly achieve the same certainty about

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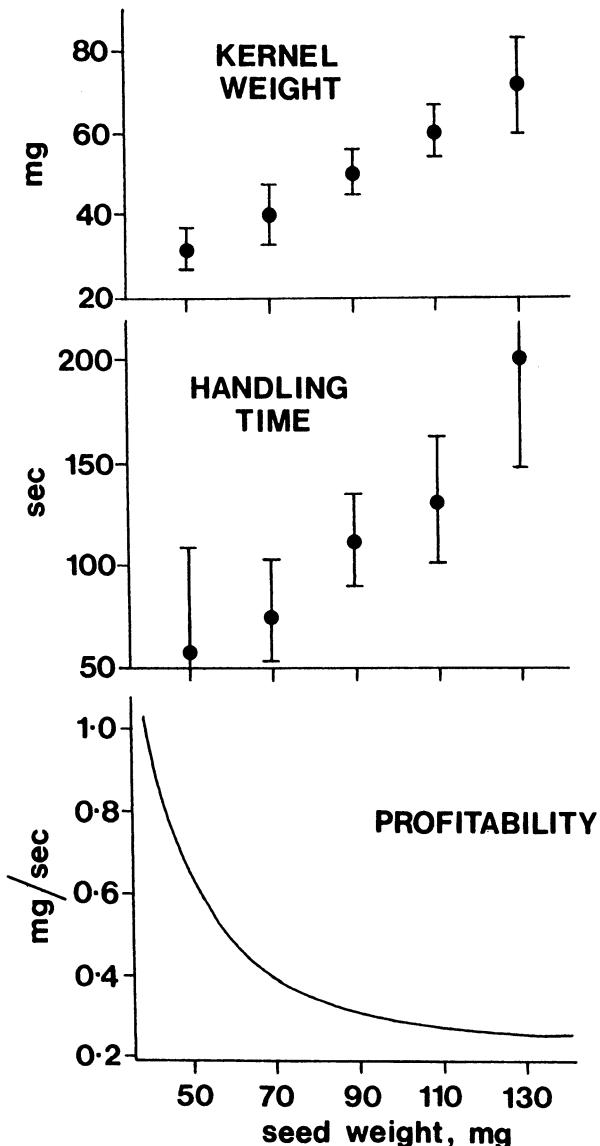


Figure 3 Variations in average kernel weight and handling time (with 95% confidence limits) in relation to seed size, and the profitability of feeding, computed as kernel weight divided by handling time.

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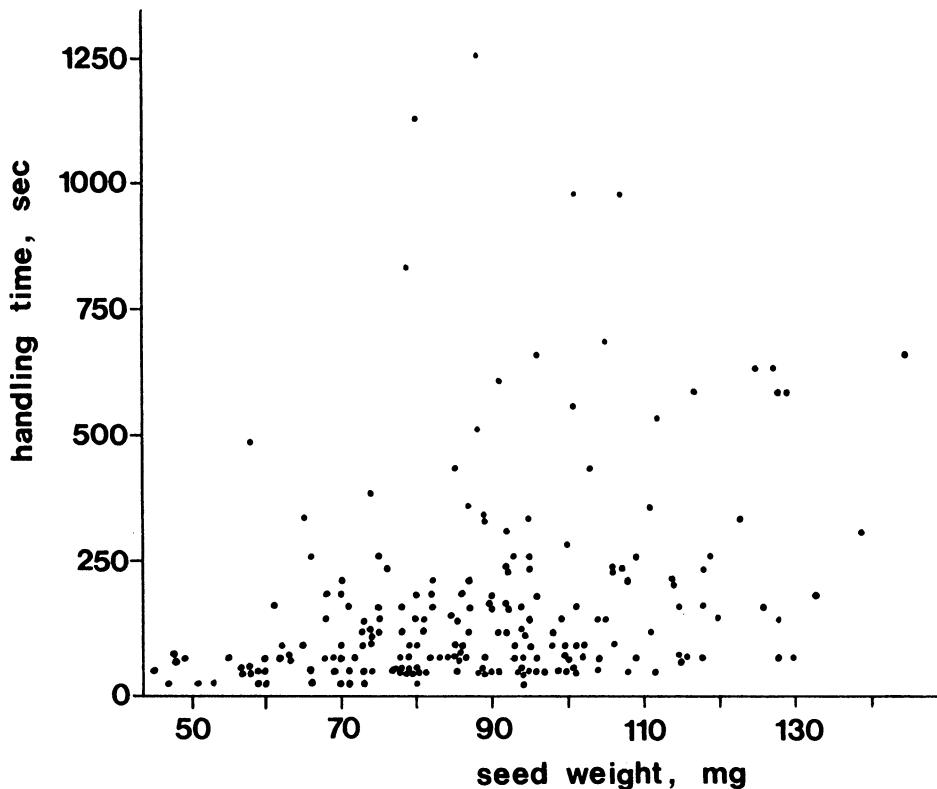


Figure 4 Individual handling times for eight Bullfinches eating sunflower seeds, in relation to seed size measured to the nearest 1 mg.

likely handling time, however, and any behaviour which would help birds to overcome this problem, and permit more accurate prediction of likely handling costs, should be strongly favoured. Results from an experiment in which Bullfinches had to choose between pairs of sunflower seeds revealed such a mechanism. On up to 75% of choices, birds undertook repeated 'exchanges' of seeds, in which they briefly handled one, then the other, often several times, before finally removing one seed for a genuine attempt to crack the husk. Examination of the sizes of the seeds involved (Table 1) showed that birds were equally likely to start a session of exchanges with the

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Table 1

Relative sizes of sunflower seeds chosen at the start and at the end of sessions in which Bullfinches repeatedly 'exchanged' seeds that were available in pairs.

	heavier	lighter	Binomial tests
First seed picked up:	32	25	NS
Seed chosen to eat:	16	41	P<0.001

heavier as with the lighter seed of the pair, but that they eventually elected to eat the lighter seed on 72% of occasions - a result with a change expectation of less than 0.1%. This strongly suggests that these exchanges constitute a direct comparison of the likely ease of handling of the alternative food items, and the time needed to do so should be incorporated with the handling time in assessing costs. This factor can introduce changes to the profitability rankings of foods when some types can be readily assessed visually but others require substantial 'recognition time' (see Hughes, 1979). Although many foraging models assume perfect knowledge for feeding prospects, it is clear that the abilities of birds to accurately estimate the costs and benefits of foods without trial and error can neither be assumed by the experimenter, nor ignored in deriving quantitative predictions (see Orians, 1981).

6. UNFINISHED SEED-EATING

The tactic discussed in the previous section, of briefly 'testing' the suitability of seeds before choosing one to eat, introduces a further area of difficulty. This is connected with the calculation of average handling times for food types, and arises because not all periods of handling end with the seed being eaten. Indeed, the distribution of 'unfinished' handling times (Figure 5) comprises records of three different kinds. As described above, many short spells of handling probably represent preliminary assessment of seeds (these appear to predominate in the highly skewed distribution of Figure 5). However, some seeds were clearly dropped accidentally while being manipulated in the bird's bill, and on other occasions, behaviour suggested that seeds were abandoned 'deliberately', usually after very lengthy periods of unsuccessful attempts to crack the husk. The problem posed for an experimenter trying to estimate a bird's likely handling costs is one of how to combine these possibilities with the distribution of the readily measurable 'successful' handling times. Should the risks of dropping seeds, and failing to open the

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husks be treated separately from actual handling times, as probabilities of the outcome, or can the distribution of measured times be modified by the addition of estimated 'missing values' for such seeds? In either case, it is necessary to distinguish between these three kinds of failure to finish eating a seed (and perhaps other possibilities, such as being robbed by a competitor), which may be operationally difficult to achieve.

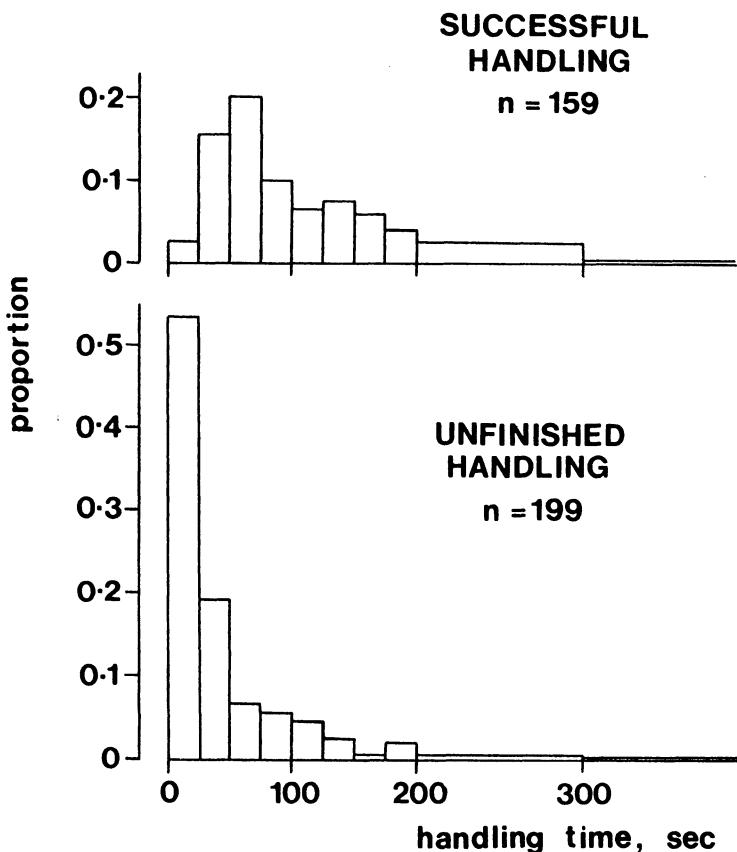


Figure 5 Frequency distributions of 'successful' and 'unfinished' handling times for Bullfinches eating sunflower seeds

Seed-eating by Bullfinches

These problems are serious only for birds which frequently fail to handle seeds successfully (Bullfinches may do so with 80% of certain size classes of sunflower seed), but they have passed apparently unrecognised in most studies, even when unsuccessful attempts at handling have been recorded (e.g. Sherry and McDade, 1982; Grant, 1981). The use of easily-handled food types in experiments may circumvent the problem, but prevents generalisation to the full range of the animal's foods.

7. SEED-EATING IN NATURAL ENVIRONMENTS

It may reasonably be argued that the behaviour of an animal in an alien laboratory environment, eating foods which it does not encounter in the wild, is unlikely to correspond to that displayed in natural feeding conditions. One of the major winter foods of wild Bullfinches is the seed of ash trees (*Fraxinus excelsior*), which in some years can account for over three-quarters of the diet (Newton, 1964; Summers, 1981; Greig-Smith, unpublished data). These seeds are analogous to sunflower seeds in several respects - they provide a relatively large food reward (20-60 mg per seed), hidden by a fruit coat which the bird must remove; they entail a lengthy handling time (up to 130 sec, average 35 sec); and they are variable in both size and shape. As with sunflower seeds, kernel weight is well predicted by external dimensions, whereas handling costs show much greater variance (unpublished data).

Observations of the behaviour of feeding Bullfinches showed that many ash fruits were dropped during handling, in circumstances comparable to those seen in the laboratory. Indeed, the overall distributions of 'successful' and 'unfinished' handling times obtained for birds feeding in ash trees were very similar in form to those shown in Figure 5. Also, though birds usually fed in the canopy, plucking fruits from the twigs, they did sometimes eat fallen seeds on the ground, and adjustments of handling techniques associated with the risk of losing a dropped seed in cage experiments may be directly relevant to foraging opportunities in the wild.

In many respects, therefore, the features of seed-eating behaviour in the field appear to be similar to those that were explored in the laboratory experiments with unfamiliar seeds. However, this correspondence should never be lightly assumed, since apparently small changes in experimental procedure may encourage different behaviour (e.g. Figure 2, and the difference between successive and simultaneous food choices; Waddington, 1981). Laboratory studies can only benefit by continual reference to behaviour in natural conditions, to ensure their relevance to an understanding of the evolved feeding strategies of the animals.

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ACKNOWLEDGEMENTS

I am grateful to Nicola Kemp and Diana Richardson for assistance with experiments, and Joe Crocker for his comments on the manuscript.

MODELS TO DESCRIBE RAZORBILL MOVEMENTS

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SUMMARY

Accumulated ring recovery data provide information on the movement behaviour of Razorbills (*Alca torda*). Earlier, descriptive work has been done to investigate the movements of British ringed Razorbills. The present paper outlines some random walk or stepping-stone type models which might be used to describe the movements of these birds.

Keywords: RAZORBILL MOVEMENTS, RANDOM WALK MODELS, STEPPING-STONE MODELS, RING RECOVERIES

1. INTRODUCTION

Razorbills (*Alca torda*), spend most of their lives at sea, since they only need land in order to breed (Mead, 1974). When they move, they also travel by sea routes. Recoveries of ringed Razorbills provide information on the patterns of their movements: see Lloyd (1974). Her approach to the data analysis was very simple and North (1980a) discusses associated problems and the interpretation of Razorbill ring recovery data generally.

The data (kindly provided by Dr. Lloyd) which are discussed in this paper all refer to dead birds. Extreme care needs to be exercised in the interpretation of such data and, for example, cause of death needs to be taken into account (see North, 1980a). Mead (1974) states that Razorbills do not normally breed until they are four years old, and they may or may not return to the breeding colony at the end of their first year of life. Therefore, just two age groups of the birds are considered here, namely

- (i) first year birds; and
- (ii) fifth year and older birds (henceforth called "adults").

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This is because if any differences in movement behaviour exist for distinct age groups of Razorbills, we might reasonably expect the two age groups chosen to show up the most extreme differences. (Lloyd, 1974, also considered different age groups of birds and North, 1980a, used just the two groups examined here).

Although the purpose of the present study is to attempt to model the movement patterns of live birds, as we have seen the only available data refer to ring recoveries of dead birds, and this causes problems when trying to make inferences from the data. For example, rings are often not recovered where birds die, e.g. when birds die at sea and are subsequently washed ashore. Even if a ring is recovered from the place where the bird died, it is not known whether the bird was in transit.

This paper presents models which might serve as useful descriptors of Razorbill movement patterns, as reflected by ring recovery data. Unfortunately the amount and nature of the data available precludes formal fitting and checking of the models, and choosing between them.

2. BACKGROUND TO THE MODELLING

We shall be concerned here with two types of movement, namely migration and dispersal. The distinction between these movement types has been of interest to ornithologists before: see, for example, Lloyd (1974). We illustrate the discussion here with data sets from two distinct time periods in the yearly cycle, namely the period when birds are in transit to their winter quarters (for migration) and the period when birds are in their winter quarters (for dispersal), for reasons given below.

We shall need an assumption to define these two periods. Now, adult Razorbills first start to attend the breeding colonies regularly from March onwards (Mead, 1974); immature birds may attend later. After the breeding season Razorbills from the South Irish Sea colonies are first reported in the Mediterranean in November, and are most numerous there in December (Lloyd, 1974). We therefore assume that recoveries of birds in the period August to October inclusive correspond to birds in transit, and that recoveries in the period November to February inclusive correspond to birds in their winter quarters. Recoveries from birds known to have been killed directly by man's actions (e.g. shooting) are omitted from consideration here, and attention is given solely to birds "found dead" or "oiled". Further discussion of the division of the available data into subgroups is given by North (1980a).

Razorbill movements

In the modelling that follows, to maintain simplicity we make the important assumption that for birds not killed directly by man's actions, the ring recovery and reporting rates are constant over space and time. While this assumption is unlikely to be strictly true in practice, it is hoped that it provides a reasonable approximation to reality. If not, the available data cannot be used to indicate whether any of the models proposed here are suitable. A similar concern underlies the assumption of a constant ring reporting rate in many bird survival studies: see, for example, Anderson, Wyrialowski and Burnham (1981), and also Lakhani (1985).

Since on their journeys Razorbills either cross stretches of sea, or follow coastlines, in the models that follow we consider motion to be along a straight line, as an approximation to reality.

The recoveries that are considered in this paper are grouped into equal-width (100 miles = 160 km) distance zones, as in Lloyd (1974) and North (1980a). Movement between these zones can be considered analogous to jumps between the points of a one-dimensional random walk, which forms the basis of the models discussed here. Holgate (1971) has previously considered random walk models for animal behaviour, with particular reference to home ranges and trapping problems.

In a random walk along a straight line a bird proceeds in a succession of independent steps. After any one of these steps the probabilities associated with the different possibilities at the next step are as follows:

$$\begin{aligned} P(\text{step forward}) &= p \\ P(\text{step backward}) &= q \\ P(\text{no movement}) &= 1 - p - q \end{aligned} \tag{1}$$

This may be represented diagrammatically as in Figure 1.

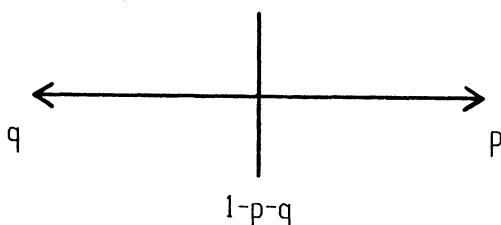


Figure 1 Illustration of a random walk model

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3. MODELS FOR MIGRATION

We first consider models for migration. A simple model of this type is as follows. We suppose that the Razorbills undergo a two-stage process at each time point under consideration (e.g. daily), of the form:

- (i) a transition stage (according to a random walk modelling the movement); then
- (ii) a mortality stage.

Although a simplification of reality, this modelling by stages is similar in concept to that of Pennycuick (1969), when modelling a Great Tit (*Parus major*) population and of North (1983) in his development of birth-death-maturation bird population models.

North (1978) gives the zone occupancy probabilities, and their eventual form after n (large) double stages, for the following model of the above type. The transition stage is described by a simple random walk allowing only forward movement, or no movement (i.e. $q = 0$ in (1)), and after each step of this random walk the bird survives with probability s , or dies with probability $1 - s$.

It can be shown that when p , the transition probability, is small and s is large, the predicted form of the distribution of dead birds eventually approximates a geometric distribution. (We would expect the survival probability over short time periods for Razorbills to be large, and the transition probability, p , to be fairly small, since the movements are assumed to take place over three months.)

Because this model cannot be homogeneous in time (since if movement continued for a long time in this manner, some birds would just move further and further away from the breeding colony) and because a death process has been superimposed on the movement process, the time period whose data are appropriate for illustrating this model is that from August to October, when the birds are moving to their winter quarters. Figure 2 shows the distribution of such recoveries for first year birds (there are too few recoveries of adult birds in this period to warrant representation in this way). Inspection of Figure 2 suggests that a death-migration model of the type introduced above might describe these data reasonably well.

The models of Bailey (1968), Adke (1969) and Renshaw (1972, 1974, 1977) can also be considered as the basis for a Razorbill movement model. In particular, Renshaw's (1972) birth-death-migration model can be applied to the Razorbill

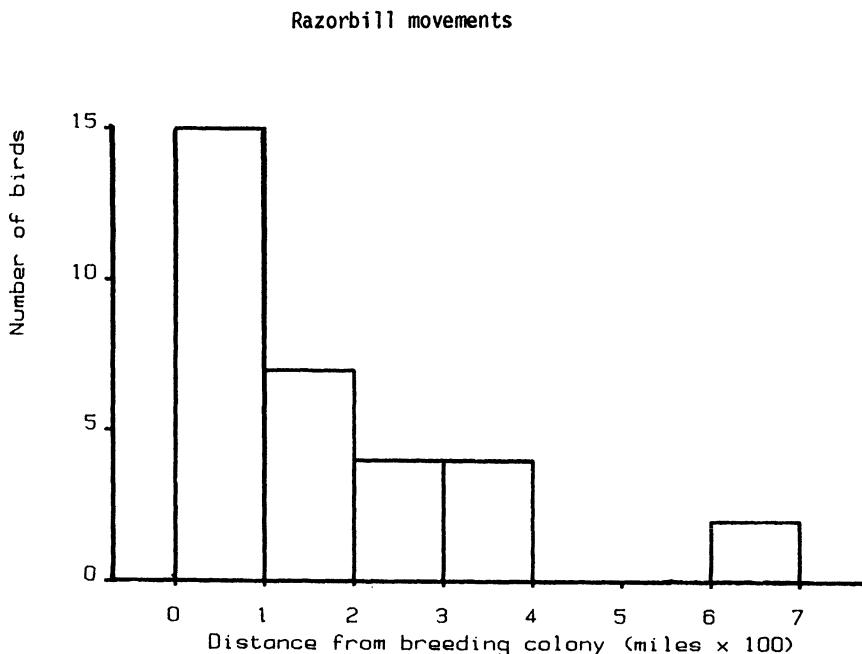


Figure 2 Distribution of recoveries of first year Razorbills, not known to have been killed directly by man's actions, from Skokholm and Skomer in the period August to October inclusive.

recovery data in the autumn movement period in the special case where the birth rate is zero (see North, 1978, for further details). Also presented there are further details of the simple death-migration process, in which motion is in one direction only among the zones, now assumed to be infinite in number. This model also appears to be a plausible descriptor of the Razorbill autumn recovery data, and the geometric distribution again occurs as a limiting distributional form.

4. MODELS FOR DISPERSAL

In the model to describe dispersal from the breeding colony, the colony corresponds to zone 0 and constitutes a 'reflecting barrier' in the random walk proposed. Suppose the possible transitions for a bird in zone i , in a small unit of time (e.g. one day) are as follows:

- (i) move to zone $i + 1$ with probability p ($i \geq 0$)
- (ii) move to zone $i - 1$ with probability q ($i \geq 1$)

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- (iii) remain in zone i with probability $1 - p - q$ ($i > 1$)
- (iv) remain in zone i with probability $1 - p$ ($i = 0$).

Such a model is too simple and one which is likely to be more reasonable as a descriptor of the Razorbills' movements has some position-dependence built into the transition probabilities (for otherwise, if $p > q$, there is a tendency for drift further and further away from the breeding colony). A simple case of position-dependency arises if the forward and backward transition probabilities are p_1 , p_2 and q_1 , q_2 respectively ($p_1 > q_1$, $p_2 < q_2$), according to whether $i < k$ or $i > k$, for some fixed integer k , where i is the number of the zone occupied just before the transition. Of course, other more complex models could be proposed in which transition probabilities change over all the zones, but will not be considered further here.

An equilibrium distribution exists for this process: the zone occupancy probabilities are given by North (1978). They increase with i for $0 < i < k$ and decrease with i for $k + 2 \leq i < \infty$, the modal zone being at k or $k + 1$, or both, depending on the relationship between p_1 and q_2 .

This model for dispersal incorporates movement only, and the equilibrium distribution indicates what the distribution of live birds would be after a large number of steps of the random walk.

The appropriate data set to illustrate this model is from the period November to February, when birds will have undergone their (possibly) dispersive movements to reach their winter quarters. Although it is dead birds that are recovered, their distribution should reflect that of the live birds if the birds are stationary within their winter quarters in this period.

Figure 3 shows the distributions of Razorbill recoveries in the period November to February, for first years and adults separately. Note the suggestion that the favoured wintering area for first years is somewhat further from the breeding colony than for the adult birds. A dispersal model of the type described above could describe the data for first year birds well. The data for the adult birds suggest a distinct preference for localities up to 400 miles away, with very few birds being found further away - suggestive of migratory movement. However, whether this result is real, or merely a spurious outcome of the small data set available is not known.

Razorbill movements

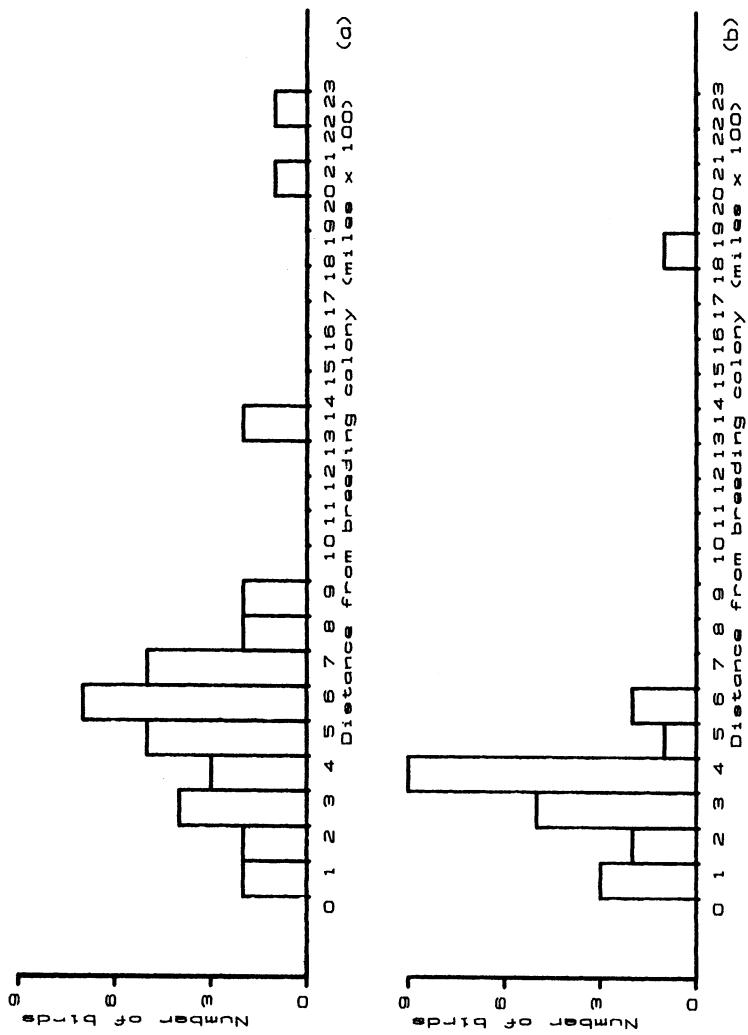


Figure 3 Distributions of recoveries of Razorbills, not known to have been killed directly by man's actions, from Skokholm and Skomer in the period November to February inclusive. (a) First years, (b) Adults.

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5. DISCUSSION

It has been implicitly assumed in this paper that the movement behaviour of the birds is similar in each calendar year. Since this study uses data from a period of about 40 years this assumption may not be true in practice, and may not even be so over a shorter period. Again, however, it is hoped that the assumption is not too far from the truth. A further potential problem in this study is that of ring wear and loss: Mead (1974) discusses this for auks.

Models have been proposed here to describe both migratory and dispersive movement. Unfortunately we do not have readily available the appropriate data for deciding between these models. Indeed, by examining data from the different, appropriate time periods within the year, we have seen that either type of model might be compatible with the data. Further investigation of the use of such models to describe Razorbill movements must await the availability of more data.

An interesting suggestion of the dispersal model is that Razorbills might move both forwards and backwards in reaching their winter quarters. If this were thought to be a valid possibility, further data could be collected to check it. This exercise might involve counts of Razorbills moving along the coast, out at sea, possibly watching from bird observatories. In this volume, Upton (1985) discusses the problem of counting birds on a sea watch, particularly when they may move in opposite directions; Darby (1985) discusses more general problems with observatory data.

ACKNOWLEDGEMENT

I would like to thank Byron Morgan for his extensive, constructive comments on earlier drafts of this paper, which have led to its improvement.

ACCOUNTING FOR VISIBLE MIGRATION

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SUMMARY

A simple algorithm is presented for calculating an improved estimate of the minimum number of birds present during a day's visible passage. The technique is described in the context of inshore sea-bird passage though it has wider applications.

Keywords: BIRD COUNTS, CUMULATIVE SUMS, SEA-BIRD PASSAGE.

1. INTRODUCTION

Before moving to Essex I had the good fortune to spend some years in Northumberland. My interest in ornithology led me to make frequent visits to the coastal observatory at Seaton Sluice. In autumn the passage of sea-birds visible from this observatory could be most spectacular. This visible passage depended upon the weather conditions: in unfavourable conditions there was either no passage at all or the passage was too far out to sea to be visible from the observatory. When there was visible passage it generally consisted almost entirely of movements in a particular direction (e.g. 95% of all birds of a given species were seen flying south). Occasionally, however, there were days on which the movements were "confused" with birds of a given species flying both north and south in roughly equal numbers. The question then arose as to whether the birds seen flying south at 11 o'clock included any of those seen flying north at 9 o'clock. The purpose of this short paper is to suggest a very simple method of analysing the daily movements which provides an improved estimate of the number of birds involved during a day of confused migration.

2. TRADITIONAL REPORTING TECHNIQUES

A widely used method of reporting a confused movement is to report the separate totals (N and S , say) for the movements in the two directions, together with the

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conclusion that there were at least $|N - S|$ birds involved. We could also regard $N + S$ as a measure of overall bird activity. Of course, here and subsequently, we are implicitly concentrating on the visible passage.

A drawback of the technique of reporting totals is illustrated by considering an extreme example. Suppose that the daily summary has $N = 300$ and $S = 300$. Reporting totals alone we must conclude that there were between 1 and 600 birds involved (the minimum value is $\max(1, |N - S|)$). These fictitious data could refer to 600 individual birds or it could refer, for example, to a single party of 300 birds that pass the observer on their way to the feeding grounds and subsequently repass on their return to their roost. Alternatively, it might refer to a single (very tired) tern travelling backwards and forwards in front of the observer during the course of its desperate search for sand eels along the tide line.

Naturally, in extreme cases, the bald entry in the daily log will be suitably annotated so that the county recorder would pay the appropriate attention to the record. In more realistic instances of confused movements, however, it will not be so clear as to how many birds are involved.

3. THE NEW ACCOUNTING PROCEDURE

The new procedure requires only that each sighting of a bird, or party of birds, should be recorded as a separate event, with both the size of the party and the direction of passage being noted. The computations, which involve only simple addition and subtraction, are probably best performed at leisure at the end of the day. A crucial assumption of the procedure is that a bird seen travelling in one direction does not repass the observer unseen during the period of interest. Thus the procedure would be upset by any birds which flew in circles past the observer, travelling north inshore but south far out to sea. However this assumption cannot be verified in the field.

The accounting procedure requires the use of two running 'totals', one for the birds heading north, the other for the birds heading south. These 'totals' are not, however, simply the sums of the numbers flying in each direction, but are obtained as follows: suppose that the next observation is of x birds flying north, and that the current values of the 'totals' are T_N and T_S . The new values of the 'totals' are $T_N + x$ and $\max(0, T_S - x)$. Corresponding adjustments are made for birds

Accounting for visible migration

flying south. The effect of ' $\max(0, T_S - x)$ ' is that neither 'total' is ever negative. The useful side-effect is that the minimum number of birds so far observed is equal to the current value of $T = T_S + T_N$.

There is an easy partial check on one's arithmetic. After any observation, the value of T is always equal to its previous value unless one or other of T_S and T_N is equal to 0, in which case the value of T may be greater than its previous value.

The algorithm has a peculiarly magical flavour to it, but, in fact, is only automating common sense, as the following examples illustrate.

Table 1
Example of the accounting procedure

Observation	T_S	T_N	T
10S	10	0	10
20S	30	0	30
10N	20	10	30
5S	25	5	30
40N	0	45	45
15S	15	30	45
Lunch-break: no birds pass by			
50N	0	80	80
20S	20	60	80
5N	15	65	80
40S	55	25	80
5S	60	20	80
100S	160	0	160
40N	120	40	160

3.1 Example: Fictitious Data

The fictitious data given in Table 1 illustrate the accounting procedure. By lunchtime the aggregate flow is 50 birds north and 50 birds south; the minimum number of birds involved is, however, not 1 but 45.

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After lunch the flow of birds becomes more spectacular and terminates with the assurance that at least 160 birds were involved. From where did this figure of 160 arise? Consider the sequence of observations (20S, 5N, 40S, 5S, 100S): during this sequence 165 birds flow south while only 5 fly north - therefore there must be at least 160 birds involved.

Table 2

Gannets, Sula bassana, on 2nd October 1983 at Bardsey bird and field observatory

Observation	T _S	T _N	T
22S	22	0	22
39S	61	0	61
9S	70	0	70
3N	67	3	70
13S	80	0	80
5S	85	0	85
2N	83	2	85
5S	88	0	88
1N	87	1	88
13S	100	0	100
12S	112	0	112
1N	111	1	112
3S	114	0	114
2N	112	2	114
6S	118	0	118
1S	119	0	119
1N	118	1	119
7S	125	0	125
1N	124	1	125
5S	129	0	129
16S	145	0	145
12S	157	0	157
5S	162	0	162
2N	160	2	162
7S	167	0	167
1S	168	0	168
2N	166	2	168
1S	167	1	168
2N	165	3	168
4S	169	0	169
2N	167	2	169
2S	169	0	169
3S	172	0	172
1N	171	1	172

3.2 Further Example: Real Data

Table 2 contains data from Bardsey Bird and Field Observatory per P. Hope Jones,

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together with the new accounting procedure applied to them. The data are for Gannets, *Sula bassana*, on the 2nd October 1983. As can be seen, passage was predominantly in a southerly direction. Indeed, seabird data from Bardsey generally reveal little problem with 'confused passage' such as might be encountered in other localities.

With such a predominantly one-way passage, the advantage in the precision of the new accounting procedure is not so obvious. Given total flows of 191S and 20N we are scarcely surprised by the conclusion that at least 172 birds were involved. Similar results were obtained for additional Gannet data, as well as data on auks (Guillemots, *Uria aalge*, and Razorbills, *Alca torda*), also kindly furnished by P. Hope Jones.

4. APPLICATIONS OF THE TECHNIQUE

The technique has been described in the context of a sea-watch. It would be equally appropriate for counts of waders, along the sea-shore, for ducks on a pond or even passerines in a hedgerow, provided, in each case, that the observer could be reasonably confident that there was no chance of an appreciable unseen reverse passage. In all these applications it is the relative motion of the birds with respect to the observer that is of importance. Thus, whilst the birds may be passing in front of a stationary observer, the accounting procedure will be equally useful for the case where the observer is moving and is passing a mixture of stationary and mobile birds.

It would be interesting to try the procedure out in the field, in a context other than a seawatch. However, there could be some difficulties involved in obtaining satisfactory records from people doing their watching whilst walking around, rather than in a static seawatch.

SECTION B

ANALYSIS OF CENSUS DATA

MULTIVARIATE ANALYSIS OF ATLAS DATA

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SUMMARY

Possible uses of principal component analysis and cluster analysis of bird atlas data are considered. Principal component analysis is shown to provide useful pictorial summaries of such data, and cluster analysis allows species to be grouped by habitat. Although only breeding data are considered here, the methods may be applied for example to presence/absence data recorded in winter.

Keywords: BIRD ATLAS; PRINCIPAL COMPONENT ANALYSIS; CLUSTER ANALYSIS;
PRUNED DENDROGRAMS

1. INTRODUCTION

In recent years, bird atlas projects have become widespread, on a local, national and international scale. Frequently, published bird distribution maps are seen as the end product of the project. Perhaps too little thought is given to the potential uses of the data that are summarised in the maps. A local atlas is currently underway in North-East Scotland (Grampian Region less Moray District). The area includes much of the Cairngorms, and the whole of Deeside and Donside. Conservation is therefore a major issue. If a site is threatened with development, a list of birds recorded at that site provides conservationists with an indicator of the value of that site. The atlas ensures that at least some records are available from every site. Records of insects and flowering plants, for example, provide further information if they exist. However, such records indicate only whether the site is important; they do not, in themselves, indicate whether the habitat which that site comprises is under threat more generally.

Most species of bird are associated with a particular habitat or habitats. If a certain species shows a marked decline in abundance or a contraction in its range, the cause may be loss of habitat. However, other causes, such as climatic factors,

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may be responsible. If species can be grouped by habitat, using for example cluster analyses, and if several species within a group exhibit a decline, then the evidence that the habitat associated with that group is under serious pressure will be greater. Atlas projects provide a source of data for calculations of this kind.

The analyses described here were used for grouping species both by breeding habitat and by winter habitat. Only the analyses of breeding data are presented. By performing the inverse analysis, the atlas sites may be clustered. The potential value of such an analysis is perhaps less, but the procedure supplies an objective way of classifying sites by habitat: habitats are "similar" when the bird species occupying them are largely the same, not when they are perceived by Man to be similar. For rare species that breed in very few sites, the analysis of sites may also provide an indicator of which further sites may be colonised.

2. STATISTICAL METHODS

The methods used were essentially those of principal component analysis and agglomerative hierarchical cluster analysis as described in Sneath and Sokal (1973). In this paper we describe Ward's (1963) method of cluster analysis as "minimum sums of squares".

Data for studies such as this are generally presented as a table of species (rows) by sites (columns); however, since the variables are congeneric (i.e. measure the same kind of attribute), a duality exists between sites and species such that the total variability in the data can always be decomposed into that due to

- the sites overall abundance (main effect)
- the species overall abundance (main effect)
- the differential profiles of species over sites (interaction).

This symmetry implies that similar analyses are equally appropriate for both the table and its transpose (sites by species).

We have carried this further than is usual by concentrating only on the interaction component of variation. That is to say, not only site means but also species means are subtracted from the observations so that (after addition of the overall mean) both row and column sums of the data table are zero. This corrects for the variation in species abundance that can be thought of as a "size" effect. Correction for size may be achieved by removal of the first principal component

Multivariate analysis of atlas data

(see, for example, Ch. 12 of Blackith and Reymert, 1971) but we feel our approach is simpler with congeneric data such as these.

3. RESULTS

Data on the 89 most widespread breeding species were extracted from the first three years' records for the 395 sites covered by the North-East Scotland bird atlas. A species was given the score of zero for a site if there was no evidence of breeding from that site. Possible breeding (as defined by the European Ornithological Atlas Committee) was scored as one, probable breeding two and confirmed breeding three. (Analyses carried out on zero-one data proved less useful. When categories one and zero were reduced to zero and categories two and three to one, relatively poor separation of species occurred, both in principal component analyses and in cluster analyses. Since most observations are zero, an increase in the number of zeroes reduces the information contained in the data. When the data were reduced to either no evidence of breeding (zero) or some evidence (unity), analyses were more closely comparable with those presented here.)

Principal component analyses proved more useful when the data were corrected for the species means, as described in the previous section. Fig. 1(a) shows the result of plotting the first principal component for the breeding data against the second. Fig. 1(b) summarises the habitats associated with the species shown in Fig. 1(a). Note that a species can take its position in Fig. 1(a) either because it typically breeds in the habitat specified in Fig. 1(b) or because it regularly occurs in two or more major habitats, and has occupied a position somewhere in the middle. For example, Lapwing (*Vanellus vanellus*) and Curlew (*Numenius arquata*) breed both on farmland and in the glens, and occupy much the same position in Fig. 1(a) as Long-tailed Tit (*Aegithalos caudatus*) and Bullfinch (*Pyrrhula pyrrhula*), which breed in woodland and forestry plantation. The first principal component is plotted against the third in Fig. 1(c), and here, Lapwing and Curlew separate widely from Long-tailed Tit and Bullfinch; species near the top of the plot and to the left are largely associated with woodland during the breeding season, whereas species of open country are mostly towards the bottom or the right of the plot.

The first four principal components explain 36.7% of the variation in the data. Components one to ten explain 19.2%, 9.0%, 4.7%, 3.8%, 2.9%, 2.7%, 2.4%, 2.0%, 1.9% and 1.8% of the variation respectively.

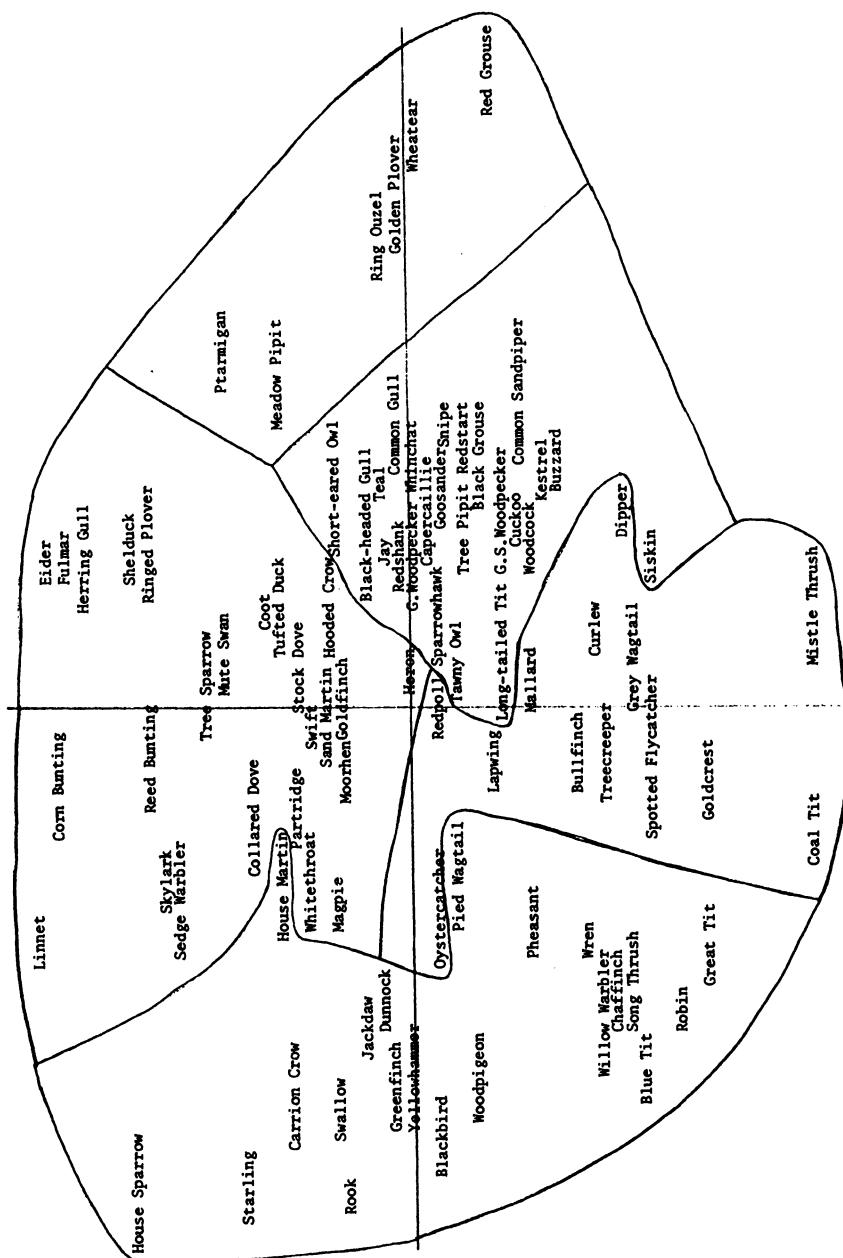


Figure 1(a) Second principal component (y-axis) against first. Also shown is the five-cluster solution from the dendrogram of Figure 2(a), employing the "minimum sums of squares" method.

Multivariate analysis of atlas data

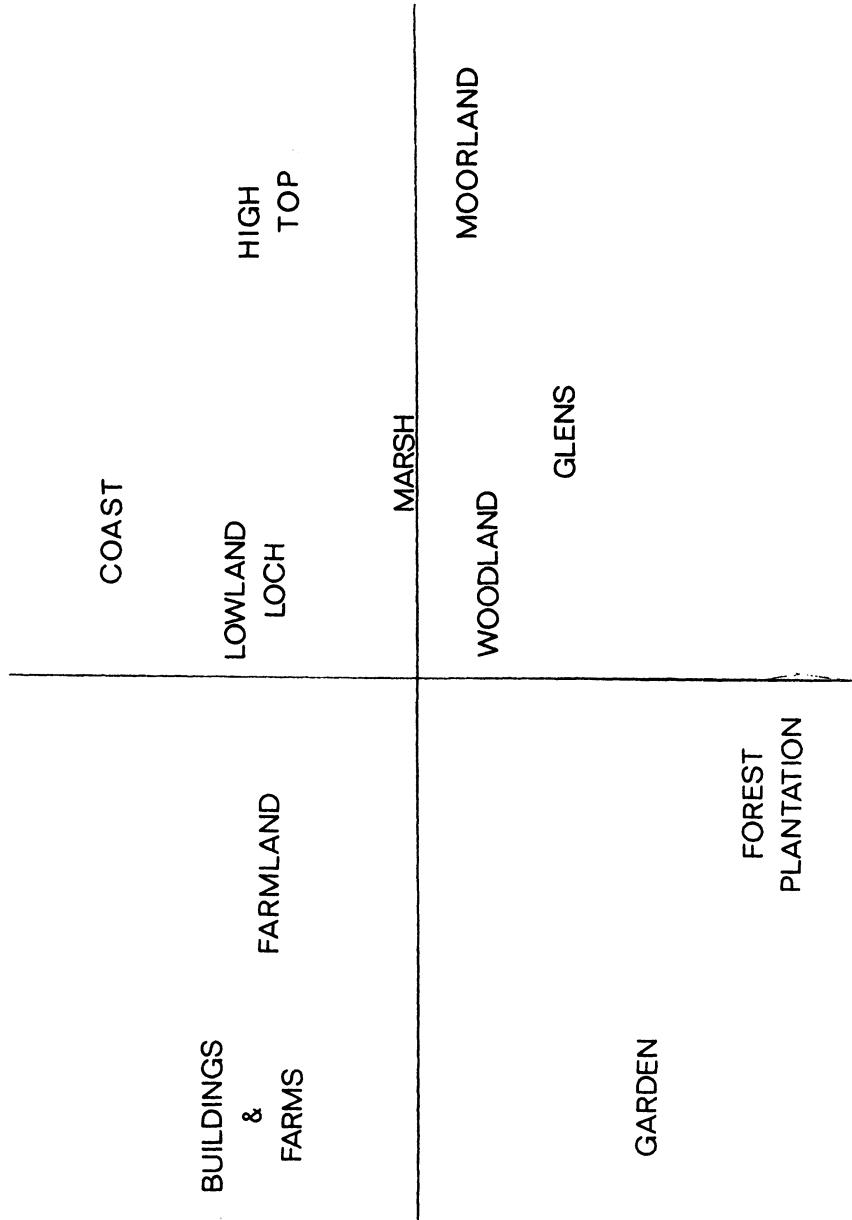


Figure 1(b) Habitats associated with the species of *Figure 1(a)*

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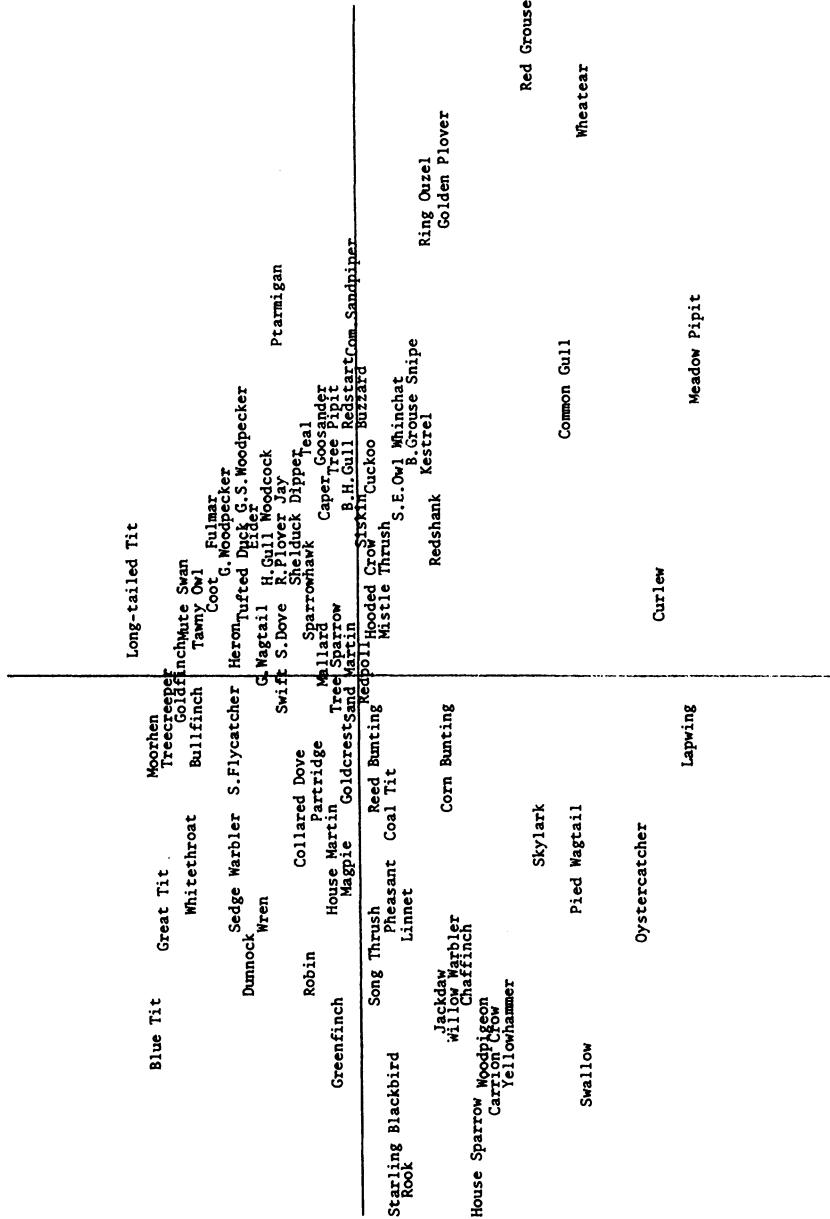


Figure 1(c) Third principal component (y-axis) against first

Multivariate analysis of atlas data

Fig. 2 shows dendograms that result from four methods of cluster analysis. Euclidean distance was used to give the measure of inter-species dissimilarity for consistency with the principal components approach. The "minimum sums of squares" method seems to provide the most useful representation of the data. If the method is applied to the 1981-82 data and the 1983 data separately, the dendograms of Fig. 3 are obtained.

The inverse analysis may be implemented to analyse the 395 sites. The inverse principal component analysis was carried out on the breeding data (corrected for site means), and the site scores on the first principal component were plotted against their scores on the second component. A summary of this plot appears in Fig. 4. Since the survey is as yet incomplete, many of the atlas sites have not been covered adequately by observers. Hence a cluster analysis on the sites is likely to be of limited use until the survey is complete.

4. DISCUSSION

The principal component analyses seem to provide useful pictorial summaries of bird atlas data. The most satisfactory two dimensional summary of the North-East Scotland bird atlas breeding data was obtained by plotting the first principal component against the second, provided the data were corrected for the species means. We recommend that atlas data should be corrected as described in Section 2. When the uncorrected data were analysed, it was found that a species' score in the first principal component was very highly correlated with the proportion of sites in which the species was recorded ($r \approx 0.99$). The most informative two dimensional summary was then found to be a plot of the second principal component against the third in the case of the uncorrected data, since this largely eliminated the effect of variable abundance. The same aim is achieved more directly by correcting the data before analysis.

Fig. 2 illustrates the well-known phenomenon that different methods of cluster analysis give rise to very different dendograms. At one extreme, the nearest-neighbour method leads to chain clusters unless there are very well defined gaps that contain no "intermediate" species in the continuum of variation. At the other, the minimum sums of squares method enforces a tight clustering that is possibly an oversimplification but is the most satisfactory summary of the main concentrations of similarly-behaving species. We recommend this latter method provided it is recognised that intermediates may considerably blur the cluster boundaries; the principal

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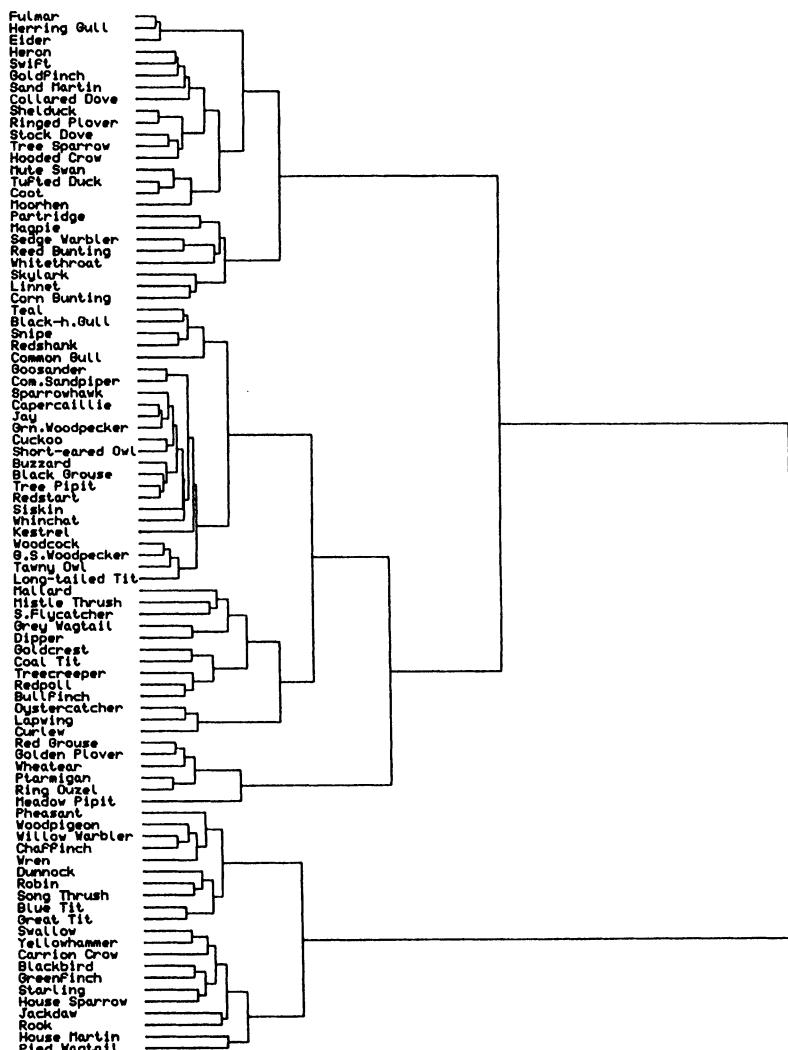


Figure 2(a) Dendrogram, minimum sum of squares

Multivariate analysis of atlas data

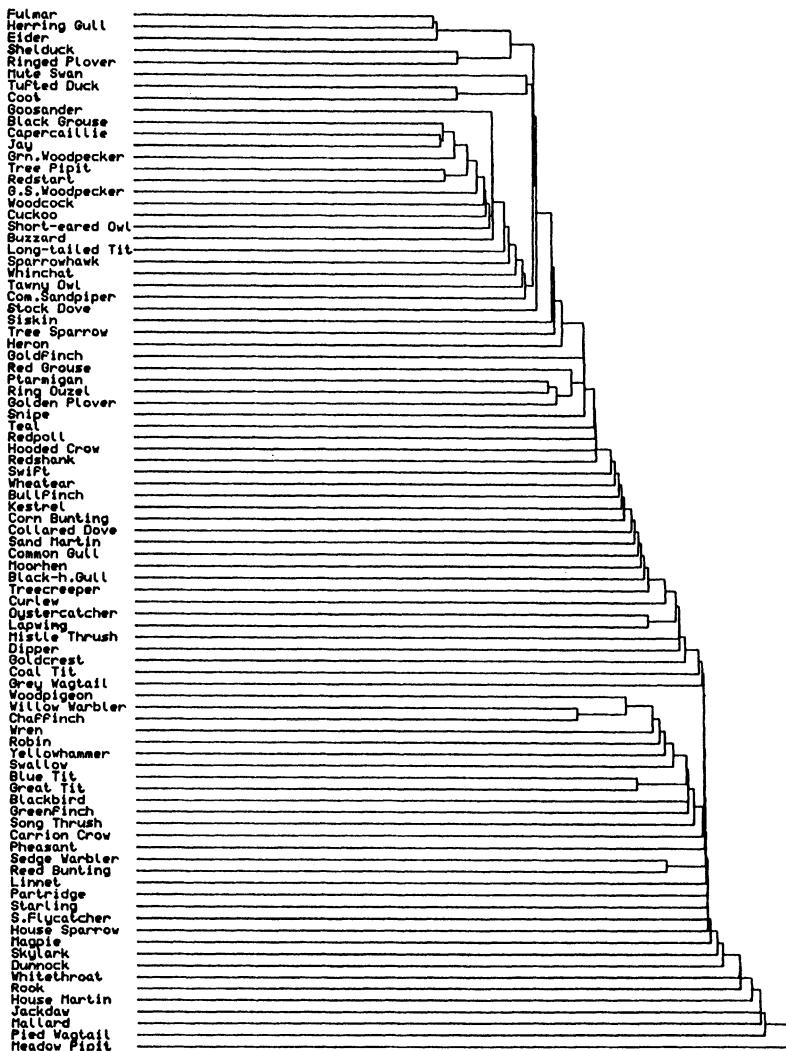
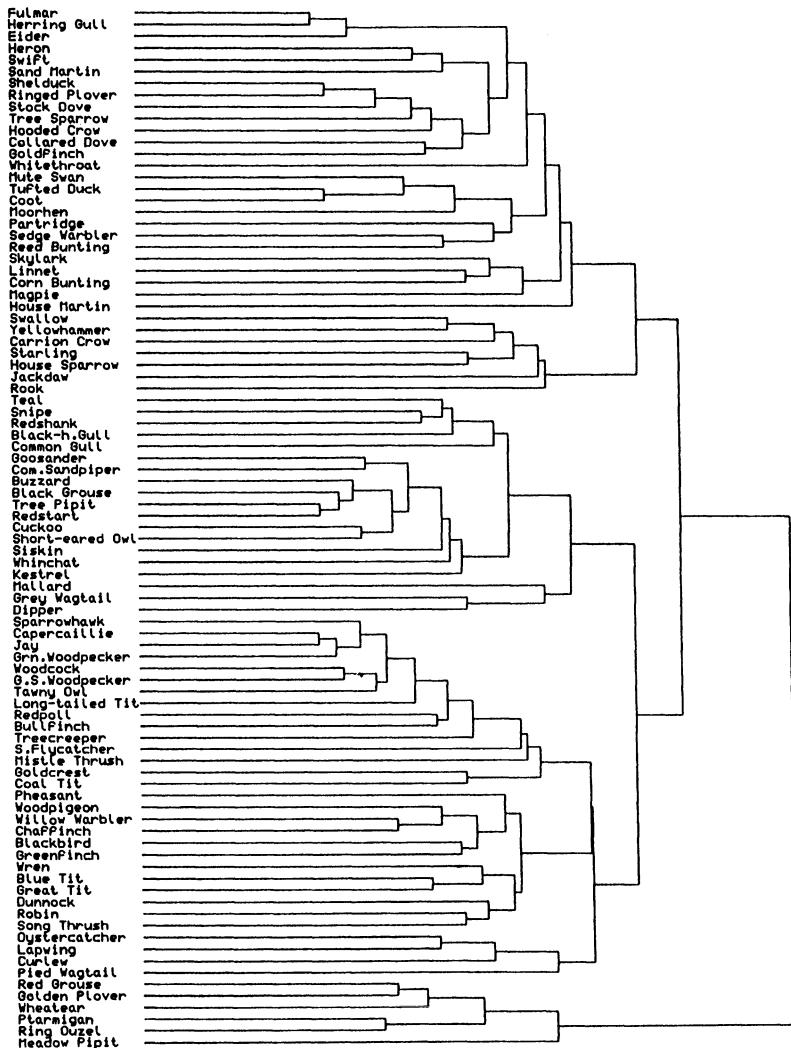


Figure 2(b) Dendrogram, nearest neighbour

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Figure 2(c) Dendrogram, furthest neighbour

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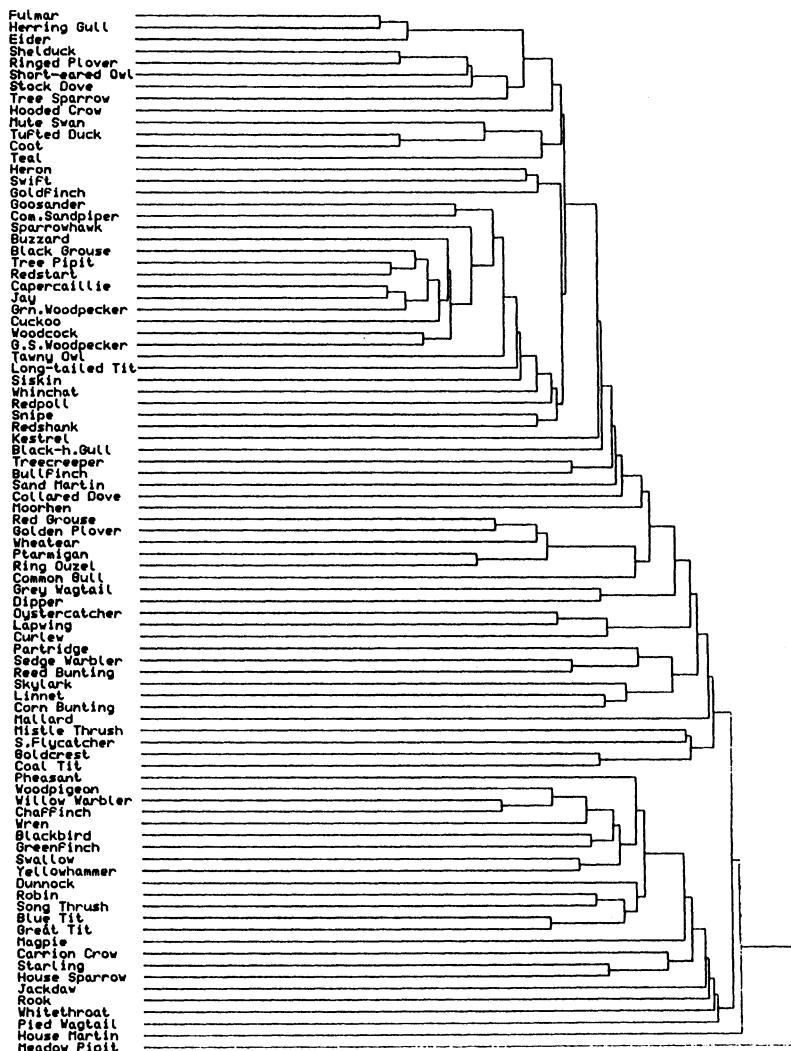


Figure 2(d) Dendrogram, group average

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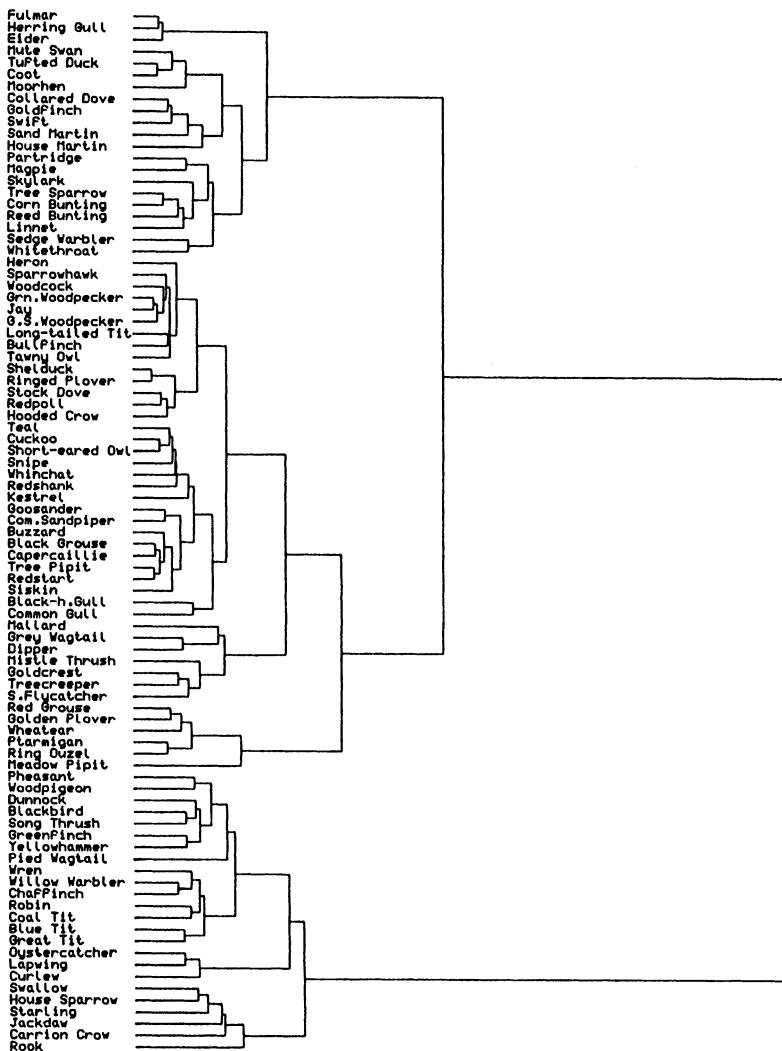


Figure 3(a) Dendrogram, minimum sums of squares, 1981-2 data

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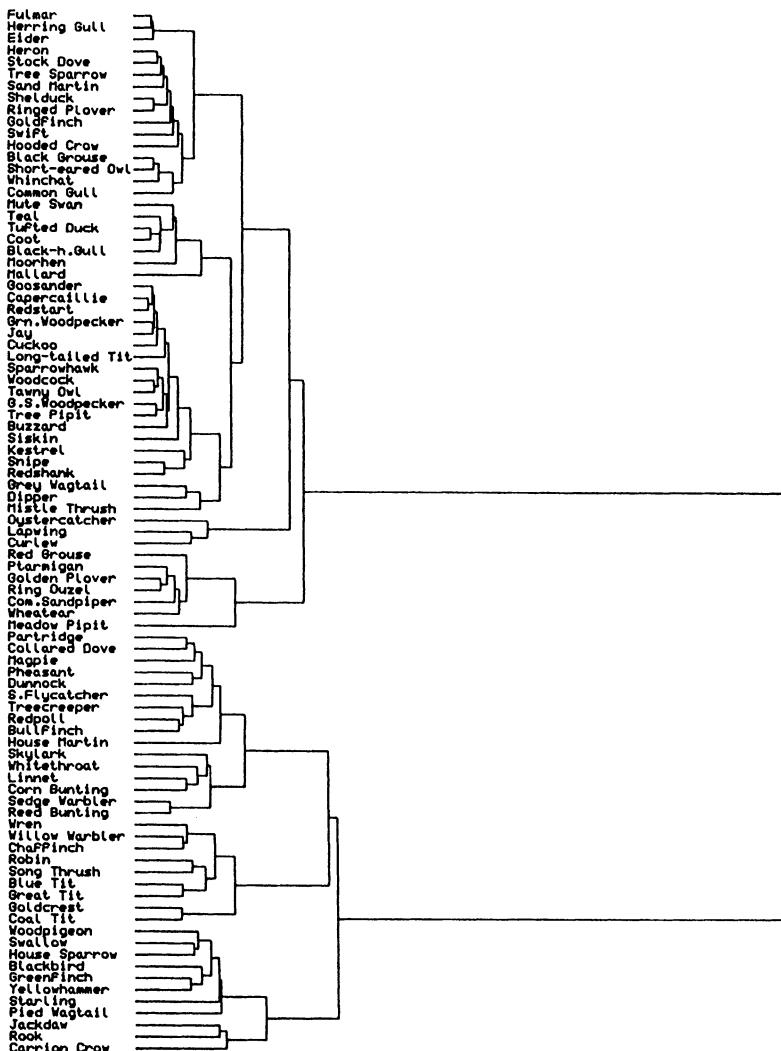


Figure 3(b) Dendrogram, minimum sums of squares, 1983 data

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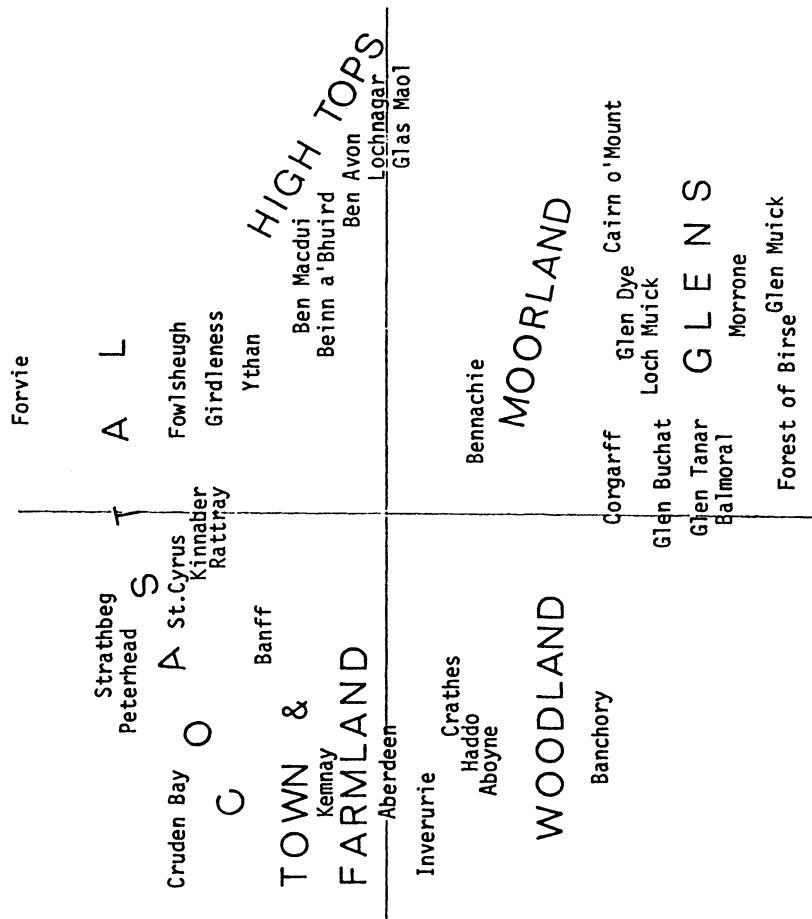


Figure 4 Summary of second principal component (y-axis) against first for sites. Only a subset of the 395 sites is presented here

Multivariate analysis of atlas data

components representation serves to aid interpretation.

Clusters of species may be obtained from any one of the dendograms. However, a more subjective approach, incorporating information from the dendograms, the principal components plots and existing ornithological knowledge, is likely to yield more useful clusters, which may then be used as described in the Introduction. The relationship between one set of clusters from the dendrogram of Fig. 2(a) and a principal component plot can be seen from Fig. 1(a). The atlas will provide the current range of each breeding species, and future studies should indicate which species are contracting. If several species within a single cluster are seen to decline, then it is possible that the habitat(s) associated with that cluster is (are) threatened.

A problem associated with cluster analyses is the stability of clusters. Fig. 3 shows the dendograms obtained by applying the minimum sums of squares method to the 1981-82 and 1983 breeding data separately. Gordon's (1980) method of cluster comparison can be applied to check the stability but experience of the technique is not yet sufficient to enable secure judgements to be made. As an illustration of his technique, we give in Fig. 5 three examples of his pruned dendograms.

ACKNOWLEDGEMENTS

We would like to thank the numerous observers who have kindly supplied data for the North-East Scotland atlas. We are particularly grateful to Dr M.V. Bell, Mr S.M. Palmer and Mrs I. Dandeker for their help in processing large quantities of records.

Dr A. Gordon kindly supplied the dendograms from which Fig. 5 was drawn. We are also grateful for the comments supplied by Dr D. French, Dr A. Watson, the editors and the referee.

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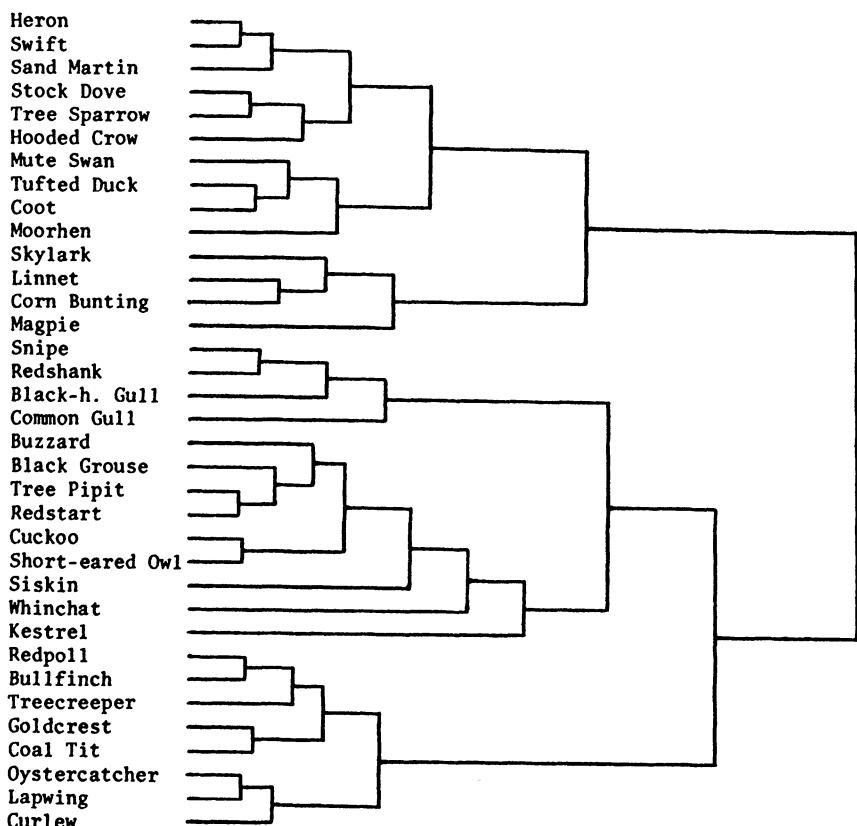


Figure 5(a) Pruned dendrogram generated from furthest neighbour and minimum sums of squares dendrograms for 1981/83

Multivariate analysis of atlas data

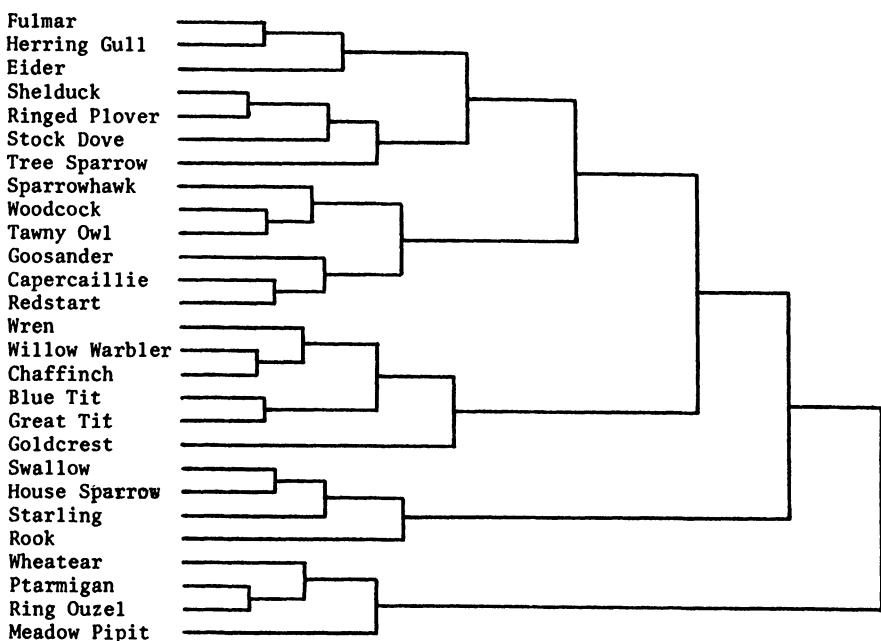


Figure 5(b) Pruned dendrogram generated from furthest neighbour dendrograms for 1981/82 and 1983

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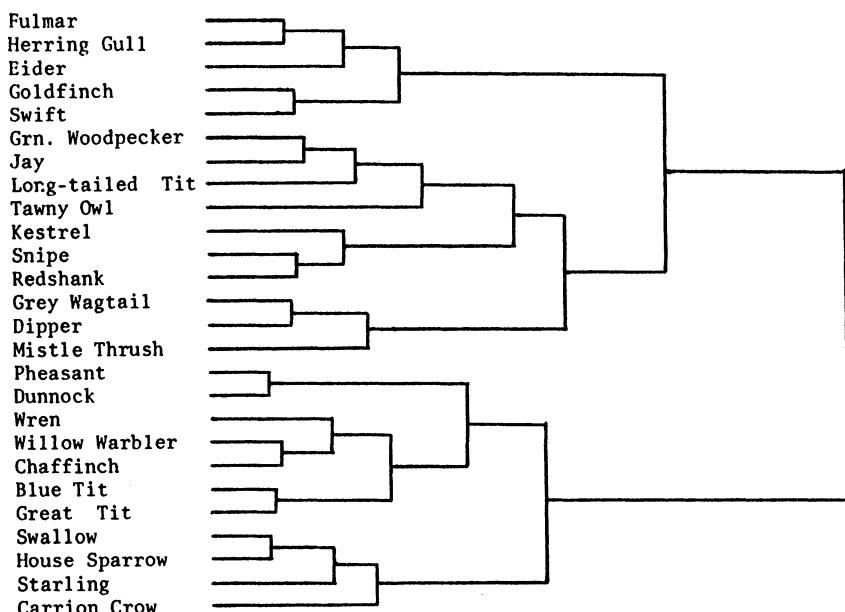


Figure 5(c) Pruned dendrogram generated from minimum sums of squares dendrograms for 1981/82 and 1983

Multivariate analysis of atlas data

APPENDIX

List of English and Latin names of species appearing in the figures

Fulmar	<i>Fulmarus glacialis</i>
Heron	<i>Ardea cinerea</i>
Mute Swan	<i>Cygnus olor</i>
Shelduck	<i>Tadorna tadorna</i>
Teal	<i>Anas crecca</i>
Mallard	<i>Anas platyrhynchos</i>
Tufted Duck	<i>Aythya fuligula</i>
Eider	<i>Somateria mollissima</i>
Goosander	<i>Mergus merganser</i>
Sparrowhawk	<i>Accipiter nisus</i>
Buzzard	<i>Buteo buteo</i>
Kestrel	<i>Falco tinnunculus</i>
Ptarmigan	<i>Lagopus mutus</i>
Red Grouse	<i>Lagopus scoticus</i>
Black Grouse	<i>Lyrurus tetrix</i>
Capercaillie	<i>Tetrao urogallus</i>
Partridge	<i>Perdix perdix</i>
Pheasant	<i>Phasianus colchicus</i>
Moorhen	<i>Gallinula chloropus</i>
Coot	<i>Fulica atra</i>
Oystercatcher	<i>Haematopus ostralegus</i>
Ringed Plover	<i>Charadrius hiaticula</i>
Golden Plover	<i>Charadrius apricarius</i>
Lapwing	<i>Vanellus vanellus</i>
Snipe	<i>Gallinago gallinago</i>
Woodcock	<i>Scolopax rusticola</i>
Curlew	<i>Numenius arquata</i>
Redshank	<i>Tringa totanus</i>
Common Sandpiper	<i>Actitis hypoleucos</i>
Black-headed Gull	<i>Larus ridibundus</i>
Common Gull	<i>Larus canus</i>
Herring Gull	<i>Larus argentatus</i>
Stock Dove	<i>Columba oenas</i>
Woodpigeon	<i>Columba palumbus</i>
Collared Dove	<i>Streptopelia decaocto</i>
Cuckoo	<i>Cuculus canorus</i>
Tawny Owl	<i>Strix aluco</i>
Short-eared Owl	<i>Aego flammeus</i>
Swift	<i>Apus apus</i>
Green Woodpecker	<i>Picus viridis</i>
Great Spotted Woodpecker	<i>Dendrocopos major</i>
Skylark	<i>Alauda arvensis</i>
Sand Martin	<i>Riparia riparia</i>
Swallow	<i>Hirundo rustica</i>
House Martin	<i>Delichon urbica</i>
Tree Pipit	<i>Anthus trivialis</i>
Meadow Pipit	<i>Anthus pratensis</i>
Grey Wagtail	<i>Motacilla cinerea</i>
Pied Wagtail	<i>Motacilla alba</i>
Dipper	<i>Cinclus cinclus</i>
Wren	<i>Troglodytes troglodytes</i>
Dunnock	<i>Prunella modularis</i>
Robin	<i>Erythacus rubecula</i>
Restart	<i>Phoenicurus phoenicurus</i>
Whinchat	<i>Saxicola rubetra</i>

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APPENDIX - continued

Wheatear	<i>Oenanthe oenanthe</i>
Ring Ouzel	<i>Turdus torquatus</i>
Blackbird	<i>Turdus merula</i>
Song Thrush	<i>Turdus philomelos</i>
Mistle Thrush	<i>Turdus viscivorus</i>
Sedge Warbler	<i>Acrocephalus schoenobaenus</i>
Whitethroat	<i>Sylvia communis</i>
Willow Warbler	<i>Phylloscopus trochilus</i>
Goldcrest	<i>Regulus regulus</i>
Spotted Flycatcher	<i>Muscicapa striata</i>
Long-tailed Tit	<i>Aegithalos caudatus</i>
Coal Tit	<i>Parus ater</i>
Blue Tit	<i>Parus caeruleus</i>
Great Tit	<i>Parus major</i>
Treecreeper	<i>Certhia familiaris</i>
Jay	<i>Garrulus glandarius</i>
Magpie	<i>Pica pica</i>
Jackdaw	<i>Corvus monedula</i>
Rook	<i>Corvus frugilegus</i>
Carrion Crow	<i>Corvus corone corone</i>
Hooded Crow	<i>Corvus corone cornix</i>
Starling	<i>Sturnus vulgaris</i>
House Sparrow	<i>Passer domesticus</i>
Tree Sparrow	<i>Passer montanus</i>
Chaffinch	<i>Fringilla coelebs</i>
Greenfinch	<i>Carduelis chloris</i>
Goldfinch	<i>Carduelis carduelis</i>
Siskin	<i>Carduelis spinus</i>
Linnet	<i>Acanthis cannabina</i>
Redpoll	<i>Acanthis flammea</i>
Bullfinch	<i>Pyrrhula pyrrhula</i>
Yellowhammer	<i>Emberiza citrinella</i>
Reed Bunting	<i>Emberiza schoeniclus</i>
Corn Bunting	<i>Emberiza calandra</i>

A TEST FOR SEASONAL OCCURRENCE

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SUMMARY

Some groups of birds, both taxonomic and ecological, show seasonal patterns of occurrence, as do single species. Sometimes a species may be present in an area in particular seasons of the year, but totally absent from that area in the other seasons. There is no need for formal statistical analysis to quantify this. However, in cases where some birds migrate while others remain resident, a formal test for seasonal occurrence may be required.

A suitable distribution for this purpose is introduced in this paper, as is the appropriate test statistic derived from it. The statistic is applied to data sets originating from the Tsavo East National Park in Kenya. Both single species of birds and ecological groups of birds are considered in these examples.

Keywords: EAST AFRICA, LAND BIRDS, SEASONAL OCCURRENCE.

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1. INTRODUCTION

Many species of animals are seasonal in their occurrence in an area, either because the various stages of their life cycle emerge only at certain seasons, or, the more interesting case, because they are migrants and move between areas to a greater or lesser extent. When a species is present in an area only at a certain period and is completely absent at another, statistics are hardly necessary to prove it to be seasonal in occurrence. This pattern applies to many species but in others, particularly among birds, some of the population remains resident in the area, while others move in or away at some periods. The net effect on the whole population is therefore one of changing the centre of gravity.

P.C. Lack

The problem of proving a seasonal change applies to these cases of individual species but is perhaps more acute with groups of birds. These groups could be taxonomic e.g. warblers or parrots, but also ecological e.g. frugivores or ground-feeding insectivores. In these latter there might be a complete turn-over in species composition but with some members of the group present all the year.

In my study of the bird community in Tsavo East National Park, Kenya I was interested both in the movements of individual species, many of which were only partial migrants, and in the ecological structure of the community at the different seasons. Full details of the area and climate can be found elsewhere (Lack, 1980, 1983), but, very briefly, the Park is a semi-arid area with savanna habitats ranging from open grassland to woodland scrub. The climate and seasons are dominated by the rainfall. The total is between about 250 and 500 mm per annum, and, on average, almost all falls from mid-November to the end of December and again during April. However, during 1975 and 1976, the years of my study, the April rains were very poor. The result was, in effect, one major wet season each year with the rest of the year dry. Rainfall produces a very pronounced change in the vegetation and in the food supplies for many birds, and many species and groups of birds showed a seasonal pattern of occurrence to a greater or lesser extent.

The main data for this study were the results of two types of census. Full details can again be found in Lack (1980, 1983). The first type was based on time. Birds were censused in periods of fifteen minutes in each of seven habitat types in each month. These were used mainly to determine the habitat preferences and seasonal occurrence of each species. The second type was designed to measure the actual density of birds, and involved censusing a series of fixed plots in each habitat once per month.

Figure 1a shows the patterns of seasonal occurrence over the two years of the study of the Spotted Flycatcher(*Muscicapa striata*). This species breeds in the Palaearctic and only occurred in Tsavo East N.P. during some of the northern winter months. It is thus a case which hardly needs statistics to prove the seasonality. Figure 1b, though, shows the occurrence of frugivorous birds in Woodland. Some birds were present all the year but numbers were apparently higher in the middle of the calendar year as compared with the northern winter period during and shortly after the rainy season in Tsavo. Is this a real increase?

Seasonal occurrence

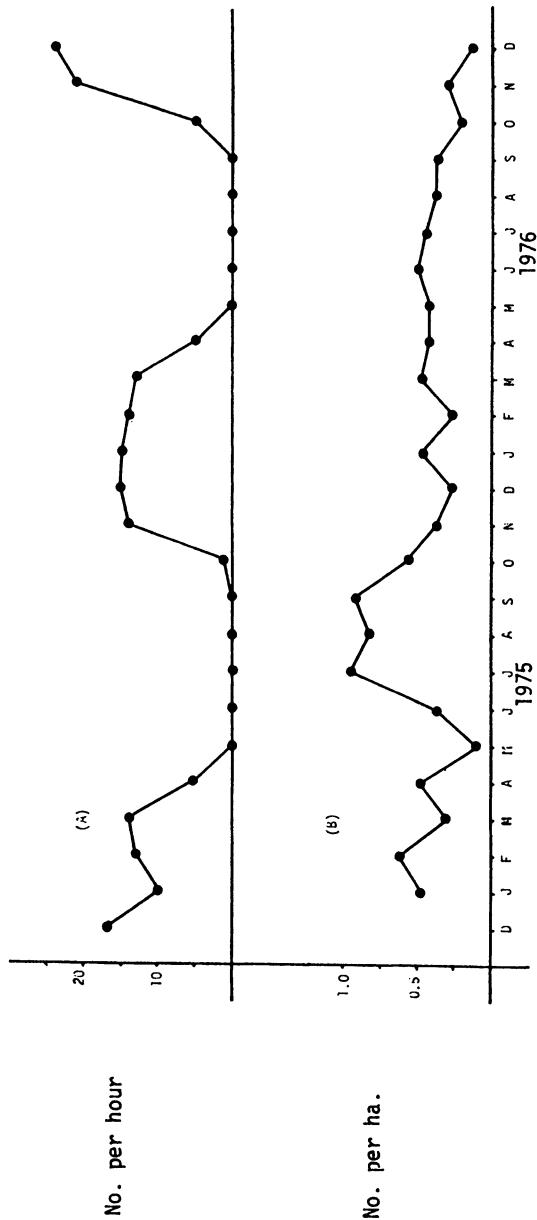


Figure 1 The seasonal pattern of occurrence over two years of (A) Spotted Flycatcher *Muscicapa striata* (B) Frugivorous birds in woodland (the density censuses were not started until January 1975 and hence there is no December 1974 figures in B either here or in Figure 2). The numbers of individual species are expressed as numbers per hour, and the numbers of groups as numbers per hectare (ha) both here and in the subsequent figures - see text.

P.C. Lack

2. THE TEST

When considered over a long period migrants occur in a cyclical pattern and therefore it is logical to test for a seasonal pattern by fitting a circular distribution, and then testing for uniformity over the year. A suitable distribution for this purpose is the von Mises distribution, whose probability density function is given by:

$$f(\theta) = \frac{1}{2\pi I_0(k)} e^{k \cos \theta} \quad (-\pi < \theta < \pi)$$

where $I_0(k)$ is the imaginary Bessel function of the first kind (see Pearson and Hartley, 1972, p.123). k is a positive constant measuring the degree of concentration.

All my censuses were based on calendar months and the circle was therefore divided into twelve sectors. The number of timed censuses in each month was not constant and all numbers of birds derived from these censuses have been converted to the number that would have been seen in 58 hours, which is the average number of hours censused each month (the range was 44-70 hours). The area censused for density estimates was the same each month (220 hectares). The numbers of the group of birds to be tested are taken as vectors from the centre of the circle and it is these vectors which are tested for uniformity. The null hypothesis is that they are uniform and therefore no seasonal pattern (which is where $k=0$) exists. If $k \neq 0$ there is a unimodal distribution with the mode along $\theta=0$.

The test involves calculating the magnitude of the resultant vector sum

$$R = \sqrt{\left(\sum_{i=1}^{12} n_i \sin A_i \right)^2 + \left(\sum_{i=1}^{12} n_i \cos A_i \right)^2}$$

where n_i is the abundance in each month and A_i is the angle of the sector representing that month. The maximum likelihood estimator of k is R/N , where $N = \sum_{i=1}^{12} n_i$ and the 5% and 1% critical values of this statistic are given in Table 56 of Pearson and Hartley (1972), which is reproduced from Stephens (1969). The table gives values for $N \leq 200$. For $N \geq 200$, and with increasing accuracy as N increases, a similar statistic, $2R^2/N$, is found to be distributed approximately as chi-squared with 2 degrees of freedom (Pearson and Hartley, 1972, p.124; see also Wilkie, 1983). In both statistics a value larger than the critical one indicates that there is a seasonal pattern.

If there is a seasonal pattern one can also find the modal vector, i.e. the angle round the circle with the peak abundance:

Seasonal occurrence

$$= \tan^{-1} \left(\frac{\sum_{i=1}^{12} n_i \sin A_i}{\sum_{i=1}^{12} n_i \cos A_i} \right)$$

with n_i and A_i as before. If the result is expressed in degrees it can be taken as equivalent to days from the arbitrary date assigned to $A=0$ - here the middle of January (15th). In the event all dates were approximated to quarter months.

3. EXAMPLES

The statistics of the two distributions shown in Figure 1 are given in Table 1. Both distributions are shown to be significantly seasonal. In other groups such as the two shown in Figure 2 there was considerable variation in numbers but no consistent seasonal pattern over the two years, and the statistics are not significant.

Table 1
The statistics of the patterns shown in Figures 1 and 2

Species/Group	N	R/N	$2R^2/N^b$	Significance	Date of peak ^a
<i>Muscicapa striata</i> (Figure 1a)	500	-	410	P < 0.001	January 2
Frugivorous birds in woodland (Figure 1b)	635	-	27	P < 0.01	August 1
<i>Halcyon chelicuti</i> (Figure 2a)	128	0.09	-	N.S.	-
African insectivores in bushland (Figure 2b)	749	-	5	N.S.	-

Notes: ^aThe date of peak is expressed as a quarter month

^b $2R^2/N$ has been used where $N > 200$

4. DISCUSSION

I calculated the statistic for all species with sufficient data and for several ecological groups of birds. In the majority of cases the statistics confirmed what I had expected from impressions gained during fieldwork for the project.

The test may demonstrate (or otherwise) a seasonal pattern with single peak distributions. A few species in my data appeared to show a more complex pattern of

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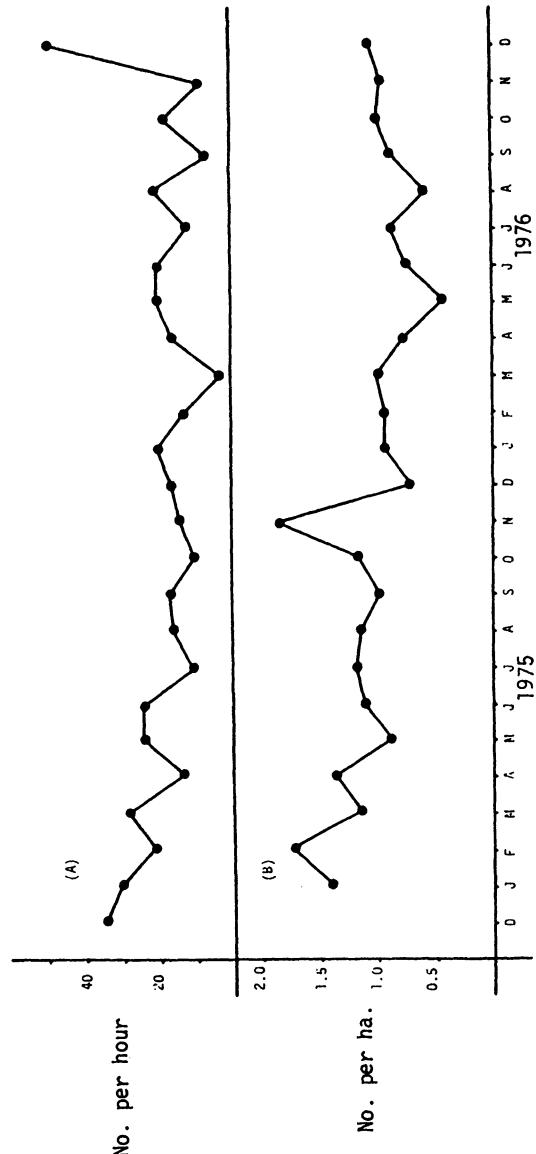


Figure 2 The seasonal pattern of occurrence over two years of (A) Striped Kingfisher (*Halcyon chelicuti*); (B) African insectivores in bushland.

Seasonal occurrence

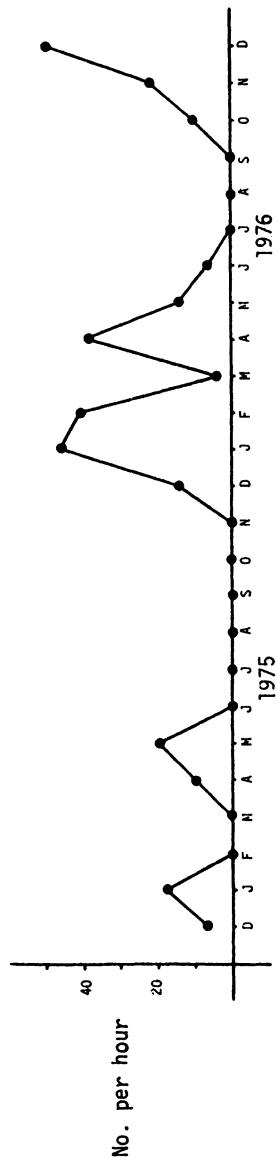


Figure 3 The seasonal pattern of occurrence over two years of Wattled Starling (*Creatophora cinerea*).

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occurrence with two peaks of abundance in the course of a year. Figure 3 shows an example of such a species, the Wattled Starling (*Creatophora cinerea*). This occurred in about equal numbers in both wet seasons, December and April. Here the statistic identified a seasonal pattern of occurrence ($2R^2/N = 295$, $N = 667$, $P < 0.001$), but the peak was identified as the last week of February, i.e. between the two actual peaks. ($2R^2/N$ is used not R/N as $N > 200$.)

Generalising this, if the two peaks are within the same six month period, as in this case, the test may still show a significant pattern although it will be reduced. If, however, the two peaks are six months apart and approximately equal any pattern will be cancelled out.

Strictly speaking, the goodness-of-fit of the von Mises distribution to the data sets should be investigated. This can be done by comparing the observed and the fitted values for each month. This should reveal instances where the test would be based on an inappropriate distribution if applied as indicated in this paper. It is also possible to provide confidence intervals for the resultant vector, using the tables of Pearson and Hartley (1972, p.127).

Pearson and Hartley (1972, p.132) mention that another way to treat bimodal data is to assume a population of two von Mises distributions superimposed, but they imply that the modes must be opposite, which is not the case here.

ACKNOWLEDGEMENTS

I am very grateful to Dr. F.H.C. Marriott for pointing out the statistic and showing me its possibilities. Dr. R. J. O'Connor kindly criticised an earlier draft. The fieldwork was supported financially by the Royal Society, the Leverhulme Trustees, the Frank M. Chapman Fund and the National Audubon Society.

AN INDEX OF POPULATION CHANGE WITH APPLICATION
TO THE COMMON BIRD CENSUS

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SUMMARY

This paper develops a model for the analysis of serially correlated unbalanced data of yearly population counts. Large-sample, minimum-variance estimates of indices of annual population size are derived. The method is used to analyse Common Bird Census data.

Keywords: POPULATION FLUCTUATION; MINIMUM-VARIANCE ESTIMATION; UNBALANCED DATA;
ORNITHOLOGY

1. INTRODUCTION

The Common Bird Census (CBC), carried out annually by the British Trust for Ornithology (BTO), monitors the changes in population size of the more common bird species. More than 250 sample plots, covering a wide range of farmland habitats, have been included in the Census. Observers make frequent visits to the sample plots during the breeding season. On each visit the observer records the species of the birds detected and the location of the birds within the plot. Using this information an estimate is made of the number of territory-holding males of each species in the plot. An objective procedure for deriving this estimate is provided by North (1977) and (1979), and further amended in North (1980). Fuller descriptions of the Census are given in Williamson and Homes (1964) and in Taylor (1965).

Till now the BTO have analysed the Census data on a year to year basis. If y_{i1} and y_{i2} are the estimated numbers of territories in sample plot i in successive years, year 1 and year 2 say, then the change in population size between the two years is measured by the ratio estimate

$$r_{12} = \sum_i y_{i2} / \sum_i y_{i1}$$

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the summation being carried out over those plots visited in both years.

The sequence of changes in the population over a period of several years is indirectly constructed from the products of the measurements of change between successive years. Thus for example the change between year 1 and year 4 is estimated by $r_{12}r_{23}r_{34}$. No direct use is made of the data for pairs of years separated by more than one year: thus the ratio r_{14} does not directly figure in the estimate of change from year 1 to year 4.

If each and every site is monitored in every year then, of course, the direct and indirect estimates of population change between any pair of years coincide. However in fact only 6 out of a total of 262 farmland plots were visited in each and every one of the 14 years. As the Census proceeded new plots were included and existing plots were discarded; gaps occur in the data corresponding to intermediate years in which a site was not visited. Overall the majority of the plots were counted in less than half of the 14 years of the Census period.

Because of this lack of balance in the data the direct and the indirect estimates of change do not coincide. In this paper a method of combining the direct and indirect types of information to produce overall estimates of change, proposed by Mountford (1982), is employed to analyse various sets of CBC data.

2. MODEL

In search of an appropriate model of territorial occupancy a preliminary examination of the data of each species was made by plotting the territory counts of each of the 14 years against each of the other years - 91 plots in all. Figure 1 shows four such graphs of the Skylark (*Alauda arvensis*) data. The straight line passing through each set of points has slope equal to the ratio estimate. The 91 graphs all reveal the same pattern: they suggest a straight-line relationship passing through the origin; they also suggest that as the time between paired years increases, then, corresponding to the decreased serial correlation, the variability about the line increases.

The model of territorial occupancy of a particular species may therefore be formulated as

$$y_{ij} = p_i g_j + e_{ij} \quad (1)$$

An index of population change

where y_{ij} is the estimated number of territories in sample plot i in year j with expected value $p_i g_j$, p_i is the i th plot effect and g_j the j th year effect. The residual error variable e_{ij} has zero mean and variance proportional to the expected value $p_i g_j$; the covariance of e_{ij} and e_{ik} decreases with increasing $|j-k|$; for $i \neq n$ $\text{cov}(e_{ij}, e_{nk}) = 0$.

The inclusion of the covariance is required to take account of the high degree of serial correlation of territory counts made in successive years. The same bird often returns to the same nest site: its offspring tend to return to the same area of farmland.

That the model incorporates the linear and proportional relationships suggested by the scatter diagrams is seen by noting that the expected ratio of the counts of plot i in year j and in year k is approximately g_j/g_k for all plots i ; other than random variation the change from year to year is assumed to be the same constant proportion over all sample plots.

Having thus defined the measures of changes in terms of the parameters of the model it is now necessary to derive estimates of the measures.

The measure of the change between year m and year n is estimated, first, by $\log r_{mn}$; secondly, indirectly via any other year p , by

$$(\log r_{mp} - \log r_{np})$$

and generally by any contrast,

$$\sum a_{ij} \log r_{ij} \quad 1 \leq i, j \leq C$$

where C is the number of years of the Census and where

$$\sum_j a_{nj} = 1 \quad , \quad \sum_j a_{mj} = -1 \quad , \quad \sum_j a_{pj} = 0 \quad p \neq n, m$$

where $a_{ii}=0$ and $a_{ji}=-a_{ij}$.

Similarly, the overall effect of year n ,

$$\log g_n - (\sum_{i=1}^C \log g_i) / C$$

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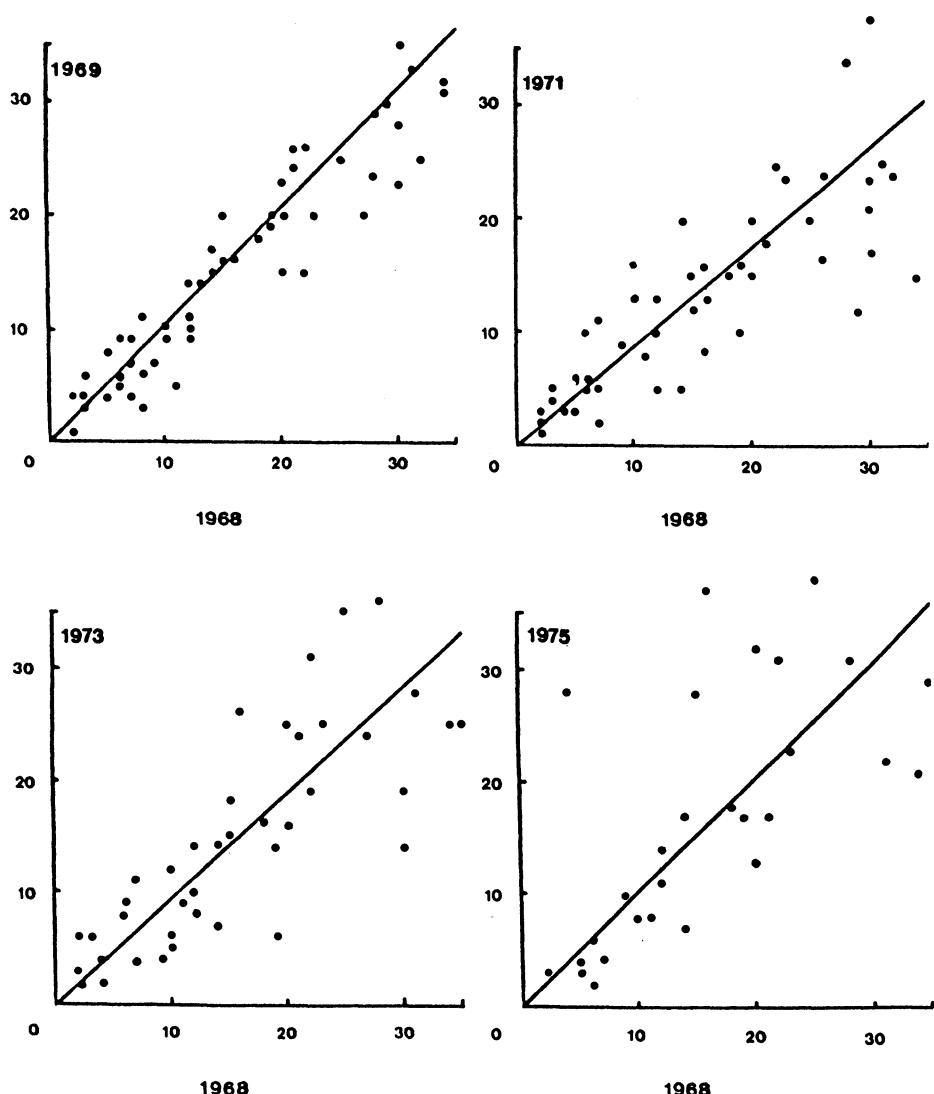


Figure 1 *Skylark counts of 1969, 1971, 1973 and 1975 plotted against those of 1968*

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is estimated by any contrast $\sum a_{ij} \log r_{ij}$ where

$$\sum_j a_{nj} = 1 - 1/C \quad \text{and} \quad \sum_j a_{pj} = -1/C, \quad p \neq n.$$

All values of r_{ij} , not merely the ratios of successive years, feature in the contrast; the available information is being fully utilised.

Of the various possible contrasts $\sum a_{ij} \log r_{ij}$ we select the one (it is unique) that is both an unbiased estimate of change and also has the smallest variance. The derivation of this estimate is straightforward: the details of the procedure as applied to the CBC data are spelled out in Mountford (1982) and will not be repeated here.

3. APPLICATION OF THE METHOD

As an example of the application of the method an analysis of the method is made of the CBC skylark data on farmland plots over the 14 year period 1963-76. An immediate question is whether a single overall analysis of the full set of 14 years' data is justified or whether the analysis of the data for a shorter period of years is more appropriate. Provided the data are connected any increase in the number of sample plots brought about by extending the length of the yearly series will provide extra information and thus improve the precision of the estimates. Thus when the method was applied first to the analysis of the data of the five-year period 1963-67 and then secondly to the analysis of the full set of data for the 14 years 1963-76, the second analysis produced estimates that were on average twice as precise, as measured by the relative magnitude of their variances, as those obtained from the first analysis. However this improvement is bought at a cost; with the passage of time there is an increasing possibility of change in the ecological characteristics of a sample plot and an increasing likelihood of the violation of the assumptions underlying the model. The answer then to the question of how many years' data should feature in a single analysis is that the series of years be as long as possible provided the assumptions of the model are met. This criterion must necessarily be ill-defined; it is not possible to lay down a fixed rule. There is an inevitable indecisiveness in judging at what stage the assumptions break down. Some guidance to the extent of the departure from the assumptions of the model is given by the test of consistency described in Mountford (1982). Another test of the model is simply to compare the estimates derived from the analysis with the standard ratio estimates. This may be done, first, by a visual comparison of the two sets of estimates and

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secondly by the following objective test.

If $d_{ij} = \log \tilde{r}_{ij} - \log r_{ij}$, $1 \leq j \leq C$, are the differences between the overall and the pairwise estimates, and if R is the variance-covariance matrix of the d_{ij} , then the quadratic form $d' R d$ is distributed approximately as χ^2 with $C(C-1)/2$ degrees of freedom. The tests indicated that with a starting point in 1963 the assumptions of the model hold only for the first nine years of the Skylark data.

That the method is applicable over the range of this particular nine-year period is of some note in that this was a period of great change; from the low numbers caused by the severe winter of 1962-1963 the population recovered to a level twice as large some five years later.

The results of the analysis of the nine years of data are given in Table 1.

Table 1

Estimates $g_i - (\sum_{k=1}^C g_k)/C$ of the yearly effects for $(1962+i)$ and their standard errors corresponding to CBC Skylark data

i	1	2	3	4	5	6	7	8	9
Effect	-0.12	-0.33	-0.04	0.05	0.03	0.13	0.17	0.07	0.04
SE	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02

Table 2 lists two estimates of the proportionate change between pairs of years. The first estimate is the standard ratio estimate; the second estimate is the antilog of the difference between yearly effects.

The two sets of estimates are in close correspondence: the average absolute difference between the two estimates is 0.03; the maximum difference is 0.10.

The bracketed figures in Table 2 are the values of the relative efficiency, as measured by the ratio of their variances, of the two estimates. The new overall method of estimation achieves considerable gains in efficiency. The bracketed figures show that there is a more than two-fold increase in efficiency; the overall method requires only half as much data to produce estimates with standard errors equal to those of the ratio estimates.

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Table 2

*Individual (1st row) and overall (2nd row) estimates of yearly proportionate change (relative efficiencies in brackets)
for CBC Skylark data*

	1964	1965	1966	1967	1968	1969	1970	1971
1963	1.21	0.98	0.92	0.92	0.88	0.79	0.90	0.82
	1.23	0.92	0.84	0.86	0.78	0.74	0.82	0.85
	(2.2)	(3.7)	(4.3)	(3.9)	(3.3)	(5.6)	(4.2)	(2.0)
1964	0.78	0.70	0.69	0.65	0.55	0.55	0.61	
	0.74	0.68	0.69	0.63	0.60	0.67	0.69	
	(2.6)	(3.3)	(3.6)	(4.3)	(5.9)	(6.7)	(7.3)	
1965	0.91	0.91	0.84	0.78	0.82	0.90		
	0.92	0.93	0.85	0.81	0.89	0.92		
	(2.2)	(2.6)	(3.1)	(6.0)	(5.7)	(4.7)		
1966	1.02	0.91	0.87	0.95	1.06			
	1.02	0.93	0.89	0.98	1.01			
	(2.1)	(2.1)	(3.0)	(3.4)	(4.4)			
1967	0.91	0.85	0.94	1.04				
	0.91	0.87	0.96	0.99				
	(2.5)	(3.3)	(3.3)	(3.0)				
1968	0.96	1.06	1.13					
	0.96	1.05	1.09					
	(3.0)	(3.6)	(2.8)					
1969	1.10	1.15						
	1.10	1.14						
	(1.8)	(2.0)						
1970	1.06							
	1.03							
	(1.7)							

4. COMPARISON OF SPECIES

One might surmise that the various territorial species, each one with its own particular behavioural pattern, life-history and ecological niche, may respond differently to the year to year changes in climate and in environment. To examine

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this conjecture the same analysis as that applied to the Skylark data was repeated on the data of five other species, selected to cover a wide spectrum of territorial behaviour; Lapwing (*Vanellus vanellus*), Songthrush (*Turdus philomelos*), Willow Warbler (*Phylloscopus trochilus*), Carrion Crow (*Corvus corone*) and Yellowhammer (*Emberiza citrinella*). The preliminary graphical examination of the year-to-year changes, some 200 scatter diagrams in all, showed the same pattern exhibited by the Skylark data; the scatter diagrams indicate straight line relationships for the paired year comparisons.

The visual inspection of the linearity of the data was supplemented by an examination of the signs, positive or negative, of the residuals of the paired observations from the line through the origin with slope equal to the ratio estimate. The paired observations were ordered according to their projection on the fitted line. Both the number of runs of residuals of like sign and also the length of the longest run were then used to test the linearity of the data. Descriptions of these two tests are to be found in Bradley (1968). On the hypothesis of linearity, and if the correlation between the paired comparisons is ignored, then for the period 1963-1971 and for each species and each test, about two out of the total of 36 paired comparisons are expected to be significant at the 5% level. Table 3 gives the actual numbers of comparisons exceeding the 5% significance level.

Table 3

Number of the 36 paired comparisons of the nine years 1963-1971 attaining the 5% significance level according to (i) the number of runs and (ii) according to the longest run

	Number of Runs Test	Longest Run Test
Lapwing	9	9
Songthrush	4	1
Willow Warbler	7	2
Carrion Crow	22	17
Yellowhammer	3	4

Both tests decisively reject the linearity of the Carrion Crow data; the Lapwing data are also somewhat suspect; the data of the remaining three species, Songthrush, Willow Warbler and Yellowhammer pass the tests at relatively acceptable levels.

The subsequent application of the main analysis produced the results shown in

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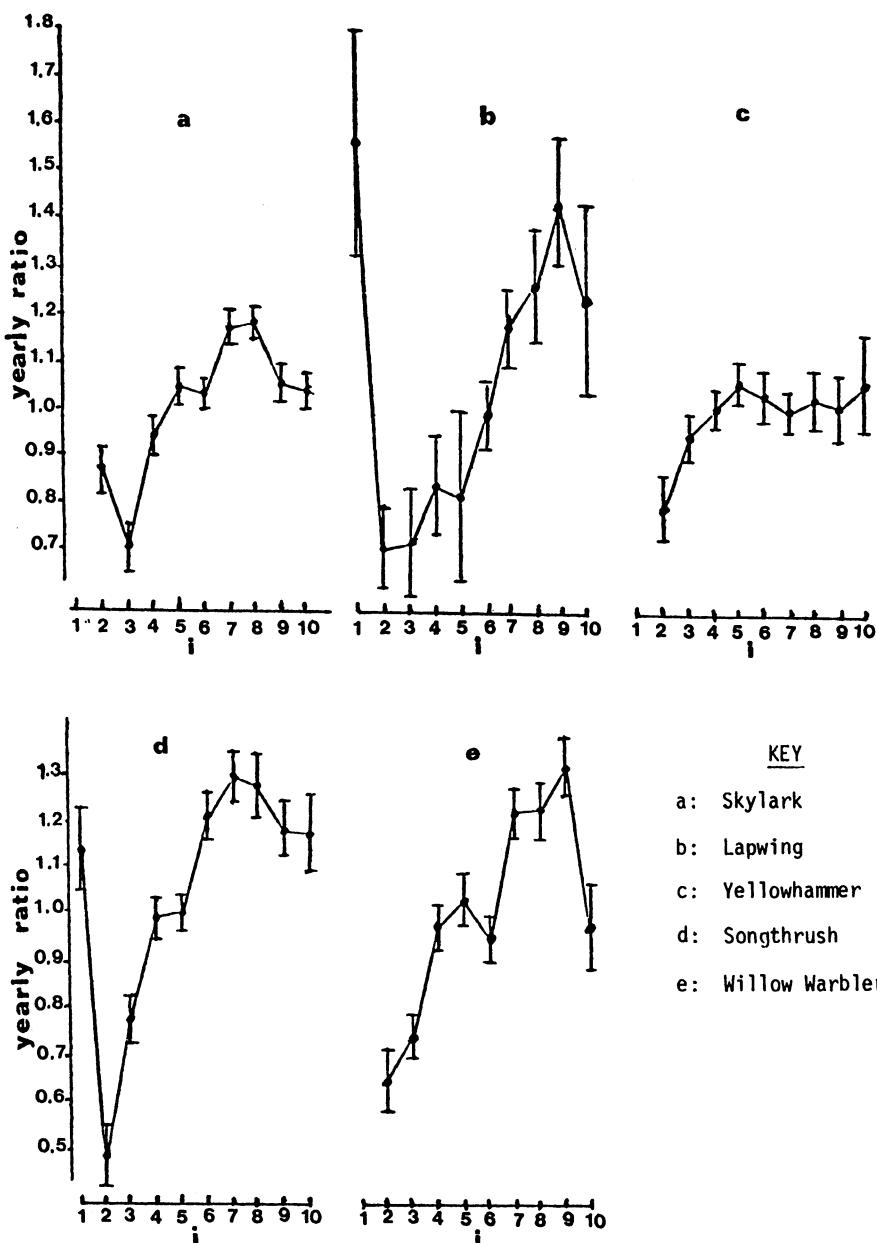


Figure 2 Ratios of yearly estimates of population index. $i=1$ denotes 1962, ..., $i=10$ denotes 1971.

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Figure 2. The analysis of the Carrion Crow data is not included in Figure 2; not only were the data rejected by the above two tests of linearity but also the tests of the validity of the assumptions of the model show that the year to year changes of this species are not mutually consistent, thus invalidating the application of the analysis. Dr. R.J. O'Connor (*pers. comm.*) of the BTO suggests that this breakdown in the model's assumptions for Carrion Crow may be the result of the difficulty of assessing territory numbers of species with large territories.

The analysis of the Lapwing data revealed a breakdown in a year to year consistency over the full period 1962-71. However the two subsets, 1962-66 and 1964-71, of the Lapwing data were both internally consistent; furthermore the relative pattern of change in the period of overlap, 1964-66, was more or less the same for both subsets and was therefore used to splice the two periods together to give the overall picture for Lapwing shown in Figure 2.

Only Lapwing and Songthrush are represented by a measure of the population size in 1962. The 1962 data of the other species were either unavailable or too inconsistent, as measured by the validity of the assumptions, to provide an estimate of the 1962 population size.

Figure 2 reveals the same broad pattern for all five species; after the long harsh winter of 1962-63 the 1963 and 1964 numbers were severely reduced; thereafter the populations increased year by year and from about 1968 onwards the numbers have fluctuated about a steady level. The Lapwing and Songthrush analyses indicate that for these two species this steady level of numbers is of the same order as that prevailing in 1962.

Within the broad pattern of recovery in numbers after the 1962-63 winter the most conspicuous differences between the five species is the degree of variability in the yearly numbers following the attainment of the steady level of population size. The numbers of Yellowhammer and to a lesser extent Skylark fluctuate less from year to year than do the yearly estimates of Lapwing and Willow Warbler. O'Connor (1980) points out that the relatively constant level of Yellowhammer numbers is a result of the density-dependent mechanism whereby birds surplus to the farmland habitat are driven off to form a reserve in the less preferred woodland habitat. The greater fluctuations in the yearly changes of Lapwing could be explained possibly by their relatively small numbers. The average number of Lapwing territories per Census plot is 3.5, compared with average numbers of 6.9, 7.7, 8.8 and 14.1 for Willow Warbler, Yellowhammer, Songthrush, and Skylark respectively. (Carrion Crow averaged 2.1

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territories per Census plot.)

In this paper the examination of the fluctuations in annual numbers has been restricted to a separate analysis for each species. The analysis could be sharpened and a closer examination be made of inter-species competition for territory and of correlations in the annual changes in the species numbers by considering jointly the data of all species found in each Census plot: it is intended to make such a multi-species analysis the subject of a future paper. North (1982) has initiated a multi-species approach; he shows that the CBC plots possess a remarkable degree of homogeneity in that the relationship between the number of species and the total number of territories in a plot is well described by the logarithmic series distribution.

5. DISCUSSION

Whereas the proposed overall method gives a single unified picture of the population changes over a number of years, the existing sequential method merely analyses the change between successive years. Even if only the changes between successive years are considered, the overall method, as is shown by the bracketed figures in the leading diagonal of Table 2, is still about twice as efficient as the year to year method. The existing sequential method measures the change in the population over a period of several years by chaining together the measures of change between successive years. The change between year 1 and year 4, is for example, estimated by $r_{12}r_{23}r_{34}$. The relative efficiency of this estimate to the overall estimate is measured by the ratio of the variances of the two estimates. For the four-year period 1963-67 this ratio equals 3.3, i.e. the confidence interval of the sequential method is 1.8 times as wide as that for the overall estimate. The relative efficiencies for periods up to 8 years apart are given in Table 4.

Table 4

Relative efficiencies of overall estimates to chained year-to-year estimates of population change between 1963 and (1963+i)

i	1	2	3	4	5	6	7	8
Relative Efficiency	2.2	3.2	3.3	3.3	3.0	3.9	4.5	5.5

There is a five-fold increase in efficiency in the estimation of the comparison of 1963 with 1971.

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The analysis of the data of the years 1962-1971 has been presented in this paper. The data for other years can be similarly analysed using different starting points and going forward and/or backward in time. Thus if, as is likely in practice, the level of the most recent year relative to the levels of previous years is of prime interest, then the last year of the 14 years is selected as the starting point of the analysis.

The question of how long the sequence should be has no simple answer. As is generally the case in statistical analysis, a gain in precision is counterbalanced by an increased dependence on the assumptions of the model. The tests of the assumptions of the model mentioned in Section 4 provide an upper limit to the length of the sequence. In the worked example given in Section 4 the test indicated an upper limit of nine years. In terms of the life histories of the six species considered in this paper this is a long time, comprising two or more generations. Moreover major ecological changes can take place in a nine-year period. It is therefore recommended, as an extra check on the accuracy of the model, that the analysis is not only applied to the data of the longest sequence allowed by the test but also to the data of sequences of shorter length. If the model is indeed a good approximation to the truth then the various analyses should give the same general picture of the year-to-year fluctuations.

The Census plots are not representative of the whole country. Upton and Lampitt (1981) report that the majority of plots are within 150 miles of London, with only seven locations outside England. Thus climatic changes which differentially affect the populations in the northern and southern halves of the country will be overlooked. The extrapolation of the results to other sites should therefore be limited to those sites that fall within the range of characters covered by the Census plots.

ACKNOWLEDGEMENTS

I am much obliged to Dr. R.J. O'Connor and to P. Whittington for providing me with the CBC data. I am indebted to the two editors Dr. B. Morgan and Dr. P. North for their many constructive comments.

AREA-SPECIES INCIDENCE RECORDING

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SUMMARY

A low-cost method for collecting extensive data from many bird-watchers at a controlled access site is described. The constraints on data collection are discussed and the uses that might be made of the data are outlined.

Keywords: CENSUS TECHNIQUES, DATA COLLECTION, COMPUTER ANALYSIS, STATISTICAL PACKAGES.

1. BACKGROUND CLASSIFICATION OF ORGANISMS, INCLUDING DEFINITION OF GROUPS (TAXONOMY) AND ALLOCATION OF INDIVIDUALS TO GROUPS (IDENTIFICATION)

Much attention has been devoted by ornithologists to systematics and to field identification. The competent amateur can often determine the age, sex and subspecies of a bird and rigorous standards are imposed before claims of sightings of rare birds are accepted. It can be argued, but never proved, that the apparent new occurrences of vagrant species in recent years owes as much to the awareness by observers of the species' existence as to new patterns of movement by the birds.

In contrast, systematic recording of the patterns of occurrence and numbers of common birds has been largely ignored. The extensive surveys carried out particularly by the British Trust for Ornithology (B.T.O.) have relied upon long term commitments by a relatively small number of trained or self-trained enthusiasts. National surveys can produce anomalous distributions of results, in that the scantiest replies come from areas known to be honeypots for bird watchers. The effort required is such that surveys have to be carried out long term at a small number of sites (for example, the Common Birds Census (C.B.C.)) or as special exercises for a limited period (for example, the Atlases).

It is customary in almost every area for local bird watchers to pool their

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records to give an overall picture of birds in their area. This method suffers severe limitations and biases compared to the B.T.O.'s surveys. Records are often very scattered in time and space and are extremely selective in the species reported; the quantities of records submitted vary widely between observers. Anyone who has collected reports for societies will know that, in Britain, House Sparrows are extremely rare eruptive migrants, Chiffchaffs are winter visitors and Blackbirds are mostly white.

Reported bird counts are arbitrary in scope and precision. From such knowledge as is available, it is apparent that more time needs to be spent in the field and in a more regulated way, to produce a reasonably accurate and reproducible count of even a single species, than to tick off all the species present. The problems of counting are well exemplified by the Peregrine and the Herring Gull. The former suffered a 40% decline in less than ten years, largely unnoticed by bird watchers until the B.T.O. survey, which was set up to monitor claims (by pigeon fanciers) of an excessive Peregrine population (Fergusson-Lees, 1957, misquoted in Ratcliffe, 1962). Coulson has concluded that the Herring Gull has been doubling its total British population every five years for the whole of this century but even this continuous and spectacular growth has not been documented in local ornithological reports (lecture at Hull University, 1980).

The majority of *ad hoc* records contain no supportive information on the weather or habitat. Again, this is largely a consequence of the overwhelming interest in field identification, which should be only the first, though critical, step in studying a bird.

The most serious criticism of casual note-takers is that negative records are often overlooked. I suspect that even when a daily log is kept, by a meeting in the evening at an observatory, the 'common residents' are ticked each day without too critical an examination.

The species-incidence form described is one attempt to tap the large number of uncontrolled observers as a source of comparable data. At a particular site it will be an interesting measure of the patterns of occurrence and gross fluctuations of numbers within species and, when comparing more than one site, the species diversity may be taken as a crude measure of the ecological interest of the site. Compared with the B.T.O. Winter Atlas scheme, (B.T.O. News 116, September 1981) the present study is more extensive in space but more extensive in time. It is hoped that the forms provided will be used as the normal way of recording by a substantial number of visiting bird watchers, without their having to undertake any formal commitment.

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A second (but not secondary) aim was to investigate ways of collecting ornithological data specifically for computer processing - methods of data entry, in particular Optical Mark Reading (OMR), were considered and whenever possible the analyses are carried out using standard packages. This related to my work in implementing, testing and supporting the use of a University computing facility and has the added motive of keeping the analyses "user-friendly". The method might be extended to other sites with comparable facilities for contacting visitors, such as reserves nature trails or observatories. Although the data collection and preparation would increase proportionately, the methods of analysis could be easily understood and undertaken elsewhere.

2. DESCRIPTION OF THE SITE

Tophill Low is a Yorkshire Water Authority (Y.W.A.) abstraction and storage site on the River Hull, approximately fifteen miles north of Hull and ten miles from the North Sea coast, which has been developed, both industrially and ecologically, since 1959. It benefits as a bird watching site by having a wide range of habitats in a small area: there are two reservoirs; the river with one small area of fringing reeds (*Phragmites*); a marsh, created in 1976, dominated by sedge (*Carex riparia*) and reed-grass (*Glyceria maxima*); shallow water "lagoons" with open mud; rough grass; lawns and gardens; deciduous and mixed woodland. Hides have been erected overlooking two of the wet areas and another is planned to overlook a reservoir. The site extends to 110 hectares and is surrounded by farmland, used for arable crops and sheep, and several small woods. Game is preserved in the area for shooting, although shooting is banned within the Tophill boundaries. Migrant birds can move easily between this site, Hornsea Mere and the coast and the Humber Estuary.

Access to the site is rigorously controlled. Bird watchers are issued permits to visit by the Y.W.A. and on arrival are required to sign-in at the Information Hut. The benefit of this is that they can also collect a hide key. A log book is left in the hut for visitors to note what they have seen; the entries tend to be scrappy but it does allow one on arrival to scan the previous few days for birds to expect or hope to spot. To date 220 permits have been issued.

There is a local committee of bird watchers who, with the permission of the Y.W.A., undertake small works to improve the area for birds and watchers. They are responsible for the hides and collate the log book records.

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3. METHODS AND RATIONALE

I approached the bird watchers' committee and obtained their agreement that I would supply questionnaires and analyse the replies. I drafted a pilot form, which was quickly modified to the layout and content currently in use, of which a specimen is appended. One clear design constraint was that the form should be a single sheet with the two sides separated in intent, so that the form is conveniently filled in while walking - I have tried using a clipboard or simply folding the sheet in four, both of which methods are quite satisfactory.

The "front" of the form asks for simple demographic information. It was agreed that completed forms should first be vetted by the committee and the name and address of observer is requested so that queries can be resolved and interesting records ascribed to the correct person. The problems of vetting are those common to any collation of records, except that all records can be seen in context. The date is essential and I think the time of arrival and length of stay are desirable items to know. The weather coding is *ad hoc* and has caused problems to people completing forms but it is, I think, worth including unless or until analysis shows that it can be ignored. It would be possible, but far more arduous and expensive, to extract general weather patterns from official data but the intention of this form is to note the local, short-term conditions.

The main part of the form is the list of species. 119 species and one extra subspecies are named; they were chosen as the 'common' species that I would expect in the area, concentrating on those that seemed to be ignored in the log book records. Certain species that are regularly seen at Tophill (e.g. Ring-necked Duck) were therefore excluded. The choice would seem to have been justified in that 111 of the 120 were reported on forms. Space is provided for extra species to be noted but it was not intended that these should be entered into the computer. Of species not named on the form, in two and a half years of operating the scheme the maximum number of extra species on any form has been three. Over any twelve month period, forty to fifty extra species might be recorded at Tophill. I hoped that the form could be used as a complete record of each visit to the site and the collection of forms would, in itself, provide a valuable account of the activities of birds and watchers over the months and years. The 'observability' of any bird is a confounding of factors to do with the species, the observer and the occasion.

The log book is still in use for day-to-day information and for more extensive notes on behaviour or descriptions of rarities.

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One advantage of having a list of species to be ticked off in the field is that it acts as a prompt. If you have been watching for some time without seeing (for example) a Starling, you can more consciously look out for one and an eventual negative record will be of more value. The asymmetry of positive and negative records must be constantly borne in mind; it is only consistent patterns of records that are to be interpreted. Strictly speaking, any bird count represents a time-series of sequential observations rather than a cross-sectional measurement. In most recording methods it seems to be assumed that the observer is constantly receptive and equally observant of all species. One counter comment on record is in Bystrak (1981). When discussing the North American Breeding Bird Survey, he writes that many observers complain that fatigue affects their results near the end of a transect.

Variations between observers could be cited as a criticism of this data collection. For example, the accuracy with which some observers can identify the more difficult species has been questioned. There are no easy solutions but some of the problems relating to pairs of species are well defined and in such cases I hope that collecting all claimed records will allow some analysis to clarify the status of the birds and the reasons for the identifications. The design of any data collection form should aim to minimise observer errors; it is unrealistic to assume that they are absent or negligible. The most comparable study is the Audubon Christmas Bird Count. Arbib (1981) discusses the problems of inter-observer variation and recommends training and grading of observers. However, this leads to expense and must reduce the number of participants. Bock and Root (1981) point out that the use of such data depends upon having large quantities over long time periods. Under these conditions, individual biases will cancel out or can be ignored.

Many people have commented that they would rather have a "simpler" form on which the numbers seen of each species are written. The multiple choice method of recording counts was deliberately chosen because, for reasons mentioned in the Background section, actual count figures are of little value unless the count is performed in a manner appropriate to the species. It is worthwhile to be able to distinguish between small and large numbers, in order to eliminate spurious occurrences caused by (for example) one sick bird that stays beyond the migration season. One may also be able to pick out marked seasonal fluctuations. However, it is far simpler to code and input to the computer grouped counts rather than figures with varying numbers of digits. Once they are used to it, it is probably more accurate if the observers categorize their own subjective or objective concepts of numbers, rather than for one coder to try and interpret a variety of accuracies and precisions. Some people at

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first ring the number category nearest to what they have seen rather than, as requested, the one below. This has now been explained to all regular contributors. Some enter both their "accurate" counts and ring the appropriate frequency class; this would make this form compatible with the B.T.O. Winter Atlas recording scheme and, for any particular species, a researcher could soon extract all the counts.

Some initial resistance was encountered because people felt that their contributions would be too meagre, either because they were novices at identification or because they intended only a short visit. The only solution to this is education. I try to persuade people that they should report those birds they can identify (and only those!) and the length of visit is, of course, noted on the form and so can be taken into account. The data are cumulative and all contributions really are well-comed. For most purposes it makes sense to aggregate all the forms within each time interval, noting a species if anyone observed it and totalling the effort as, e.g., observer-hours. The justification for this study is precisely that it collects data that are available but generally neglected. By imposing the least burden and restrictions on observers, we can hope to carry on for as long as interesting and useful results are obtained.

After vetting by the committee, to pick up interesting records and reject obviously spurious ones, the forms are passed to me in batches. I add the codes in a distinctive colour in the printed spaces and the codes are transcribed character for character into the computer by the Computer Centre data preparation service.

The codes used are mostly self-explanatory. Questionnaires are treated in the order I receive them and the "REFERENCE" is just an integer. The observer's name is coded as initials. The date is day, month, year and the time is the truncated hour below (local time). The length of stay is hours and tenths, but the latter cannot be expected to be exact and, in general, times have been recorded to the nearest quarter hour, which I call 0.3, 0.5 and 0.7 respectively. Codes for the weather types appear on the form. Each species seen is then coded with 1, 2, 3, 4 or 5. Any question unanswered or species not noted is left blank.

The data input to the computer's store consists of a text file with three lines per form. This is fixed-format data and it is essential to confirm that characters have not been missed or duplicated, as well as to pick out as many mis-typings as possible. It would be possible, but not convenient, to refer back from a character in the file to the original form but rather than do this, I run a program that reformats the data as printer output in a column layout very similar to the form. This program

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was specially written in Algol68 and is simply a formatted read and formatted write in a repeating loop. The output can be proof-read against the original forms and then kept as a copy of the forms.

Once the data have been deemed sufficiently accurate, the analysis can begin. The package SPSS has been used initially. It has several features that commend it; one in particular is the powerful labelling facility. Each variable in the data set is given a name, by which the programmer and the program can refer to it. The initial data description file contains a list of variable names, a FORTRAN-like format statement according to which the values are read and a list of text labels to explain each variable name and each permitted value (if necessary). This file is tedious to prepare but once done it need not be substantially changed again. The ability to label values means that the coding scheme of "blank" or 1 to 5 for every species does not lead to confusion when different class intervals are used; on output, a 5 for Great Crested Grebe will be labelled as meaning "5 or more", while a 5 for Greylag Goose will be labelled "100 or more".

4. ANALYSES AND PRELIMINARY RESULTS

The forms have been used since April 1981. 180 were returned for the period up to the end of 1981 and a number of analyses have been tried. Those reported here have been chosen to demonstrate the ease with which the data can be displayed in useful ways and with which hypotheses can be tested. The present paper deals only with the technical aspects of how to collect and analyse such data and any conclusions suggested with regard to particular species are very tentative.

The programming shown is in the SPSS command language (Nie *et al.*, 1975; Hull and Nie, 1979) and is mostly self-explanatory to intent. Words shown in upper case are either keywords in SPSS or variable names referring to questions on the form. Variable names are identified, on the particular computer used, by the first six characters but extra characters may be present and will be ignored. Most of the names are lengthened to be obvious in meaning.

The first analyses aim to provide additional confidence that the data are correct and consistent. Procedure FREQUENCIES produces for each of the demographic variables a table of the values found and their respective numbers of occurrences. The values can be checked, to show that they are within the allowed range and the frequencies compared with known or sensible estimates. For example, any value for YEAR

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other than 81 would probably indicate data misplaced on the line. An error that did show up at this stage was a MONTH coded as 1; on checking it was found that the observer had written the month as 1 in November. This error would not have been obvious had data been available for the whole year.

Tables of the numbers of forms returned by each observer, the times of arrival and the lengths of visits would be of interest to the management of a reserve or nature trail.

Procedures CROSSTABS and SCATTERGRAM provide bivariate summaries as contingency tables and point plots respectively. CROSSTABS allows one to notice improbable or impossible combinations of answers and the SELECT IF and LIST CASES commands can be used to identify the offending data to be re-checked against the form. Examples would be to look for fine days when it snowed or warm days when the ground was frozen. Scatter plots are easier to assimilate than tables when the number of categories or alternative answers is large. Plotting the arrival time against the month clearly shows the change of day length; I would not expect bird watchers to arrive in the dark. Again, outliers once recognised can be identified and understood.

More sophisticated analyses using these data might include attempts to identify warm and cold spells, periods of gales or periods of settled weather. The one analysis I have done was a BREAKDOWN table of the length of STAY by MONTH. Rather surprisingly, it showed little variation in the mean or variance, suggesting that there is no great need to make a general adjustment for this factor in interpreting the "observability" of a species through the year.

The bird counts pose an initial problem in their bulk. A trivial program would suffice to obtain a FREQUENCIES table for each species in turn but this would extend over an unwieldy length of paper. As a data reduction, I collapsed all the codes for numbers to the dichotomy PRESENT/ABSENT and used calendar months as convenient, if arbitrary, time periods to produce a 2×8 contingency table of occurrences for each species:

RECODE	DABCHICK TO CARRIONCROW (0 = 0) (ELSE = 1)
CROSSTABS	TABLES = DABCHICK TO CARRIONCROW BY MONTH
OPTIONS	3 , 5

This would still be far too long, largely because of SPSS's preoccupation with page and table headings and also because half of each table is redundant. Therefore this output was filed and simple use of the system text editor left just the species'

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Bird Type	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Dabchick	Forms: 3	0	0	0	0	1	8	9	9	30	
	%age: 12.5	0.0	0.0	0.0	0.0	10.0	27.6	33.3	42.9	16.9	
Great-crested Grebe	Forms: 10	24	14	10	2	0	19	24	5	108	
	%age: 41.7	77.4	73.7	76.9	50.0	0.0	65.5	88.9	23.8	60.7	
Cormorant	Forms: 14	13	9	2	1	1	19	13	21	93	
	%age: 58.3	41.9	47.4	15.4	25.0	10.0	65.5	48.1	100.	52.2	
Grey Heron	Forms: 4	6	2	4	2	5	11	9	6	49	
	%age: 16.7	19.4	10.5	30.8	50.0	50.0	37.9	33.3	28.6	27.5	
Canada Goose	Forms: 8	8	0	0	0	0	0	0	0	16	
	%age: 33.3	25.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.0	
Grey Lag	Forms: 19	25	6	3	0	4	19	17	8	101	
	%age: 79.2	80.6	31.6	23.1	0.0	40.0	65.5	63.0	38.1	56.7	
Mute Swan	Forms: 22	18	8	3	0	3	15	22	15	106	
	%age: 91.7	58.1	42.1	23.1	0.0	30.0	51.7	81.5	71.4	59.6	
Shelduck	Forms: 22	19	13	3	0	0	4	7	5	73	
	%age: 91.7	61.3	68.4	23.1	0.0	0.0	13.8	25.9	23.8	41.0	
Mallard	Forms: 24	31	18	12	4	10	29	27	20	175	
	%age: 100	100	94.7	92.3	100.	100.	100.	100.	95.2	98.3	
Teal	Forms: 22	14	10	11	4	10	28	27	21	147	
	%age: 91.7	45.2	52.6	84.6	100.	100.	96.6	100.	100.	82.6	
Gadwall	Forms: 18	28	11	5	1	2	14	19	15	113	
	%age: 75.0	90.3	57.9	38.5	25.0	20.0	48.3	70.4	71.4	63.5	
Wigeon	Forms: 14	3	1	0	0	0	23	25	19	85	
	%age: 58.3	9.7	5.3	0.0	0.0	0.0	79.3	92.6	90.5	47.8	
Pintail	Forms: 1	0	0	0	0	1	4	8	3	17	
	%age: 4.2	0.0	0.0	0.0	0.0	10.0	13.8	29.6	14.2	9.6	
Shoveller	Forms: 19	30	9	6	1	8	26	25	11	135	
	%age: 79.2	96.8	47.4	46.2	25.0	80.0	89.7	92.6	52.4	75.8	
Pochard	Forms: 22	29	15	10	3	7	28	27	20	161	
	%age: 91.7	93.5	78.9	76.9	75.0	70.0	96.6	100.	95.2	90.4	
Tufted Duck	Forms: 23	31	18	10	4	7	28	27	21	169	
	%age: 95.8	100.	94.7	76.9	100.	70.0	96.6	100.	100.	94.9	
Goosander	Forms: 0	0	0	0	0	0	0	5	9	14	
	%age: 0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.5	42.9	7.9	
Sparrowhawk	Forms: 4	5	1	2	0	0	3	5	3	23	
	%age: 16.7	16.1	5.3	15.4	0.0	0.0	10.3	18.5	14.3	12.9	
Kestrel	Forms: 7	10	8	6	2	5	21	21	17	97	
	%age: 29.2	32.3	42.1	46.2	50.0	50.0	72.4	77.8	81.0	54.5	

Figure 1 Tables of occurrences of 19 common species of birds at Tophill Low in 1981. The top line for each species is the number of forms reporting the species, the second line is this expressed as a percentage of the monthly or annual total of forms. The table runs from April to December, then the year total follows. Based on 178 forms received as of 23/2/82.

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name, monthly totals of forms reporting the species and these figures expressed as percentages of the monthly total of forms. A sample of this output is reproduced as Figure 1.

In this output comparisons can be made between species and within species between months. Again, the first uses are to spot odd or unbelievable records - Arctic Terns in December invariably turned out to be misplaced Wood Pigeons. It is then of interest to see which species have been reported. Marsh and Willow Tits provide a good test case of species that are not deemed rare enough to warrant a description to back up a record and are possibly often confused. Both were reported (Marsh twice and Willow 6 times) and the committee are satisfied that both do occur. The forms may help further to clarify their respective statuses, both by causing records to be reported and by stimulating more birdwatchers to be aware of the need for critical identification.

Although the table is intended as a summary and only the springboard to more detailed species by species examination, some features are quite striking. Species that would be dismissed as "resident" are seen by no one over extensive periods. It might be thought that such sedentary birds as tits should be present constantly if at all but one of the clearest patterns is that Long-tailed Tits were not seen from April to August although they were frequent from October onward. Other species are apparently always about but vary in their probability of being spotted. For example, it is instructive to compare Sparrowhawk and Kestrel records. Many of these variations in "observability" can be related to song or display periods, moult, weather etc. One curious observation is that the proportion of forms reporting Cormorants went up in the very cold weather in December. I have made a start in looking at the effect of windspeed on the reservoirs. Two hypotheses are that wind, by causing waves, may affect the numbers of waterfowl and/or that it may make them more difficult to spot and count.

It would be simple, using the standard data modifications of SPSS, to divide the time into periods of equal lengths or periods represented by equal numbers of forms. It would also be easy to identify weekends and holidays (see Sharrock, 1966, for rationale).

When all the counts have been RECODEd to 1 or 0, it is easy to COUNT the number of species noted on each form and it is of interest to plot this against the length of stay. This plot is reproduced as Figure 2. The point A is a genuine outlier, in that it comes from a different population - this was a moth-catcher who spent four

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hours at Tophill at night and noted the birds that called or sang! The plot suggests that one may expect to see more species as one stays longer only within the first three hours. This accords with my informal observation that it takes between three and three and a half hours to make a satisfactorily thorough tour of the site. A related discussion is found in Usher (1985).

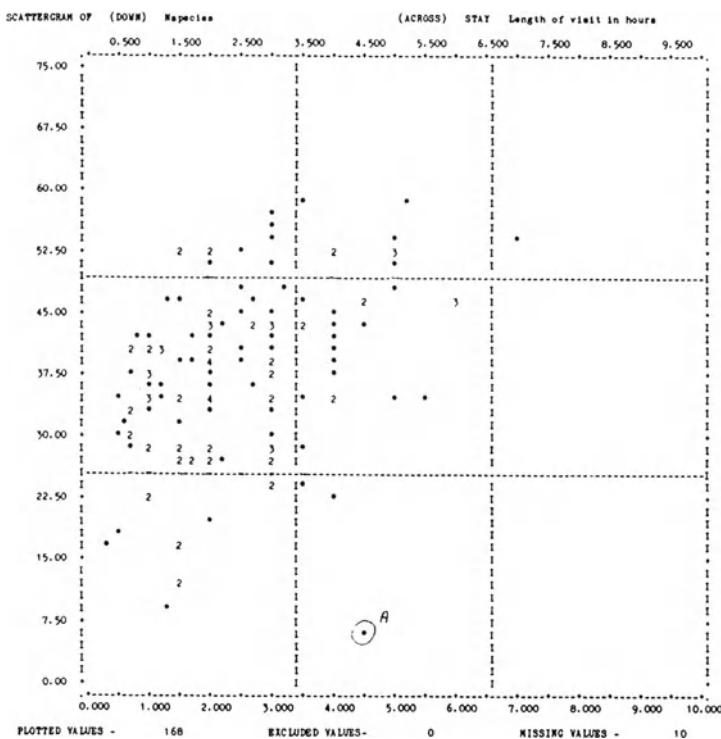


Figure 2 Tophill low bird recording sheets analysis. Implemented by University of Vermont. Run at University of Hull.

Such a plot of species-number against effort, where effort is conventionally the area sampled but is here the time expended, is termed a collector's curve. It is of interest to observe whether the species-number increases indefinitely with effort or approaches some asymptote. As presented, the data do not clearly answer that question but when aggregated into days, weeks or months, with a corresponding increase in the effort (observer-hours) for each period, it is seen that the species-number does

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indeed continue to increase monotonically with effort and no ceiling is reached. This implies an open community, which one would expect for a site where observable migration is a main interest. However, the different abilities of observers have been noted above and this work also highlights the need to measure, control or reduce observer bias when collecting any data.

Another analysis suggested by the species data recoded would be to take the 180 by 120 matrix of presences and to perform cluster analysis to group either species or dates. The choice of similarity measure should take account of the asymmetric nature of Present and Absent as data values. The large clusters could be anticipated but some small scale features might be interesting. The package CLUSTAN has an easy interface with SPSS, to allow the use of the latter's powerful data manipulation and selection. This step has not yet been taken.

All the analyses so far described have been in terms of records, i.e. forms. This is fair, in that the number of forms reporting each species within any sample is an estimate of the probability of recording that species averaged over the sample of observers. When there are several forms available for each day or defined short period, they cannot be treated as independent, as people do ask what is about and look in the log book. It might be more appropriate to merge the data from all the forms for each period; one approach would be to take the maximum count for each species and the total observer hours. Procedure AGGREGATE provides just this operation and creates a new raw data file of requested summary data. With the powerful SORT CASES facility, it is easy to input forms in the order received, extract the (say) seven-day maxima for each species and to plot these in order. This would give a simple diagnostic for identifying gross changes in numbers. This has not been done but for one or two species it is more convenient to plot the records against the chosen period. Here is an example which uses the standard SPSS function for turning a date into a day-index:

```
COMPUTE      DAYIND = YRMODA (YEAR, MONTH, DAY) - YRMODA (81, 1, 1)
COMPUTE      WEEK = TRUNC (DAYIND/7)
SCATTERGRAM   LONGTAILTIT (0, 10) WITH WEEK (2, 52)
OPTIONS .     7
```

This output is presented as Figure 3; it shows all records, whereas the aggregated file would contain only the top point for each column.

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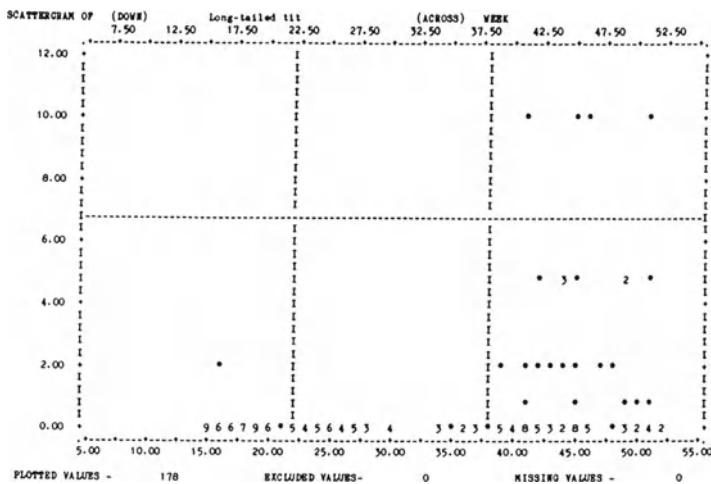


Figure 3 *Tophill low bird recording sheets analysis.*
Quick aggregate.

5. FUTURE DEVELOPMENT

An assessment of the worth of this approach to recording must depend upon the usefulness of the data ornithologically. The first results are encouraging; some expected patterns can be seen and some unanticipated patterns can be understood. It can already be claimed that the use of the forms has increased the numbers of recorded occurrences of many species without imposing an intolerable burden on the collator of an annual report. The committee and I are satisfied that the Tophill Low recording scheme is worth continuing.

The existing form could be much improved in design. The better use of space, a variety of type faces and sizes and a simplified rubric should increase the numbers of contributors and the accuracy of replies. The weather details will be changed to request those on arrival with an extra question about whether conditions then remained stable, improved or deteriorated. The form will soon be redrafted as supplies run out.

An approach that was considered was Optical Mark Reading, in which the observer would record his count by drawing a line through the appropriate answer. Such forms

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are then immediately readable by a special peripheral analogous to a punch-card reader but working by reflected light. This considerably reduces the time and effort required to transcribe the data and almost eliminates transcription errors. The technique has been widely used for stock control.

OMR was rejected firstly on the grounds of cost and secondly because of technical restrictions. The printing of forms has to be very exact and in non-reflecting ink. Few firms undertake this specialist job and, while they were very helpful and encouraging, the design, set-up and printing for a short run (5,000 forms) was estimated at £500. Reading the forms was, however, comparatively very cheap at a bureau and for a larger scale study the initial cost might well be completely offset by later savings in data transcription. The technical restriction is that the marks themselves must be drawn in pencil as most biro inks reflect the wrong spectral lines. This instruction might inhibit *ad hoc* recorders or might be ignored, leading to forms being misread or necessitating copying.

OMR would be practical and easy to use for field recording if some national service were set up, possibly by the B.T.O. Folded or crumpled forms can be read successfully and provision can be made for cancelling marks. Most importantly, if a generalised form were produced in large quantities (to reduce the cost), it is possible to overprint specific questions so as to tailor the form to a site or a study.

The techniques of analysis outlined using standard and widely available computer programs could be applied to existing presence/absence or count data, such as observatory or reserve logs.

6. FURTHER DEVELOPMENTS SINCE MAY 1982

After some initial resistance the recording forms are now well used, mainly by regular visitors to the site but also by some first-time visitors. 318 forms were returned in 1982 (*cf.* 178 for April-December 1981). The processing described has allowed these data to be incorporated in an annual report that follows the usual pattern.

The form was redesigned at the end of 1982, making the current version the third. In spite of the earlier comments that a "simpler" form was needed, my collaborators were persuaded that *ad hoc* counts are not suitable either for data capture or for processing. The number of count categories has been widened and we

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have tried to tailor the categories to each species more exactly. This has principally involved choosing as the top frequency class a number that will rarely, if ever, be attained. We also now distinguish between "1" and "Present but uncounted". The intermediate frequencies have been chosen to form a very roughly logarithmic scale. We have added a small map onto the form, so as to get an idea of the quality of coverage of the site; this information has not yet been coded and entered onto the computer.

To investigate the internal consistency of the *ad hoc* weather codes I used principal component analysis. The scale variables were assumed monotonic and the wind direction reduced to two binary variables to indicate northerly and easterly components. A more refined analysis would test the validity of these assumptions. Nevertheless, the results were encouraging: four components were identified from the nine recorded variables and all had an obvious interpretation. In order of eigenvalue, they were RAIN (weighted on general condition and precipitation), COLD (weighted on temperature and ground state), VISIBILITY (weighted on visibility and cloud cover) and WIND (weighted on speed and both directions). It will be more sensible to derive and use canonical variates when relating bird numbers to the weather, as this reduces the effects of subjectivity and individual bias on any particular scale.

Further work has been carried out on obtaining indices of ecological diversity, and evenness, of which the species-number is an example. The interpretation of such measures of "community" structure at a migration site with a high seasonal turnover of species is at least problematical. Plots of such indices against time might indicate seasonal activity.

The data have been used to experiment with correspondence analysis, implemented in GENSTAT. No immediately meaningful interpretation of the axes generated by the species came to mind, possibly because of the short time span of the data used. However, many small scale features were observed and further attempts will be made with this procedure. With a longer time sequence, I will separate groups of species for analyses (e.g. winter visitors, water-birds, breeding species), so as to look for structure within the groups. One reason for doing this is that the program is expensive in machine time.

ACKNOWLEDGEMENTS

I would like to thank Peter Izzard for his helpful criticism of the draft of this paper and for his work in administering and collecting the questionnaires as well

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filling them in. Thanks are also due to the other members of the Tophill Low bird watchers' committee and all those observers who have so far completed forms.

APPENDIX 1

Dabchick	<i>Podiceps ruficollis</i>
Great Crested Grebe	<i>Podiceps cristatus</i>
Greylag Goose	<i>Anser anser</i>
Ring-necked Duck	<i>Aythya collaris</i>
Sparrowhawk	<i>Accipiter nisus</i>
Kestrel	<i>Falco tinnunculus</i>
Peregrine	<i>Falco peregrinus</i>
Herring Gull	<i>Larus argentatus</i>
Arctic Tern	<i>Sterna macrura</i>
Wood Pigeon	<i>Columba palumbus</i>
Blackbird	<i>Turdus merula</i>
Chiffchaff	<i>Phylloscopus collybita</i>
Long-tailed Tit	<i>Aegithalos caudatus</i>
Marsh Tit	<i>Parus palustris</i>
Willow Tit	<i>Parus montanus</i>
House Sparrow	<i>Passer domesticus</i>
Starling	<i>Sturnus vulgaris</i>
Carrion Crow	<i>Corvus corone</i>

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APPENDIX 2Please leave
blank for code:

TOPHILL LOW Bird Recording Sheet

PLEASE COMPLETE A SEPARATE SHEET FOR EACH VISIT

Please complete both sides of the form. Most of the questions on this side can be answered on arrival. The species list can then be completed as you walk around the site. Record every species you see or hear; approximate or exact counts are a bonus. Unusual species or behaviour should be recorded in the Log-book in the Information Hut.

Completed forms may be left in the Information Hut, or sent to:

Allan Reese, 5 The Green, Cranswick, Driffield, YO25 9QU
or given to any member of the Hide Committee.

Contact name and Address
.....
.....

Date Number in party

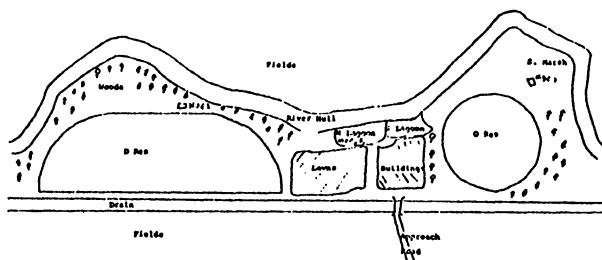
Time of arrival Duration of visit

Weather on arrival (Please ring appropriate category for each item)

Temperature:	Very Hot(1)	Hot(2)	Warm(3)	Mild(4)	Cold(5)	Very Cold(6)			
General:	Fine(1)	Showers(2)	Light Precipitation(3)	Heavy Precipitation(4)					
Precipitation:	None(0)	Rain(1)	Hail(2)	Sleet(3)	Snow(4)				
Visibility:	Good(1)	Moderate(2)	Poor(3)	Mist(4)	Fog(5)				
Cloud Cover:	(Total) 8/8	6/8	4/8	2/8	0/8 (N1)				
Ground State:	Dry(1)	Wet(2)	Frozen(3)	Snow Covered(4)					
Wind Speed:	Calm(1)	Slight Breeze(2)	Moderate Wind(3)	Strong(4)	Gale(5)				
Wind Direction:	N 1	NE 2	E 3	SE 4	S 5	SW 6	W 7	NW 8	Variable 9

During the visit, the weather (1) improved (2) deteriorated (3) was steady.

Please mark areas examined, on the sketch-map below, with crosses or notes.



Thank you for contributing

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APPENDIX 2 (Cont'd.)

Fill in this side as you proceed around the site. Ring a number if you have seen or heard AT LEAST that number or ring P for PRESENT if you make no count. Enter actual counts by the species' name.

Dabchick	10	5	4	3	2	1	P	Swift	100	30	10	5	2	1	P
Great-c. Grebe	10	5	4	3	2	1	P	Kingfisher	10	5	4	3	2	1	P
Cormorant	10	5	4	3	2	1	P	Skylark	100	30	10	5	2	1	P
Grey Heron	10	5	4	3	2	1	P	Sand Martin	100	30	10	5	2	1	P
Canada Goose	50	30	20	10	5	1	P	Swallow	100	30	10	5	2	1	P
Grey lag	50	30	20	10	5	1	P	House Martin	100	30	10	5	2	1	P
Mute Swan	10	5	4	3	2	1	P	Meadow Pipit	100	30	10	5	2	1	P
Whooper Swan	10	5	4	3	2	1	P	Yellow Wagtail esp.	100	30	10	5	2	1	P
Bowicks Swan	10	5	4	3	2	1	P	Grey Wagtail	10	5	4	3	2	1	P
Shelduck	50	30	20	10	5	1	P	Pied Wagtail esp.	100	30	10	5	2	1	P
Mallard	500	300	200	100	10	1	P	Wren	100	30	10	5	2	1	P
Teal	500	300	200	100	10	1	P	Dunnock	100	30	10	5	2	1	P
Gadwall	100	30	10	5	2	1	P	Sedge Warbler	100	30	10	5	2	1	P
Wigeon	500	300	200	100	10	1	P	Reed Warbler	100	30	10	5	2	1	P
Pintail	10	5	4	3	2	1	P	Grasshopper Warbler	10	5	4	3	2	1	P
Garganey	10	5	4	3	2	1	P	Garden Warbler	10	5	4	3	2	1	P
Shoveller	100	30	10	5	2	1	P	Blackcap	10	5	4	3	2	1	P
Pochard	500	300	200	100	10	1	P	Whitethroat	10	5	4	3	2	1	P
Tufted Duck	500	300	200	100	10	1	P	Lesser Whitethroat	10	5	4	3	2	1	P
Goldeneye	100	30	10	5	2	1	P	Willow Warbler	100	30	10	5	2	1	P
Rd-b. Merganser	10	5	4	3	2	1	P	Chiffchaff	10	5	4	3	2	1	P
Goosander	10	5	4	3	2	1	P	Goldcrest	100	30	10	5	2	1	P
Sparrowhawk	10	5	4	3	2	1	P	Spotted Flycatcher	10	5	4	3	2	1	P
Kestrel	10	5	4	3	2	1	P	Whinchat	10	5	4	3	2	1	P
Partridge	100	30	10	5	2	1	P	Stonechat	10	5	4	3	2	1	P
Rd-l. Partridge	100	30	10	5	2	1	P	Wheatear	10	5	4	3	2	1	P
Pheasant	100	30	10	5	2	1	P	Robin	100	30	10	5	2	1	P
Water Rail	10	5	4	3	2	1	P	Fieldfare	100	30	10	5	2	1	P
Moorhen	100	30	10	5	2	1	P	Blackbird	100	30	10	5	2	1	P
Coot	500	300	200	100	10	1	P	Redwing	100	30	10	5	2	1	P
Ringed Plover	10	5	4	3	2	1	P	Song Thrush	100	30	10	5	2	1	P
Little R. Plover	10	5	4	3	2	1	P	Mistle Thrush	100	30	10	5	2	1	P
Golden Plover	100	30	10	5	2	1	P	Long-tailed Tit	100	30	10	5	2	1	P
Lapwing	100	30	10	5	2	1	P	Marsh Tit	10	5	4	3	2	1	P
Dunlin	100	30	10	5	2	1	P	Willow Tit	10	5	4	3	2	1	P
Curlew Sandpiper	10	5	4	3	2	1	P	Coal Tit	10	5	4	3	2	1	P
Ruff	100	30	10	5	2	1	P	Blue Tit	100	30	10	5	2	1	P
Rodshank	100	30	10	5	2	1	P	Great Tit	100	30	10	5	2	1	P
Greenhank	10	5	4	3	2	1	P	Tree Creeper	10	5	4	3	2	1	P
Spotted Redshank	10	5	4	3	2	1	P	Corn Bunting	100	30	10	5	2	1	P
Green Sandpiper	10	5	4	3	2	1	P	Yellowhammer	100	30	10	5	2	1	P
Wood Sandpiper	10	5	4	3	2	1	P	Reed Bunting	100	30	10	5	2	1	P
Common Sandpiper	10	5	4	3	2	1	P	Chaffinch	100	30	10	5	2	1	P
Curlew	10	5	4	3	2	1	P	Brambling	100	30	10	5	2	1	P
Woodcock	10	5	4	3	2	1	P	Greenfinch	100	30	10	5	2	1	P
Snipe	100	30	10	5	2	1	P	Siskin	10	5	4	3	2	1	P
Jack Snipe	10	5	4	3	2	1	P	Goldfinch	100	30	10	5	2	1	P
Black-h. Gull	100	30	10	5	2	1	P	Linnut	100	30	10	5	2	1	P
Lesser B-b Gull	10	5	4	3	2	1	P	Redpoll	100	30	10	5	2	1	P
Herring Gull	100	30	10	5	2	1	P	Bullfinch	10	5	4	3	2	1	P
Greater B-b Gull	100	30	10	5	2	1	P	House Sparrow	100	30	10	5	2	1	P
Common Gull	100	30	10	5	2	1	P	Tree Sparrow	100	30	10	5	2	1	P
Black Tern	10	5	4	3	2	1	P	Starling	100	30	10	5	2	1	P
Common Tern	10	5	4	3	2	1	P	Magpie	10	5	4	3	2	1	P
Arctic Tern	10	5	4	3	2	1	P	Jackdaw	100	30	10	5	2	1	P
Wood Pigeon	100	30	10	5	2	1	P	Rook	100	30	10	5	2	1	P
Stock Dove	100	30	10	5	2	1	P	Carrion Crow	10	5	4	3	2	1	P
Collared Dove	10	5	4	3	2	1	P	10	5	4	3	2	1	P
Turtle Dove	100	30	10	5	2	1	P	10	5	4	3	2	1	P
Cuckoo	10	5	4	3	2	1	P	10	5	4	3	2	1	P
Barn Owl	10	5	4	3	2	1	P	10	5	4	3	2	1	P
Tawny Owl	10	5	4	3	2	1	P	10	5	4	3	2	1	P
Short-eared Owl	10	5	4	3	2	1	P	10	5	4	3	2	1	P

ANALYSES OF NEST SPACINGS

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SUMMARY

A large effort has been spent on mapping the nest sites of complete populations of a bird species within a study area. This paper considers how such maps have been summarised, in particular the problems of extracting simple summaries which can be related to habitat measurements. This is a difficult problem in spatial statistics, compounded by the patchy nature of most habitats.

Keywords: EDGE-EFFECTS; NEAREST-NEIGHBOUR DISTANCES; NEST SPACINGS; POINT PROCESSES; SPATIAL STATISTICS; TERRITORIAL BEHAVIOUR

1. INTRODUCTION

An enormous amount of effort has been spent on recording and mapping the nest sites of as far as is practicable complete populations of a bird species within a restricted study region. The quantitative results of such studies do not seem to fully exploit the labour involved in mapping. This paper attempts to survey what analyses have been done and how they might be supplemented by more sophisticated techniques. A particular problem is to produce realistic estimates of spacing when nesting sites are confined to a patchy habitat, such as British woodlands.

The practical difficulties involved in mapping have restricted the species studied to two classes; large birds such as duck, game birds and raptors, and communal-nesting seabirds. For the latter aerial photographs can provide complete maps of, for example, gull and gannet colonies. Communal cliff-nesting species provide examples in which the local habitat (the availability of a suitable nesting site) may modify or even dominate any innate spacing behaviour. Some studies of gull colonies are discussed in the next section.

British ornithologists have been studying the breeding population of raptors for some years and have contributed much to our knowledge of their territorial and spacing behaviour. Brown (1976) surveyed the work up to that date (see also Newton, 1979).

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Notable studies include Ratcliffe (1962, 1969) on Peregrines (*Falco peregrinus*), Brown and Watson (1964) on Golden Eagles (*Aquila chrysaetos*), Dare (1961) and Tubbs (1974) on Buzzards (*Buteo buteo*), Newton *et al.* (1977) on Sparrowhawks (*Accipiter nisus*) and Cadbury and Balfour (unpubl.) and Picozzi (1978) on Hen Harriers (*Cyrus cyaneus*). Because raptors are large, conspicuous and use the same or nearby nest sites from year to year one can be relatively sure of having located the complete population. Thus they are ideal subjects for testing quantitative measures of spacing behaviour. The next section discusses methods used in earlier studies, whereas the rest of the paper is devoted to the particular problems associated with woodland-nesting species. It remains to be seen whether measures which prove useful for raptors work well for smaller birds.

Study of spacing behaviour is related to but not the same as study of territorial behaviour. Most but not all of the species for which a regular nest spacing has been found do defend a territory round the nest, but this is almost always too small to completely explain the degree of regularity. It is sometimes not realized how a remarkable degree of global order and regularity can arise from local competition effects, both through direct territorial display and for food. Thus there is no need to postulate global cooperative behaviour to explain the regular nest spacing that has frequently been reported. In many of the species discussed below no satisfactory explanation of the spacings found has been given.

2. PREVIOUS WORK

The usual form of analysis has been *via* nearest-neighbour distances (abbreviated to NNDs henceforth). For each nest the distance d to the nearest nest is recorded. An alternative way to view these distances (Brown and Rothery, 1978) is to regard πd^2 as the "area swept-out" in searching for another nest. Typical published analyses quote the average of d and perhaps frequency counts in fairly coarse intervals (*cf.* Table 1 below). The observed distributions are always heavily skewed, so the mean may not be a very good summary. Further, the mean of d , \bar{d} is often converted into an "area of theoretical circular territory" $\pi(\bar{d}/2)^2$ for which the mean of the squared distances might be more appropriate.

I am aware of only one attempt to model nesting patterns from NNDs. Bartlett (1974, 1975) reported work by MacDonald and himself on communally nesting Herring and Lesser Black-backed Gulls (*Larus argentatus* and *L. fuscus*). This indicated that, as might be expected, small distances occurred less often than in a "random" pattern but

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no totally satisfactory alternative was found. Diggle (1979, 1980) has since refined modelling techniques for NNDs.

Bartlett's study encountered a common problem, that of assigning a total area available for nesting. This is particularly important when performing a significance test for a random pattern. The preferred test (which Ripley, 1979, shows by simulation to be the most powerful of those suggested) compares the average of the NNDs to a normal distribution with mean and variance depending on the total area, and so is inapplicable. Bartlett used the index $n\Sigma d^2/(\Sigma d)^2$ of Eberhardt (1967), where n is the number of nests. Brown (1975) provided two alternative tests for the studies on duck of Newton and Campbell (1975). These are the ratio of the geometric mean to the arithmetic mean, and the squared coefficient of variation, of the squared NNDs. None of these statistics depends on the overall scale, and hence they are independent of the total area available. However, their distributions do depend on the shape of the study region, and no convenient approximations to their distributions are available. (cf. Brown and Rothery, 1978.)

Brown's work raised the problem of edge effects. The NNDs from nests near the edge of the study region will tend to be larger than those in the centre, because it will only be possible to search inwards for other nests. Thus d will be inflated by a factor which could be on average as large as $\sqrt{2}$ (because only half the circular territory is searched). In some circumstances it may be possible to estimate the area searched (in particular, if the possible nesting region is completely known) and equate this to πd^2 . Unfortunately, the suitable nesting habitat often fades out rather than have a clearly defined edge. Edge effect problems in spatial processes are considered more generally in Ripley (1982).

A completely different approach has been taken by Ogata and Tanemura (1981) for data on Gray Gulls (*Larus modestus*) from Howell, Araya and Millie (1974). Howell *et al.* found no departure from a "random" pattern whereas Ogata and Tanemura fitted parametric models from statistical physics to the map of nests using an approximation to maximum likelihood.

3. WOODLAND NESTS

Edge effects are particularly severe in woodlands, where every nest may be near the edge. However, the nesting habitat is well-defined, at least on the scale of the

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nest spacing of large birds such as sparrowhawks and buzzards. Newton *et al.* (1977) recognised the problem for Sparrowhawk nests, and divided the NNDs into two classes, according to whether the line joining a nest to its neighbour was wholly within woodland or not. The average of those NNDs within woodland was then used as a measure of territorial spacing to be related to other explanatory variables (altitude, food supply...). This average still has the upwards bias caused by edge effects, plus an opposite bias towards small distances, since large distances are less likely to be contained wholly within woodland. Consider a woodland made up of a number of small copses. Then the method would only consider NNDs within a single copse, which might be a very small part of the set of NNDs and not representative of the spacing behaviour. In Newton *et al.* 25% of the distances were discarded, with less than half being kept in the most extreme region.

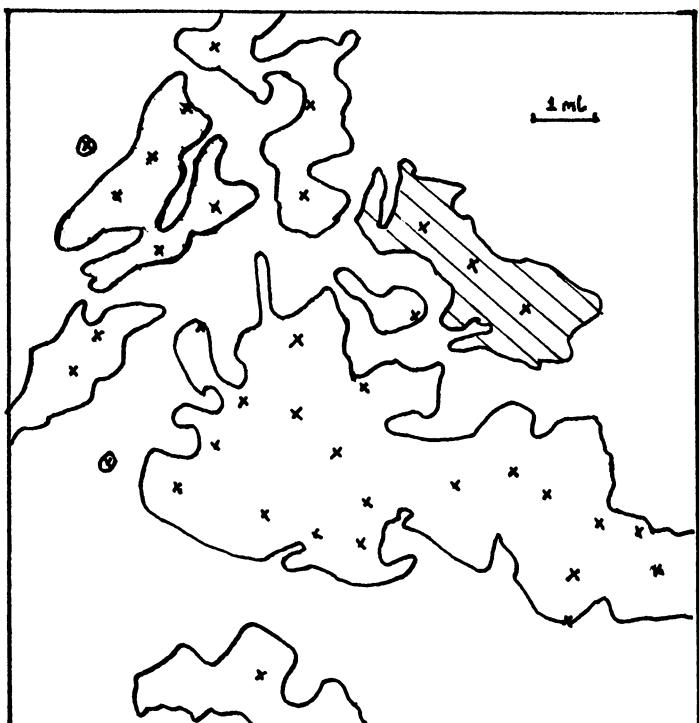


Figure 1 Locations of 37 nests of Buzzards (*Buteo buteo*) shown by crosses, together with the approximate boundary of woodland. The hatched patch is referred to in the text. (Adapted from Tubbs, 1974)

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Figure 1 illustrates the problem (adapted from Tubbs, 1974). Thirty-seven nests of Buzzards in the New Forest in Southern England from 1971 are shown by crosses, together with the approximate boundary of the woodland area. Table 1 shows their NNDs. The mean NNDs are, in miles, 0.96 or 0.90 excluding those 7 crossing non-woodland areas, as suggested by Newton *et al.*

Table 1
*Nearest-neighbour distances for Buzzard
 (Buteo buteo) nests of Figure 1*

Distance in miles	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	≥ 1.4
Number in woodland	2	6	7	5	4	2	1	1	2(each 1.6)
Number across gaps	-	-	-	-	-	-	4	1	1(2.6)

Estimating the swept-out area yields a root-mean-square of 0.70 for d against 0.95 for the within-woodland distances. Thus in this case the Newton *et al.* adjustment is minor compared to the edge effects.

4. MODELLING WITHIN WOODLANDS

The most promising approach to fragmented study regions such as woodland appears to be to attempt to model the pattern of nests within the study region. To do so will involve hypotheses on how the birds select their nest sites, and in particular, whether their spacing behaviour involves the pure spatial pattern of the nests or is modified by the shape of the nesting habitat. Without hypotheses it seems impossible to separate the nesting pattern from the habitat pattern.

The second-moment approaches described in Ripley (1981, Chapter 8; 1982) enable one to estimate the second-moment properties of a spatial point process viewed through an arbitrary "window". This corresponds to an assumption that birds nest in a pattern which extends throughout space, but only that part of the nesting pattern within the study region is observed. This is fine for the nests of duck, where one can take an artificial boundary and avoid the ill-defined edge of the study region. As it stands it is inappropriate for woodlands which are usually too patchy to allow a simply artificial boundary. However, there are other hypotheses which have the same effect.

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Suppose birds nest at random within the available woodland, subject to the condition that no new nest is established within distance D of an existing nest. The pattern of nests produced may be similar to one assuming hypothetical unobserved nests within the non-woodland areas.

We will apply the method of Ripley (1981, Chapter 8) to Figure 1. The reference gives fuller details and illustrates nest data of Golden Eagles and Peregrines analysed by the same method. The quantity estimated is $\hat{K}(t)$, the expected number of nests within distance t of an arbitrarily chosen nest, divided by the density (the expected number of nests per unit area). This is defined for a point process model of nests within a large continuous forest, and estimated by

$$\hat{K}(t) = n^{-2}A \sum k(x,y)$$

where the sum is over all pairs (x,y) of nests which are distinct and up to distance t apart. Also, n denotes the number of nests, A the area of the woodland, and $k(x,y)$ is a correction factor for edge effects which can be described as follows. Consider the circle centred on x passing through y . If this is wholly within woodland then $k = 1$. Otherwise $1/k(x,y)$ is the proportion of the circumference of the circle within woodland. The idea is to compensate for nests which might have been present in the non-woodland area had this been suitable nesting habitat.

Looking at all $n(n-1) = 1332$ pairs would clearly be an onerous task. Fortunately, we only want $\hat{K}(t)$ for small t ; Figure 3 plots it up to 2 miles, for which only 81 pairs are involved (each considered twice, once as (x,y) and once as (y,x)). Estimating $k(x,y)$ by eye is quite easy with a device such as Figure 2 copied onto a transparent sheet.

Figure 3 shows the effect of the correction, which is appreciable even at 0.9 miles, the average nearest-neighbour distance. Notice too that the shape of $\hat{K}(t)$ is changed by the correction. The corrected curve is very similar to plots from simulations of the model described above, in which birds are prevented from nesting closer than 0.6 miles (*cf.* Ripley, 1981, Figures 8.11 and 8.12). This cannot be the actual mechanism, for nests do occasionally occur appreciably closer than this distance (Tubbs, 1974). Nevertheless, severe inhibition at distances less than 0.6 miles does seem a simple and adequate description of the observed pattern of nests.

The large correction factors applied to the pairs of nests in the upper righthand strip of woodland (hatched in Figure 1) indicate a deficiency of the method. These

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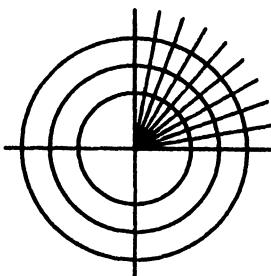


Figure 2 A device to estimate $k(x, y)$. A copy on a transparent sheet is centred on x , and the markings used to estimate the proportion of the circle through y which is within woodland.

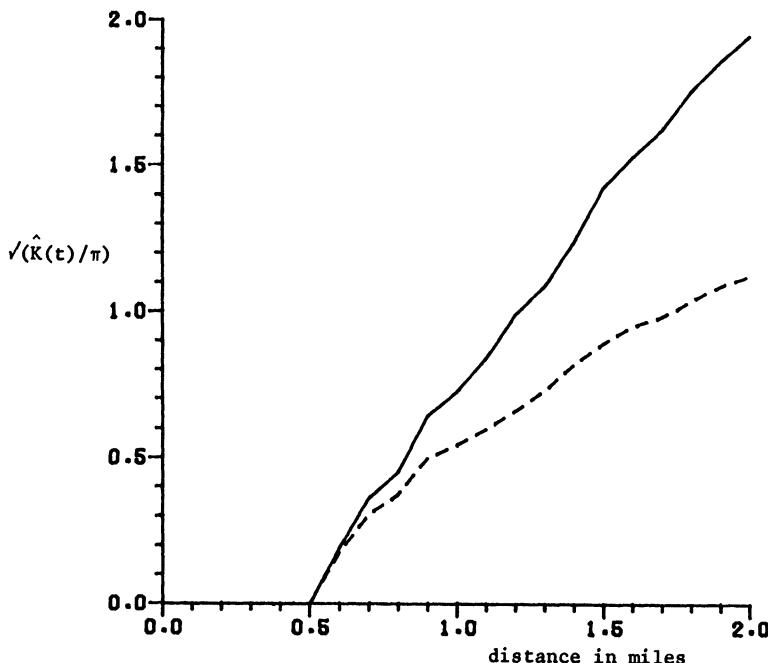


Figure 3 The effect of edge correction on $\hat{K}(t)$ for the data of Figure 1. The solid curve is $K(t)$. The dashed curve is obtained by ignoring the edges and taking $k(x, y) \equiv 1$.

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three nests are regarded as significant, because the "choose a nesting position at random" hypothesis makes their pattern unlikely. It is more plausible biologically that if the position at which the bird arrives is unsuitable, it will move locally to see if it is possible to satisfy the hypothetical competition criterion. Under such a model these nest positions are more likely. It seems impossible to formulate this process in a mathematically tractable way, although it might be possible to simulate it. It is related to the "molecular dynamics" methods of simulation used in statistical physics.

A maximum-likelihood analysis of pair-potential models (Ripley, 1981, Chapter 8), with nests confined to the woodlands would be biologically attractive. Unfortunately such an analysis is not yet possible even for a rectangular study area, for the attempt by Ogata and Tanemura (1981) applies only at very low densities and for specific models.

5. CONCLUSIONS

The patterns of birds' nests present difficulties of analysis which have often not been appreciated, and are at or beyond the current limits of knowledge. The example explored here has shown that edge effects can cause severe biases in nearest-neighbour methods, which might mask any useful information about variations in nesting patterns from study region to study region. The approach *via* \hat{K} provides a way to compensate for the shape of the nesting habitat. However, the precise assumptions made by any method need careful consideration, for it seems impossible to separate an assessment of the nesting pattern from assumptions as to how it is affected by the habitat pattern.

AN ASSESSMENT OF SPECIES-AREA RELATIONSHIPS
USING ORNITHOLOGICAL DATA

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SUMMARY

The concept of species-area relationships is reviewed, and a few models are discussed. Data on Royal Society for the Protection of Birds reserves (woodlands, islands, other habitats) fit the most frequently used model

$$S = CA^z$$

where S is the number of species, A is the area, and C and z are positive constants.

An analysis of British Trust for Ornithology data for 30 woodlands over five years shows no significant year to year variation in the species-area relationship. It is suggested that one of the most important factors in determining the constant z of the species-area relationship is the amount of time spent by the recorders in a wood during their Common Birds Census. Lack of time has probably led to incomplete sampling of larger areas.

What relevance does the species-area relationship have in studies of birds or their conservation? It is argued that the relationship is probably of more theoretical than practical importance, though it may be useful in thinking of conservation strategies.

Keywords: COMMON BIRDS CENSUS; ISLANDS; NUMBER OF SPECIES; REGRESSION;
SPECIES-AREA RELATIONSHIPS; WOODLAND BIRDS

1. INTRODUCTION

There is nothing particularly startling about the assertion that as one searches a larger piece of land one finds more species. Indeed, it could be argued that this positive correlation between area and number of species was self-evident to any biologist who has observed plants or animals in the field, and hence that scientists

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need not be concerned with what has become called the "species-area relationship". In practically all sets of data which have been analysed (see Rafe, 1983, for a review), there is a correlation between the number of species and the area or length or volume of habitat searched. As many data as were available for the reserves of the Royal Society for the Protection of Birds (R.S.P.B.) are shown in Fig. 1. These data cover 69 reserves, of which 35 are in England, 23 in Scotland, 7 in Northern Ireland and 4 in Wales. If one considers just one habitat type, say woodlands, then one can see that in general the larger the woodland the greater the number of breeding bird species in it. Similarly for islands off the shore of the British Isles, there is a relationship of the same type. These R.S.P.B. data (Usher, in press; Rafe, 1983) can be fitted to a model that was originally proposed in 1921 by Arrhenius. His model related the logarithm of the number of species to the logarithm of the area, and hence it can be formulated by the equation

$$\ln S = K + z \ln A \quad (1a)$$

or

$$S = C A^z \quad (1b)$$

where S is the number of species, A is the area, and C , K and z are constants ($K = \ln C$). Since that model was first used, there has been a considerable controversy about which particular model best fits species-area data. It has become fashionable to review large numbers of sets of data, and attempt to fit a variety of different models by least squares regression analysis. Basically these models are forms of the linear equation

$$Y = a + bX$$

where Y can be S , \sqrt{S} or $\log S$, and X can be A or $\log A$. A brief review of the results of two of these studies, by Connor and McCoy (1979) and by Stenseth (1979), is given in Table 1. The approach has been to conduct a form of popularity poll; that is, to see which of these models best fit each data set (based on the largest r when X and Y are correlated), and then looking at the best fits from a large number of data sets finding which particular model seems to be generally the most applicable. The consensus of opinion seems to be that the model described in equations (1) is generally the most applicable, though the model

$$S = K + k \log A \quad (2)$$

where K and k are constants, also generally seems to give a reasonable fit to the data. In view of the general utility of equations (1) over both equation (2) and the other forms of the relationship, equations (1) will be used for most of the analyses included in this paper.

Species-area relationships for birds

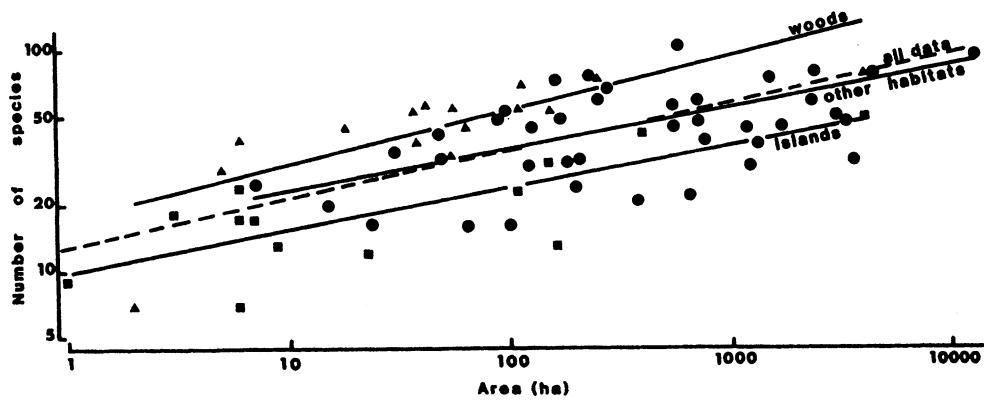


Figure 1 Data for 69 nature reserves managed by the R.S.P.B. relating the number of breeding bird species to the area of the reserve. Triangles represent woodlands, squares offshore islands, and all other habitats are represented by circles. Regression equations have been fitted to each of these three categories of data (continuous lines) and to all of the data unclassified by habitat (dashed line).

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Table 1

Four of the models which have been used to relate the number of species, S , to area, A . Connor and McCoy (1979) fitted all four models to 100 sets of data (including plants and animals). In some cases two models fitted approximately as well, and hence the number of "best fits" exceeds 100. Stenseth (1979) used his data to distinguish between a stable system, which he considered to be best fitted by model IV, and a disturbed system, which he considered should be fitted best by model II. The table records his analysis of 26 sets of bird data: in 3 cases both models fitted the data as well as each other and hence the number of "best fits" exceeds 26. In the four models C and z are constants.

Model	Number of data sets best fitted by	
	Connor & McCoy	Stenseth
I. $S = C + zA$ (S, A)	35	-
II. $e^S = CA^z$ ($S, \log A$)	27	20
III. $S = Ce^{zA}$ ($\log S, A$)	14	-
IV. $S = CA^z$ ($\log S, \log A$)	43	9

2. BIRDS BREEDING ON R.S.P.B. RESERVES

The data for R.S.P.B. reserves have already been mentioned, and are illustrated in Fig. 1. If one takes the woodland reserves, then the equation is

$$S = 16.75A^{0.245}$$

(in the form of equation (1a), $F_{1,13} = 17.95$ ($P = 0.001$), $se(z) = 0.058$, $se(K) = 0.25$). This equation indicates a relatively slow rate of acquisition of new breeding bird species with increasing woodland area (the number is approximately doubled for a 17-fold increase in area). An analysis of the islands reserves gives

$$S = 9.80A^{0.186}$$

(in the form of equation (1a), $F_{1,12} = 22.05$ ($P < 0.001$), $se(z) = 0.040$, $se(K) = 0.15$). This equation has a slope (z in equation (1a)) similar to that for the woodland data, but the constant term is now smaller. Using the heterogeneous category of all other habitats, the regression line lies between the woodland and island lines, having the equation

$$S = 14.59A^{0.189}$$

(also in the form of equation (1a), $F_{1,38} = 15.85$ ($P < 0.001$), $se(z) = 0.048$, $se(K) = 0.28$). Although it might be appropriate to fit equations to a variety of data, it is perhaps more interesting to ask questions about a comparison of the

Species-area relationships for birds

equations. Table 2 shows a comparison of the regression equations, where it can be seen that the three classes of reserves can be considered to have a common value of slope, $z = 0.199$, whereas the values of the constant C differ considerably. The constant C indicates the number of breeding birds per unit of area, and hence one

Table 2

Analysis, fitting equation (1) by least squares regression, of the data shown in Fig. 1. The sample sizes are 15 for woodland reserves, 14 for island reserves, 40 reserves of other habitat types, and hence 69 for all reserves without habitat grouping. r is the correlation coefficient (based on $\ln A$ and $\ln S$).

Habitat	C	z	r
Woodland	16.75	0.245	0.76
Islands	9.80	0.186	0.80
Other habitats	14.59	0.189	0.54
$F_{2,63}$ for comparing slopes, 0.30 (not significant)			
$F_{2,65}$ for comparing intercepts, 10.07 ($P < 0.001$)			
All reserves (with common C and z)	12.94	0.213	0.69
All reserves (with common z)*	-	0.199	-

*C takes the values 20.07, 9.46 and 13.84 for woodlands, islands, and other habitats respectively.

would have hypothesised that woodlands would be richer than islands. Hence, C gives a measure of species-richness for the habitat under investigation. For the mixed habitat, the value of C will give some average value, and it is of less interest than that for either woodlands or islands. Rafe (1983) has experimented with a number of methods of sampling communities, and has clearly shown that the value of the slope, z, is dependent to some extent on the method of sampling which was used in the collection of data. In these R.S.P.B. data, the species lists were compiled over a number of years, and represent cumulative lists of the bird species breeding on the reserves. As the reserves are visited by ornithologists, and as they are often wardened, the values of S indicate as good an estimate of the complete number of species present as can be gained. Hence, the problems of sampling that Rafe (1983) investigated are unlikely to be applicable to this data set.

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3. COMMON BIRDS CENSUS DATA

The previous data were collected over a period of time (varying from reserve to reserve), and hence the number of species used in the analyses represent cumulative totals. To what extent is a species-area relationship something that is fixed and repeatable, or might it vary from year to year? In order to analyse this question, the data held by the British Trust for Ornithology (B.T.O.) were analysed by Woolhouse (1983). He selected 30 woodland sites, widely distributed geographically in Great Britain, which were all that were available with complete data for the 5-year period 1976-1980 inclusive. The method of surveying was that of the Common Birds Census (Marchant, 1983), and in fact the sites selected were a subset of the national data available from that census.

Pooling all 150 datum points gives the relationship

$$S = 13.90 A^{0.227} \quad (3)$$

(in the form of equation (1a), $F_{1,148} = 109.6$ ($P < 0.001$), $se(z) = 0.022$, $se(K) = 0.59$). Woolhouse (1983) shows that two other models relating the number of species to area fit the data well: these are a linear regression of a number of species on area and a regression of the number of species on the logarithm of the area.

When each of the five years is analysed separately, the five regression equations are shown in Fig. 2. This illustrates that the regression equations are all very similar, with the possible exception of 1980, and on analysis there is neither a difference between the slopes nor a difference between the intercepts ($F<1$ for both comparisons). Data for the five regression equations are given in Table 3. Hence the pooled equation (3) quoted above is a reasonable approximation to these data, and it indicates that we need not consider year to year variability as being terribly important. This result differs from that of Usher (1979) for higher plants on nature reserves in Yorkshire: due to improved surveys of the plants the species-area relationship altered significantly over a 10-year period.

Woolhouse (1983) continued to investigate why the species-area relationships existed. Arguing from Preston's (1962) work, which was concerned with species abundance distributions, Woolhouse showed that the number of species increased with the number of individuals recorded during the census of a particular woodland. This relationship can be expressed by the equation

$$\ln S = 1.538 + 0.347 \ln I \quad (4)$$

Species-area relationships for birds

Table 3

Coefficients, and their standard errors, of the five regression equations shown in Fig. 2. The regression model used was equation (1a), and all variance ratios (F) have 1,28 degrees of freedom.

Year	z	$se(z)$	K	$se(K)$	F
1976	.219	.045	2.64	.12	24.1
1977	.199	.052	2.74	.14	14.6
1978	.204	.047	2.70	.13	18.8
1979	.227	.055	2.62	.15	17.0
1980	.287	.047	2.44	.13	36.8

where I is the number of individuals and $F_{1,148} = 364.1$ ($P < 0.001$). An assumption might have been that the number of individuals was directly proportional to area, but on analysis it was found that this linear dependence, i.e. an assumption of constant density, was not appropriate. The number of individuals can be related to area by the equation

$$\ln I = 3.082 + 0.679 \ln A \quad (5)$$

where $F_{1,148} = 271.8$ ($P < 0.001$). Substituting equation (5) into equation (4) gives

$$\begin{aligned} \ln S &= 2.607 + 0.236 \ln A \\ \text{or} \\ S &= 13.56 A^{0.236}. \end{aligned} \quad \left. \right\} \quad (6)$$

This compares closely with equation (3), the direct regression of the logarithm of the number of species on the logarithm of the area.

Since all of these regressions are significant ($P < 0.001$), Woolhouse (1981) investigated why there might be relationships between the number of species, the number of individuals, and the area of the woodland. Since one might expect a constant density of birds in woodlands, it is of particular interest to ask why the number of individuals increases more slowly than area (it approximately doubles for a 2.8-fold increase in area). The recorders for the Common Birds Census noted the time spent in each woodland, and these data are plotted as sampling efforts (measured as hours per hectare of woodland) in Fig. 3. The data clearly show that the amount of time spent per unit of area in smaller woods tends to be much greater than the

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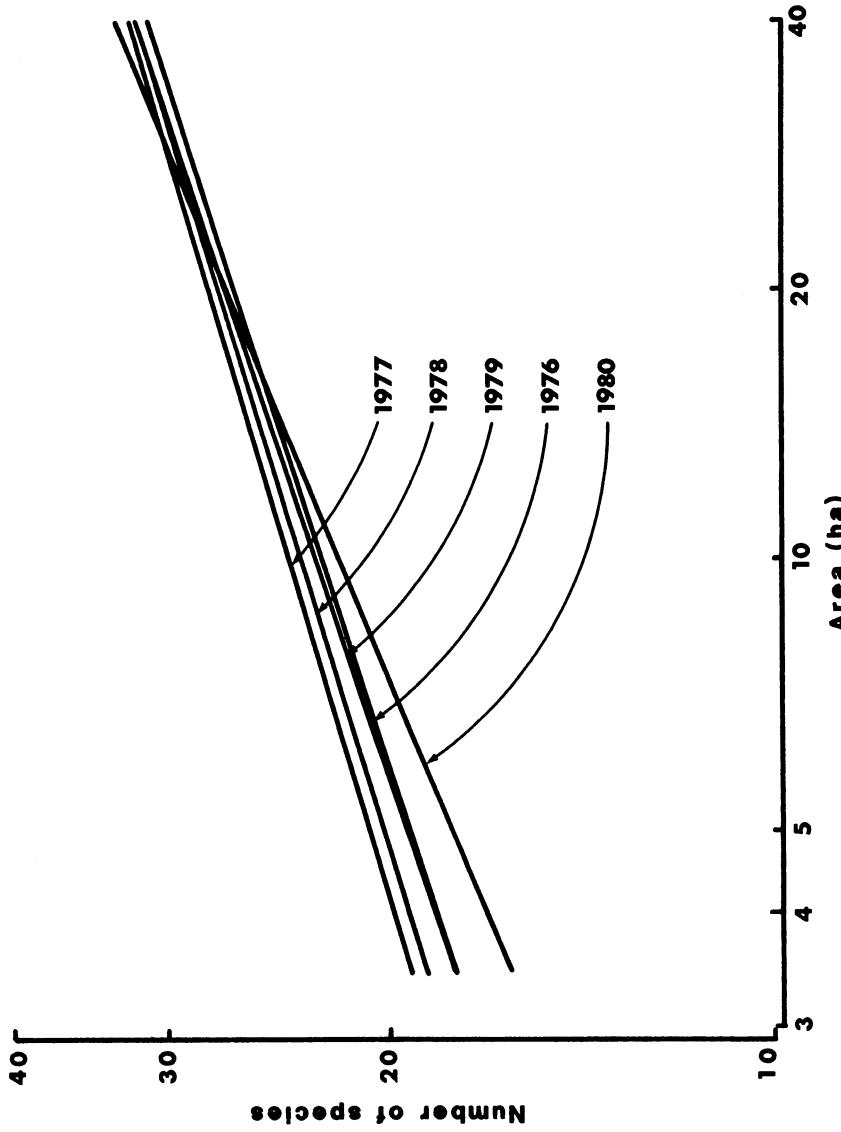


Figure 2 Common Birds Census data for 30 woodlands surveyed in each of the 5 years from 1976 to 1980 inclusive. Only the regression equations are shown: the individual datum points have been omitted for clarity (the complete data are in Woolhouse, 1981).

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time spent per unit of area in larger woods. Hence, small woods are probably reasonably well sampled, whereas large woods are likely to be undersampled. Thus, although an assumption of constant density of birds may be appropriate, it is unlikely to be upheld by a method of data collection where the recorders have spent proportionally longer in smaller woods than larger woods.

4. DISCUSSION

Analyses of this sort raise three questions. First, there is the question of how to collect the data: what is the appropriate method of sampling? Second, there is a statistical question: is a least squares regression analysis really the most appropriate way of analysing such data? Third, having shown that a relationship exists, does this have any practical application, for example in conservation studies?

Looking first at the collection of the data, Woolhouse's (1981) study showed that the sampling effort during the Common Birds Census was inversely proportional to the area of the woodland being studied. It is, in fact, a credit to the census that data like these were available to analyse, since many sets of data just record numbers of species (or a list of named species) and do not outline all of the details of the sampling procedure. It does, however, seem possible to recognise three different strategies of sampling in species-area studies. First, one might try to obtain a complete enumeration. Almost certainly the Common Birds Census aimed to do this, but, as can be seen from the analysis above (Fig. 3), it fell short of this aim, particularly for the larger woodlands. Second, it may be possible to sample in a proportional way. Thus, a fixed percentage of the area may be searched for, say, wild flowers or nesting birds, and these data are then used to represent the whole. Again, the aim will be to try to obtain a complete enumeration of this sample area. Alternatively, a constant sampling effort, i.e. a constant time per unit of area, could also be used to give a proportional sample. Third, a fixed sample may be taken. This strategy has been used in a number of plant studies, for example those of Ward and Evans (1976) who spent a constant amount of time on each limestone pavement, irrespective of the area of that pavement. Studying the plants in hedgerows, Lagden (1983) indicated that the proportional and complete methods gave very similar results, whereas the fixed sample size gave rather different results. Rafe (1983) used a simulation model to compare various sampling strategies, and he concluded that the observed result, of a steeper species-area relationship (larger value of z) with proportional as opposed to fixed sampling, was indeed due to the system of sampling employed. The crucial importance of sampling methodology seems all too often to have been forgotten in studies of the species-area relationship. See also Reese (1985).

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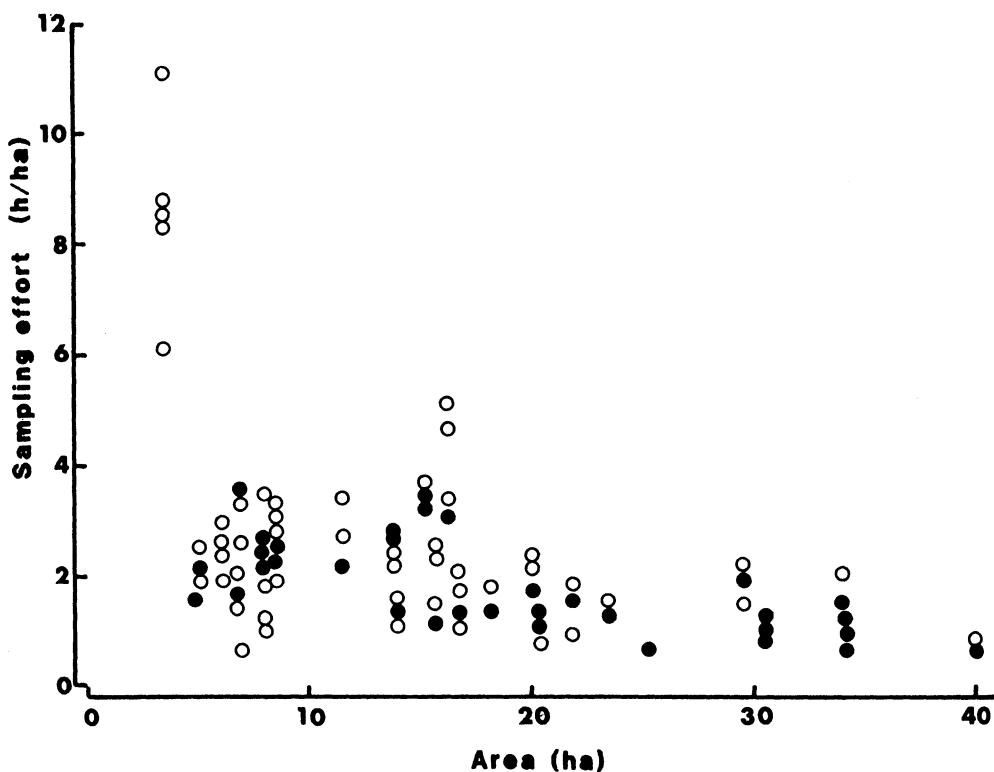


Figure 3 The relation between sampling effort (the time in hours spent per hectare of woodland) and the area of woodland in the Common Birds Census data shown in Fig. 2. Although no equation is fitted to these data, the general decline in sampling effort with increasing area is discussed in the text. Many of the points are multiple datum points (shown as solid circles).

Species-area relationships for birds

Turning now to the statistical treatment of the data, when using the logarithmically transformed regression model, as in equation (1a), it seems that the assumption of homoscedasticity is reasonable. In the majority of plots the variance does not seem to increase (or decrease) with increasing area. However, how does one actually measure the area of the habitats concerned? There is the problem of the boundary round the area, and whether one makes allowance for a boundary zone. It is likely, ecologically, that a boundary zone will differ significantly from the centre of the habitat. Particularly in woodlands, there is the difficulty of assessing where the actual margin occurs, especially when some of the woodlands are extremely small. This problem seems not to have been realised by Moore and Hooper (1975), who dealt with the birds of British woodlands, and who considered woodlands down to the size of 10 m^2 , where the whole wood (one bush) is in reality all boundary. Also, it is unlikely that the numbers of species will be normally distributed for a variety of sites with the same area. This is because S cannot be overestimated, i.e. a complete count cannot be more than a complete count, but S can be, and probably often is, underestimated. Hence the distribution of S 's for any particular A is likely to be skewed to the left, though this skewness is likely to be corrected to some extent by the logarithmic transformation.

The species-area relationship is more a description of the set of data than a tool of practical use to the conservationist or ecologist. Thus, an equation such as equation (3) describes the set of Common Birds Census data, and can be used to show that per unit of area (with these data one hectare) there are an average of 13.9 species of breeding birds. The data for the R.S.P.B. reserves, again per hectare, indicated an average of 16.8 species of breeding birds. Nature reserves have generally been selected for their diversity (see the criteria in Margules and Usher, 1981), and hence it would be expected that R.S.P.B. woodland reserves (where diversity of birds is likely to have been an important factor in the decision to establish a reserve) would be more species-rich than a variety of woodlands surveyed under the Common Birds Census. The increase of the number of species with area, the power in equation (3) and Table 2, is very similar with both the Common Birds Census woodlands and R.S.P.B. reserves.

The species-area relationship may also have some relevance in conservation studies, especially when reserves are to be selected. If a species-area relationship is known, and a number of candidate sites are plotted on a graph with this relationship, then the sites with the maximum positive residuals are those which are most diverse, for a given area. If, as is usually the case (Margules and Usher, 1981), diversity is the criterion at a premium, then a species-area relationship can

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be useful to indicate which are at present the most diverse sites on an area-eliminated basis. This approach was used by Adriani and Maarel (1968) in their case to preserve the Voorne Dunes in The Netherlands. As is usual with conservation studies, they used the plant species diversity of a number of dune systems, and compared it to the species-area relationship for plants in The Netherlands. It was, however, the first published example of the use of a species-area relationship in presenting a case for conservation. Although botanical data have been used since then, ornithological data are now much more extensive, and with a concentration on the number of species of breeding birds rather than on total lists of birds seen, it is possible that species-area relationships for birds as well as plants will be a more useful tool for conservationists in the future.

ACKNOWLEDGMENTS

I should particularly like to thank Mr Mark Woolhouse and Dr Richard Rafe for permission to use data which are included in their theses. The British Trust for Ornithology and the Royal Society for the Protection of Birds are also thanked for making their data available to us.

APPARENT SYSTEMATIC EFFECTS ON SPECIES-AREA
CURVES UNDER ISOLATION AND EVOLUTION

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SUMMARY

The species-area relationship for birds is usually linear in the form $\log \text{species} = \text{constant} + \text{log area}$. On distant archipelagos, in the dispersive stage of the taxon cycle, the species-area line is depressed at the island of largest area, and its slope decreased. In the south-west Pacific the slope decreases from 0.22 to 0.053 over four archipelagos. In the later stages of the taxon cycle, involving evolution in the archipelagos, the slope increases again. In the West Indies the change is from 0.075 to 0.42. The evidence for both these phenomena is thin, and confirmation of them is needed.

Keywords: SPECIES-AREA RELATIONSHIP; TAXON CYCLE; DISPERSAL; ARCHIPELAGOS

1. INTRODUCTION

It has long been known that there are fewer bird species on oceanic islands than on broadly comparable continental ones. What has not been clear is the effect on bird species number of the island being part of an archipelago. In this paper I draw together a few studies on archipelagos to suggest a family of relationships. The results can only be speculative, as the archipelagos studied are too few. There are also some uncertainties about the data sets, and the statistics that should be used, but these are, as will be seen, less important.

There has been uncertainty about the best way to represent the relationship between island area and the number of bird species. From a variety of studies, it is now clear (Williamson, 1981) that the plot of the logarithm of the number of the species against the logarithm of the area produces a linear plot more frequently, but certainly not universally, than other plots. This view was first urged by Arrhenius (1921). The relationship is frequently written as $S = cA^z$, where S is the

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number of species, A the area, c and z constants. I will, for convenience, refer to the slope of the Arrhenius plot as z.

Hamilton, Barth and Rubinoff (1964) and MacArthur and Wilson (1963, 1967) all suggested that Arrhenius plots were steeper for distant islands in the Pacific. However, they compiled species lists from whole archipelagos, rather than from individual islands, and they included archipelagos of very different physical types, some being mainly low, dry atolls, others mainly high, wet volcanic islands. The inclusion of Hawaii was also unfortunate, as the origin of its avifauna is quite different from that of the other Pacific archipelagos (Williamson, 1981). Studying islands within archipelagos, Schoener (1976), Diamond and Marshall (1977) and Connor and McCoy (1979) all agree that the more distant the archipelago the flatter the slope of the Arrhenius plot. Unfortunately, the values of z they give for the same archipelago appear to disagree. For the Solomons and New Hebrides respectively, Diamond and Marshall quote 0.09 and 0.053, while Schoener's graph indicates values of 0.22 and 0.19. None of these authors consider the value of the other constant, c, of the Arrhenius plot. Both Gould (1979) and Williamson (1981) suggest that a major effect of distance (or its equivalent, isolation) on the number of species is to depress the species area curve, to make c smaller. Before considering the interaction of these effects, it is necessary to deal with some background biological and statistical points.

2. BACKGROUND CONSIDERATIONS

Some of the biological processes that lead to a particular number of species occurring on an island are clear enough. In the first place, a bird species must immigrate to an island. Once there it may be subject to evolution or extinction, and the rate and pattern of evolution may well be affected by the pattern of islands within the archipelago and its isolation. There are also considerations of population dynamics for a species which arrives on an island. There must be sufficient food, not too many enemies, sufficient nesting sites and so on, for a population to be maintained. For these reasons very small islands necessarily have impoverished breeding populations. For land birds, the minimum area worth considering in a comparison with larger islands is probably about one kilometre square (Diamond and Mayr, 1976; Williamson, 1981). The mixture of immigration, evolution and extinction may possibly lead to a phenomenon named the taxon cycle, a term used to describe the states of taxonomic diversity and distributional patterns that can

Effects on species-area curves

sometimes be seen in archipelagos (Williamson, 1981). Greenslade (1968) describes the taxon cycle for the Solomon Islands, while Ricklefs and Cox (1972) describe it for the West Indies. The four stages recognised by Ricklefs and Cox are:

- 1 widespread species with little or no subspeciation,
- 2 widespread species that show considerable differentiation into subspecies,
- 3 species with fragmented and reduced distributions and well-differentiated populations,
- 4 species endemic to single islands.

It is generally held that in the early stages of the cycle, species are characteristic of marginal, or at least lowland, habitats, while later stages are more likely to be confined to mountains. However, the habitat distinctions do not closely match the stages. Regarded as an empirical classification of different distribution patterns, the taxon cycle has its uses, as will be seen. Its reality as a set of evolutionary stages, let alone the timing involved, is difficult to demonstrate.

The statistical problems in studying species-area relationships are also well known. Studies discussed below all attempt to refer to the breeding populations of land, or sometimes land and freshwater, birds. The archipelagos are mostly tropical, and as Diamond (1970) points out it is even harder for an expedition visiting such islands to determine which birds have breeding populations than it is for the resident ornithologist in a temperate zone, because 'breeding of a given species may be spread over much of the year, different species have peaks at different times, and many bird individuals in most localities at most times are non-breeding and non-territorial'. Similarly, the area of the islands is frequently known only roughly. Douglas (1969) is unable to give an area for very many of the islands in the archipelagos of the southwest Pacific discussed below, though estimates can of course be made from such maps as are available. Having got a table of reputedly breeding species and of notional areas there can be dispute about how to estimate the parameters of the relationship. As Gould (1979) points out, this is also true in the similar field of allometry. One can calculate regressions or various sorts of major axes, the estimates can be from linear algebra on transformed variables, or from non-linear least squares, or by other methods. In this paper, as what I want is the best prediction of the number of species to be found in an area of a particular size, a regression of species on area is appropriate. It is clear in nearly all data sets that the Arrhenius plot normally gives satisfactory homoscedasidity at different areas. The set of graphs showing this most clearly are to be found in Slud (1976). So, all z's have been estimated from linear regressions of Arrhenius plots.

Of the two parameters of the Arrhenius plot, z's can be compared for any data,

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but, as Gould (1979) points out, it is only easy to compare c 's when z 's are the same. Where the z 's appear different (see later), I use two techniques. The first is to compare the position of the curve at a standard size of island. Most biologically interesting islands are between 1 and 10^4 square kilometres (see the endpapers of Williamson, 1981) and the largest island in the Santa Cruz group is just over 10^2 square kilometres. I have therefore taken 10^2 square kilometres as being within the range of all the archipelagos considered, and towards the middle of the range of most of them. Looking at the difference of position at the size of the largest island in archipelagos is also informative.

3. RESULTS

The major effect of isolation on species-area curves is to depress at least the right hand end of the curve. On top of this there are two other phenomena. The first is that for initial stages of the taxon cycle, the dispersive stages, the curve gets flatter with greater isolation. The second is that through the taxon cycle the curve gets steeper again. At least, that is what the examples that are known to me seem to show. They are rather few and need confirmation for birds from other archipelagos, and from other groups of organisms.

On the depression of the curve, Williamson (1981) showed a conspicuous depression in two data sets. The first was Slud's (1976) assembly of lists from individual islands in the warmer seas throughout the world, which means in practice particularly from the Caribbean and the Pacific. The other set was a comparison of the Azores and the Channel Islands. The same phenomenon can be seen in Diamond and Mayr's (1976) data for the Solomon Islands, where the main chain has a predicted 53.3 species at 100 sq kilometres, but the isolated islands only 34.2. Gould (1979), using unpublished data sets assembled by J.E. Cohen and T.W. Schoener, showed the same phenomena for sets that have the same z , although the geographical positions within each set were remarkably heterogeneous.

The reason for the depression is no doubt that relatively few species are able to disperse out to the distant islands, though there is no doubt also the fact of ecological impoverishment on these islands. These two effects have been disputed between Diamond and Lack (see Diamond, Gilpin and Mayr, 1976), and both are probably involved to some extent, and both depend on well-founded observations. The impoverishment of plants and insects on isolated archipelagos can be shown, and, at least for the Azores, impoverishment is as great in the birds as in other dispersing groups (Williamson, 1981). Which of the effects is the more important in any data

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set has to be established. The critical depression, though, seems to be associated with the largest island in an archipelago. In the first stage of the taxon cycle, where the species are good dispersers that have not undergone appreciable evolutionary change, having once reached the archipelago, the species are likely to reach every populous island within it. The effect is to produce a flattening of the species-area curve, and in archipelagos of sufficient size this can produce the unexpected effect that smallish islands in isolated archipelagos can have more bird species on them than smallish islands nearer the continent. This flattening can be seen, but only as a statistically insignificant phenomenon, in the birds of the Azores, in various isolated islands in the region of Australia and New Zealand (Abbott and Grant, 1976) and in Slud's data. The data sets in which the phenomenon is most striking are those for Diamond and his associates in the southwest Pacific.

The enormous island of New Guinea, slightly less than 10^6 square kilometres, is a source area for several South Pacific archipelagos. Diamond has given species-area relationships for islands close to New Guinea, particularly at its northern and western end (Diamond, 1972), for New Britain and the Vitiaz-Dampier islands, which are scarcely more isolated, at the northeast end of New Guinea (Diamond, 1974), and then progressively further from New Guinea for the Solomon Islands (Diamond and Mayr, 1976), for the Santa Cruz islands which are between the Solomons and New Hebrides, and for the New Hebrides (Vanuatu) (Diamond and Marshall, 1977). For the Solomons and Vanuatu, island areas and species lists are given, and the data are shown in Figure 1. Diamond has the interesting habit of calculating species-area curves for the lowland birds only, though still using the area of the whole island, and the very odd habit, at least to a statistician, of using only such points as he thinks sensible. For instance, for New Britain he uses seven of his eight control islands, and there are a further nine non-control islands. For New Guinea he uses 34 islands 'presumed to be at equilibrium', excluding 16 others. In the Solomons the excluded islands are the isolated ones only. In Vanuatu twelve islands are used, seven excluded. It is this selection of bird species and islands, no doubt, which make his results different from Schoener's. Diamond's slopes are: for the New Guinea islands 0.22, for New Britain 0.18, for the Solomons 0.087 and for Vanuatu 0.053. The progressive flattening of these curves is clear enough and the apparent standard errors small, e.g. ± 0.00507 for the Solomons (Figure 1). Taking the predicted number of species on islands of 100 square kilometres, we get New Guinea 33.7, New Britain 43.3, Solomons 53.3 and Vanuatu 33.4.

The diminution of species with isolation is in fact not seen in these selected sets except at the largest island size. It would, in fact, be difficult to argue

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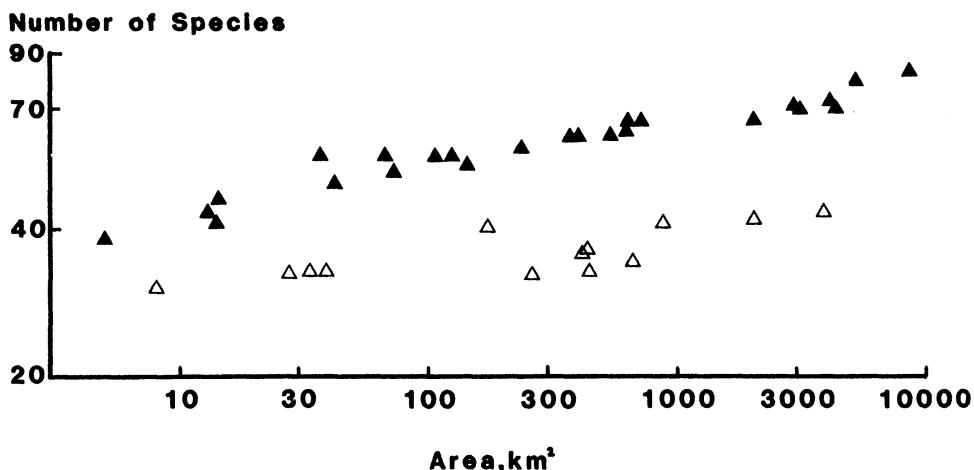


Figure 1 The species-area relationship for lowland breeding land and freshwater birds in the Central Solomons ▲ and in the central islands of Vanuatu △. These data refer to stage 1 of the taxon cycle. Data from Diamond and Mayr (1976), Diamond and Marshall (1977). Note that log scales are used.

that New Britain is more isolated from New Guinea than the other ones that Diamond discusses round New Guinea. It is therefore not surprising that at the area of New Britain (37,800 square kilometres, Cumberland, 1956) the New Guinea regression predicts 124 species, the New Britain one 126 species, while the actual figure appears from Diamond's graph to be slightly less than this. From the New Britain regression, the prediction for Bougainville, the largest of the Solomons, would be 96.5 lowland species, compared with 82 observed. Going out from the Solomons, the next island group is the Santa Cruz group, where the largest island, Ndeni, is stated by Diamond to be 438 square kilometres and have 24 species. The prediction for an island this size in the central Solomons would be 60.6 species. In Vanuatu, the prediction from the Solomons regression would be 73 lowland species as against 43 estimated by Diamond and Marshall. Schoener (1976), using the total area of the archipelago rather than the size of the largest island, shows the same combined effect of isolation and island size on the position and slope of the species-area relationship.

All the studies so far discussed, except Slud's, are dealing with the early stages of the taxon cycle. For instance on the Azores there are no endemic species, only endemic sub-species. On the Santa Cruz islands there are only three endemic

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species (Mayr, 1945). The only data set known to me showing the effects of later stages in the taxon cycle on the species-area relationship in birds are those of Ricklefs and Cox (1972) for islands in the Caribbean and fully discussed by them. For Stage 1, z is about 0.075, for Stage 2 about 0.15, for Stage 3 about 0.32 and for Stage 4 about 0.42 (Figure 2). At 100 km square the effect is to predict 12 species in Stage 1, 6 in Stage 2, 4 in Stage 3, and 1.5 in Stage 4, approximately.

Number of Species

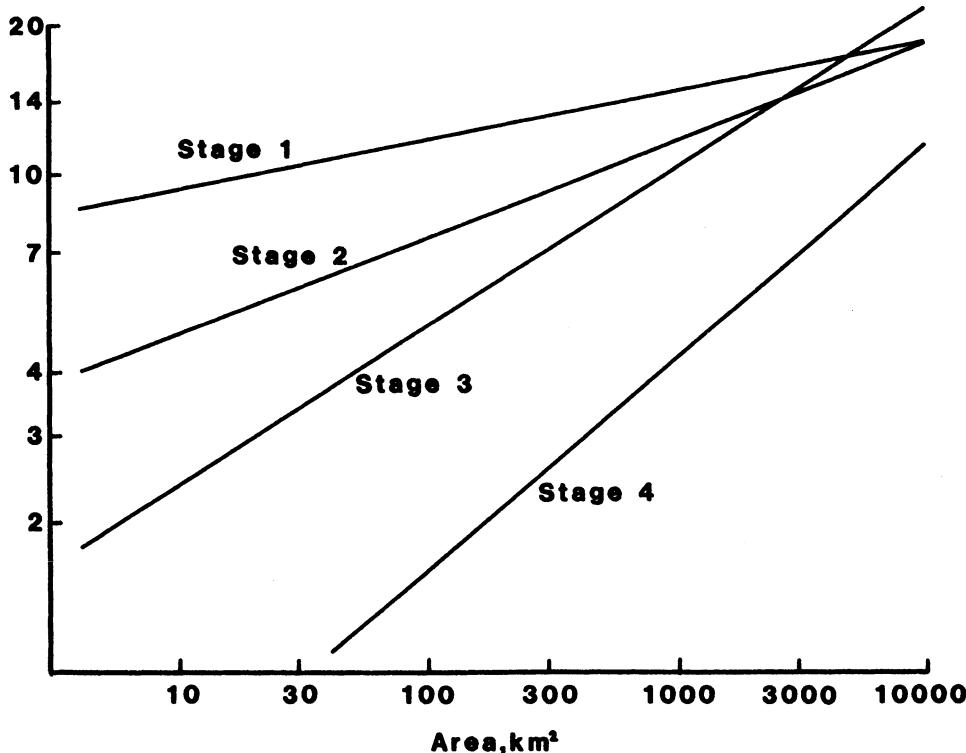


Figure 2 Linear regressions for the four stages of the taxon cycle in the West Indies. Derived from Ricklefs and Cox (1972), who give the scatter diagrams for the four stages. Note that the scaling of the axes is the same as in Figure 1.

The emphasis here has been on qualitative, rather than quantitative, comparisons. While standard statistical analyses are clearly possible, calculated standard errors, for example, are probably quite a lot smaller than the real doubt about the values.

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4. CONCLUSION

From this rather small set of sets of data, with all the doubts about the validity of species lists and island sizes, and the concern that might well be felt about some of the techniques that have been used, the general pattern described at the beginning of the last section is nevertheless consistent. The major effect of isolation seems to be to lower the species/area curve at the largest island, the amount of lowering will be greater the smaller the largest island is. From there the slope of the curve will be determined by the balance between the flattening caused by good dispersion in the early stages of the taxon cycle, and the steepening caused by progression to the later stages. For instance, the species/area curve for the indigenous extant or recently extinct birds of Hawaii is 0.335, reflecting the dominance of the species list by the endemic drepanidids (Williamson, 1981). Further studies are clearly needed to see if the patterns found here are sufficient to account for the variation in slopes in other archipelagos.

SECTION C

SURVIVAL

ARE HUNTING LOSSES OF YOUNG
BLACK DUCKS (*ANAS RUBRIPES*) TOO HIGH?

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SUMMARY

There are 2 to 3.5 million North American Black Ducks in early autumn, of which about 900,000 are shot, about 60% in Canada, where the kill has been increasing in the Atlantic Provinces and falling in Ontario. Numbers found in January in the US have decreased. So has the kill in New England and in the northern states east of the Mississippi River. An apparent slow reduction in Black Duck numbers since 1955 has been attributed to excessive killing of young ducks in their first winter. Over 11,000 recoveries of 72,000 Black Ducks ringed in Canada in July-September, 1968-1981, are used to estimate annual survival-, recovery- and kill-rates, using a stochastic model (Brownie *et al.*, 1978). The mean first-year survival of young Black Ducks in 1968-1980 was $42.2\% \pm 2.83\%$ in Ontario, $43.4\% \pm 3.29\%$ in Quebec and $38.4\% \pm 3.16\%$ in the Atlantic Provinces, or $39.7\% \pm 1.46\%$ in all. These rates are much less than that of young Mallard ringed throughout Canada in 1968-1981, $51.8\% \pm 0.62\%$, but not than those of young Mallard ringed in Ontario, $47.8\% \pm 1.26\%$ and Quebec, $37.9\% \pm 2.53\%$. The corresponding kill-rates were 24.8% for Black Ducks and 24.2% for Mallard ringed in Ontario, 25.6% for Black Ducks and 33.1% for Mallard ringed in Quebec and 27.1% for Black Ducks from the Atlantic Provinces, where there are few Mallard. Mallard are increasing rapidly in southern Ontario and southwest Quebec, where Black Ducks have decreased greatly. The estimates of survival- and kill-rates fail to account for those changes in abundance. The lack of correlation between survival and kill of young Black Ducks and Mallard suggests that at present levels of hunting increased losses from hunting are compensated for nearly completely by reduced deaths from other causes.

Keywords: BLACK DUCK (*ANAS RUBRIPES*); DUCK SHOOTING; SURVIVAL ESTIMATES;
WATERFOWL MANAGEMENT

H. Boyd and C. Hyslop

1. INTRODUCTION

In North America "waterfowl management" forms a substantial part of the activities of the federal, state and provincial agencies with responsibilities for the conservation of wildlife. Giving effect in the USA and Canada to the Migratory Birds Convention of 1916 involves, *inter alia*, the setting each year of regulations limiting where, and how ducks, and other migratory game birds, may be taken and limits on the numbers of birds that may be shot in any one day or be in the possession of hunters. There are regional differences in the dates of open seasons, which cannot exceed 109 days in all, within the outer limits of 1 September-10 March, and in other limitations, designed to correspond to changes in the distribution of birds as they leave their breeding places and move more or less rapidly towards their winter quarters. The taking of rare species is prohibited and additional restrictions are imposed on the taking of scarce ones. Though compliance with the published regulations varies, in accordance with regional traditions and attitudes towards the use of waterfowl and with the effort put into enforcing regulations, there is considerable evidence that the annual hunting regulations do affect the amount of waterfowl hunting and the size of the resulting kill; see Boyd and Finney (1978) for the situation in Canada, and the US Fish and Wildlife Service (USFWS) *Final Environmental Statement on the Issuance of annual regulations permitting the sport hunting of migratory birds* (FES 7/-54, June 1975, 710 pp., plus 11 Appendices).

For a long time it was also believed that the regulated size of the sport "harvest" (kill) had direct, and perhaps decisive, effects on the annual mortality rates of the principal quarry species. That belief has been shown to have been the result of unsound methods of analysing and testing the apparent relationships between hunting kill and losses from other causes. Anderson and Burnham (1976) studied the effect of exploitation on survival by analysing recoveries of ringed Mallard (*Anas platyrhynchos*). The Mallard is the most abundant game duck. There were 8-12 million alive in North America at the start of each nesting season in the 1970s, originating chiefly from the Canadian prairie provinces and the North-Central US, though increasingly also from Ontario, the Great Lakes states, and the Pacific coastal states. The combined reported kill in the USA and Canada during the same period was 4-7 million. Anderson and Burnham demolished earlier arguments that hunting mortality of Mallard is completely additive to other losses and showed that at the hunting intensities prevailing up to 1971 increased hunting of Mallard was compensated for by a corresponding decrease in other forms of mortality. They were unable to demonstrate that survival rates increased in years when kill rates were low because of restrictive hunting regulations. The large USFWS Mallard investigation, of which the study

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by Anderson and Burnham formed the most interesting part from a theoretical point of view, was in that respect very discouraging. It was based on over 400,000 recoveries from 1.5 million Mallards ringed in North America "pre-season" (i.e. in July-September), chiefly in the years 1961-1971. That was by far the largest such data set existing, other ducks having been marked less abundantly and tending to be recovered in proportionally, as well as absolutely, lower numbers. Such a massive effort having yielded so little insight into the possible relationships between hunting regulations and total mortality, what chance is there of doing better, with less information, about other species?

The Black Duck (*Anas rubripes*) is a very close relative of the Mallard, breeding in eastern North America from 100°W to the Atlantic coast and from 60°N to about 40°N, wintering in the southern parts of its breeding range. Formerly the ranges of the Black Duck and Mallard overlapped very little but during the last half century or so the Mallard has spread eastward into the range of the Black Duck from Manitoba to southern Quebec, though still scarce as a breeding bird east of 75°W, except where large-scale release programs have taken place in the US. Where the two species overlap, the Mallard seems to be more successful, at least in those areas that are relatively densely peopled and modified by human activities. In the relatively undisturbed boreal forests, where no ducks are abundant but which produces many by virtue of its great extent, the Black Duck seems still to prevail. Where they meet Mallard and Black Ducks readily form pairs and produce fertile hybrids showing mixed plumage characteristics. In some areas, such as south-west Ontario, up to one-fifth of the Mallard and Black Ducks appear to be hybrids.

Mallard numbers over most of their range can be estimated by means of breeding surveys, in May and early June, production surveys in July and midwinter counts. Black Ducks have only been monitored by counts in midwinter, because they are too difficult and expensive to find and count in all parts of their breeding range on a regular basis. The numbers of Black Ducks found in winter have decreased slowly since the midwinter counts began some 30 years ago, the decline having been steepest in the 1950s. The Black Ducks found are thought by the USFWS to comprise only 1/4 to 1/3 of those alive in January. As the winter inventory has not been conducted in conformity with any rigorous sampling scheme it is not practicable to estimate the total numbers of Black Ducks in a reliable way, so that the apparent slow decline in the numbers found is not easy to interpret. It has nevertheless been used to argue that "something must be done" to restore Black Duck numbers. A convenient way of "being seen to do something" is to put additional restrictions on the hunting of Black Ducks.

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In Canada very little has been done to restrict hunting of Black Ducks, in relation to the hunting of ducks in general. The only remnant still in place of an attempt made over a decade ago to cut down Black Duck hunting in the Maritime Provinces is that in Prince Edward Island the daily bag limit for Black Ducks is four, against the general limit of six ducks a day, of any species, prevailing throughout the eastern provinces.

In the US Atlantic Flyway states (i.e. those on the Atlantic seaboard from Miami to Florida, together with Pennsylvania and West Virginia) Black Duck hunting is much more severely restricted. There are many complications but, in summary, the daily bag limit for Black Ducks is now either two or one and in some states the 50-day Black Duck open season is shorter than that for ducks in general.

The combination of "restrictive" regulations in the US and "liberal" regulations in Canada has brought about a situation in which the kill of Black Ducks in the US has decreased while it has increased in Canada, so that since 1977 more than half the reported kill has been in Canada (Table 2). This has led to emphasis in the US on the need to reduce the kill in Canada if pressure on Black Ducks is to be eased.

The USFWS recently sponsored extensive reviews of Black Duck population dynamics, in order to update the work by Geis, Smith and Rogers (1971), which had provided the basis for management actions during the 1970s. The principal new research was that conducted on recoveries of ringed Black Ducks by Blandin (1982a,b).

The key passage in Blandin (1982a) is in the section on management recommendations (at page 160): 'That restrictive regulations can reduce the size and rate of the waterfowl harvest has been demonstrated clearly (Martin *et al.*, 1979; Rogers *et al.*, 1979; Patterson, 1979; Geis *et al.*, 1969; Martinson *et al.*, 1968). Although this study has not demonstrated that Black Duck harvest has affected survival (average harvest = 680,000; 1968-1979, or about one-fourth the estimated average population size of 2.8 million), the weight of evidence suggests that relief from intensive hunting pressure, especially in young birds, would benefit the Black Duck resource'.

The urgent management questions for the Canadian Wildlife Service (CWS) are three: (1) Has hunting affected the survival of Canadian-breeding Black Ducks? (2) If so, would restricting the Canadian kill be likely to result in the growth of Canadian Black Duck stocks, or at least arrest any tendency to decrease? (3) If hunting seems not to have affected the survival of Canadian Black Ducks, may it still be desirable to follow the US lead in further restricting the hunting of Black Ducks?

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Scientific evidence is clearly relevant to the first two questions.

2. DATA SOURCES AND METHODS OF ANALYSIS

In what follows we concentrate on evidence from "pre-season" ringing (i.e. in July-September) of Black Ducks in Ontario, Quebec and the Atlantic Provinces in the years 1968-1981, together with ringings of Mallard in Ontario and Quebec during the same period. (Few Mallard live in the Atlantic Provinces.) Comparison between the two species is especially relevant because the Mallard is gaining ground in eastern Canada while the Black Duck is losing, so that it is reasonable to expect corresponding differences in productivity and survival. We draw also on results of the Canadian and US national harvest and species composition surveys, described in Boyd and Finney (1978) and the USFWS FES 35-54 (1975) respectively. The data are published annually in CWS Progress Notes and in USFWS Administrative Reports. These are backed up in the US by annual Waterfowl Status Reports published in the USFWS Special Scientific Reports - Wildlife series, though these appear only after delays of several years and do not include details of the age- and sex-composition of the reported kill.

Blandin (1982a,b) found that there were differences between adult females and males in mortality-rates and proportionate kill of Black Ducks, but that no clear differences existed in those respects between males and females in their first year of life. As we are primarily concerned with those young birds, we have used the simple classification into "young" and "adults", ignoring the relatively small differences between adult females and males. (The survival of adult males is higher than that of adult females by 4-10%.)

In estimating survival- and recovery-rates we have used the stochastic models and methods of Brownie, Anderson, Burnham and Robson (1978). Again in the interests of simplicity and comparability the results used here were all obtained using their "Model under H1", which involves the assumptions that: "(1) Annual survival, reporting and harvest rates (hence recovery rates) are year-specific; (2) annual survival and harvest rates are age-dependent for the first year of life only (i.e. young and adult birds have different survival and harvest rates); and (3) reporting rates "are not dependent on time of release" (*lit. cit.* page 59). The model under H1 was usually, though not always, the simplest model (i.e. with fewest parameters) that adequately described the data. For reasons that will emerge, the annual estimates are for most purposes less useful than the mean estimates for the entire period, but no

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corresponding advantage emerges from the use of the restricted Model 3 of Brownie *et al.*, in which survival and recovery rates are constant, and the mean estimates under the two models differ little arithmetically. In testing the evidence for the effects of exploitation on survival we have followed Anderson and Burnham (1976).

Before reporting on and discussing the ringing analyses we outline information on the population size and regional distribution of the Black Duck in May and September (Table 1) and on the size and distribution of the kill (Tables 2 and 3). The sources are given in the captions to the tables. It is not possible to attach standard errors to the numbers. Some of the field data show large year to year variations, but the major weakness, especially in the very large areas in Ontario and Quebec, is uncertainty about the true variability of numbers within each wetland region in the same year, given that the proportion of Black Ducks present that can be detected is small (10-30%).

3. RESULTS

Table 1 demonstrates the extent to which Canada dominates the population size and production of Black Ducks, holding about 86 percent of the breeding population and producing about 90 percent of the young, Quebec (39 percent) and Ontario (30 percent) being the principal sources, with few further west. In the northern US, New England is the principal stronghold but has shown the greatest decline (Spencer, 1979).

The regional distribution of the kill (Table 2), including some guesses at illegal and otherwise unreported kill, shows that Black Ducks from different parts of the breeding range mostly suffer 20-25 percent losses to hunting each year, although those from the Atlantic Provinces may suffer as much as 38 percent and those from the northwest (Manitoba and Saskatchewan) only 14 percent. Although in 1977-1981 the reported kill in Canada averaged $348,000 \pm 27,000$, 52.3 percent of the kill in both countries ($665,000 \pm 69,000$), when full allowance is made for unreported kill the mean Canadian total may have been as high as 568,000, or 62 percent of the total kill. "Native kill" refers to ducks taken by Indians who are not required to buy Migratory Game Bird Hunting Permits and so are not sampled by the national harvest surveys. There is little reliable information on their kill of Black Ducks, but the allowance of 10% is more likely to be too high than too low.

Table 3, based only on the reported kill, shows that the average kill in Quebec

Black Duck hunting losses

Table 1

Breeding numbers and production of fledged young Black Ducks in different regions of Canada and the US, late 1970s. Numbers in thousands, to nearest 5.0. (After CWS, 1979; Cooch, 1981; Spencer, 1979)

Region	Numbers in May		Number of flying young in September ¹			"Fall flight"	Region % Total fall flight
	total	potential breeding females	A	B	C	P+(A+B+C)/3	
	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Western Boreal	30	10	30	25	90	80	21
Ontario	450	150	450	375	1330	1170	30.7
Quebec	600	200	600	500	1770	1560	40.9
Atlantic Provinces	240	80	240	200	540	570	15.0
Canada	1320	440	1320	1100	3730	3380	88.7
N. Miss. Flyway	35	10	35	25	105	90	2.4
New England	120	40	120	100	170	250	6.5
Middle Atlantic	45	20	45	50	40	90	2.4
U.S.	230	70	200	175	315	430	11.3
Total	1520	510	1520	1275	4045	3810	100.0
	(1-2 million)		(2-5.5 million)				

¹ Estimate A assumes that on average 3 flying young are produced per breeding pair (CWS, 1979), so that Column (3) equals Column (1), which assumes one non-breeding adult for every breeding pair. Estimate B (Spencer, 1979) assumes that only 50 percent of breeding pairs are successful, each with an average of 5 flying young. Estimate C, using results from a later section, assumes negligible losses of adults from May to September, and multiplies P by the ratio of young and adults in the hunting kill, after adjustment for the greater vulnerability of young to the gun.

and the Atlantic Provinces was higher in 1977-1981 than in 1972-76, that in Ontario, the Mississippi Flyway states, New England and the Middle Atlantic states it was lower in the later period and that in the Atlantic Flyway from Delaware and Maryland southwards it was little changed. The kill per 1,000 hunter-days (a measure of all duck-hunting effort, not necessarily directed at Black Ducks) was much higher in the Atlantic Provinces and Quebec than elsewhere. From 1971-76 to 1977-81 it rose in the Atlantic Provinces, remained unchanged in the Middle and South Atlantic states and fell elsewhere.

Thus there is considerable evidence in support of the view that if Black Duck

Table 2

mean annual kill of Black Ducks, 1977-78 to 1981-82, by regions of take and of origin: "Reported Kill" = estimates from national harvest surveys; "Additions" = illegal kill (20% in Canada, 10% in US) + native kill in Canada (10%) + tridipping loss (25% in Canada, in US included in reported kill).

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Table 3

*Reported seasonal kill of Black Ducks by regions, 1972-73 to 1981-82:
(a) mean kill, in thousands; (b) kill per 1,000 hunter-days*

	1972-76	(a) Mean Kill 1977-81	Kill 1972-81	(b) Kill per 1,000 1972-76	1977-81	Hunter-Days 1972-81
Ontario	92.0	85.7	88.8	115	101	108
Quebec	108.9	120.3	114.6	245	231	238
Atlantic Provinces	112.0	142.3	127.1	269	294	284
Canada	312.9	348.3	330.6	188	184	189
North Miss. ¹	65.1	41.3	53.2	36	29	33
South Miss. ¹	44.3	32.4	33.4	80	47	63
New England	99.5	72.9	86.2	191	152	172
Mid. Atlantic ²	99.6	93.2	96.4	87	89	88
South Atlantic ^{1/3}	74.5	73.2	75.8	91	90	90
U.S.	383.0	317.0	350.0	105	92	98

¹ In calculating kill per 1,000 hunter-days limited to states with mean kill > 5.0: Michigan, Ohio and Indiana in North Miss. and Tennessee, Kentucky and Alabama in South Miss.

² New Jersey, New York, Pennsylvania

³ Delaware, Maryland, Virginia, North Carolina

abundance is to be restored by reducing hunting the effort to do so must include Canada as well as the US.

Table 4 summarizes the mean survival-(S), recovery-(f) and harvest-rates (K) of ringed Black Ducks in 1968-1981, derived from Model H1. The mean harvest rate can be estimated from $K = f/W$, where W is the mean reporting rate for ringed birds shot. Using a finding from a recent USFWS reward ring study (USFW Research Information Bulletin No. 82-40, October 1982, 1 p.), that the mean reporting rate (W) of regular rings was 43.0 ± 0.4 percent, $K = 2.326 f$. The mean adult survival rates are close to 60 percent, those of young birds are around 40 percent, lower in the Atlantic Provinces than further west. The recovery- (and hence the harvest-) rates of adults decrease from west to east while those of young birds increase, so that the highest harvest rate is that of young ducks in the Atlantic Provinces (27.1 percent) where the adult harvest rate is lowest (11.7 percent).

For the specific purpose of this inquiry - is the kill of young Black Ducks too high? - the most important result in Table 4 is that for the samples of young birds

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Table 4

Estimates of mean annual survival- (\bar{S}), recovery- (\bar{f}) and kill-rates (\bar{K}) of Black Ducks ringed in eastern Canada, 1968-81, and of sampling correlations, using Model H_1^L , which assumes that: (1) annual survival- and recovery-rates are year-specific and (2) young birds have different survival- and recovery-rates from those of adults

	Ontario	Quebec	Adults	Atlantic	Canada	Ontario	Quebec	Young	Atlantic	Canada
survival, S , %	57.92	61.90	61.22	60.21	\bar{S}^1	42.24	43.40	38.41	39.72	
s.e.	2.40	3.12	3.71	1.31	\bar{f}^1	2.83	3.29	3.16	1.46	
recovery-rate, f , %	6.16	5.34	5.02	5.51	\bar{f}^1	10.67	11.02	11.64	11.19	
s.e.	0.34	0.33	0.32	0.17		0.28	0.27	0.19	0.13	
kill-rate, K , %	14.33	12.42	11.67	12.82	\bar{K}^1	24.81	25.63	27.07	26.03	
corr (\bar{S}, \bar{f})	-0.3888	-0.4005	-0.2156	-0.3918	(\bar{S}^1, \bar{f}^1)	-0.0409	-0.0401	-0.0253	-0.0395	
corr (\hat{U}, \hat{K})	-0.3921	-0.2392	-0.1239	-0.5272	(\hat{U}^1, \hat{K}^1)	-0.4040	-0.1506	-0.3190	-0.5783	

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the correlation coefficients $r(S^1, f^1)$ are close to zero (-0.025 to -0.041). As recovery-rates tend to reflect intensity of hunting, this negative result implies a lack of decisive impact of hunting.

The last row of Table 4 introduces the relationship between the kill (K) and losses from other causes ($U = 1 - S - K$). Though in all six cases the coefficients are negative, even for the Ontario samples these fall short of the conventional level with a probability of less than 0.10.

Thus, in accordance with Blandin's findings (1982a, 1982b) for earlier years and other areas, the evidence that the kill of Black Ducks at current levels is influencing their survival is weak.

Similar information on the estimated survival- and recovery-rates of Mallard originating in Ontario and Quebec is summarized in Table 5. The estimated survival of the adults is much the same as that of the Black Ducks, that of the young rather greater in Ontario and less in Quebec. As with young Black Ducks, the correlation between estimators of survival- and recovery-rates is non-existent for young Mallard, although the inverse correlation between K^1 and U^1 (estimated losses from causes other than hunters) is quite strong (-0.55 and -0.58).

The estimated annual values of the survival- and recovery-rates of young Black Ducks and Mallard provide some additional guidance. Table 6 records marked departures from the mean in particular years. The survival estimates yield fewer anomalous values than the recovery-rates. It does not appear that young ducks originating in different regions are similarly afflicted by unusually large or small losses in particular years. Nor are anomalous survival rates for ducks from one region necessarily shown by both species.

The recovery-rate of young Mallard from Ontario has declined markedly from 1968 to 1981. The Black Duck and Quebec Mallard rates show no such trend but have fluctuated quite widely and more often together than independently. This is not surprising, given the extent of their mixing during the hunting season.

The relationship between hunting mortality (K') and non-hunting mortality (U') of young ducks is explored further in Table 7, which records the results of estimating the slope b in the relationship $U' = U'_0 + bK'$ on the alternative hypotheses of compensatory and additive relationships between U' and K' . The methods of estimation are described by Anderson and Burnham (1976). The relevant points that emerge are

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Table 5

Estimates of mean annual survival- (\bar{S}) , recovery- (\bar{F}) and kill-rates (\bar{K}) of Mallard ringed in Ontario and Quebec, 1968-1981, using Model H1.

	Ontario	Adults Quebec	Canada *		Ontario	Young Quebec	Canada
survival, \bar{S} , %	57.79	57.17	64.92	\bar{S}^1	47.82	37.86	51.82
s.e.	0.86	0.21	0.28		1.26	2.53	0.62
recovery-rate, \bar{F} , %	6.44	6.78	5.01	\bar{F}^1	9.93	13.56	8.29
s.e.	0.15	0.32	0.04		0.12	0.34	0.07
kill-rate, \bar{K} , %	15.71	16.54	11.65	\bar{K}^1	24.22	33.07	19.28
corr (\bar{S}, \bar{F})	-0.4238	-0.3706	-0.4802	(\bar{S}^1, \bar{F}^1)	-0.0506	-0.0619	-0.0591
corr (\hat{U}, \hat{K})	-0.3195	-0.5296	-0.2471	($\hat{U}^{-1}, \hat{K}^{-1}$)	-0.5548	-0.5802	.0.1486

* Includes samples from western provinces.

that at current levels of hunting: (1) the kill of young Mallards from Ontario and Quebec can be regarded as completely compensatory to other kinds of loss; and (2) the kill of young Black Ducks from Ontario, Quebec and the Atlantic Provinces is largely compensatory and certainly not a completely additive form of mortality. This line of inquiry needs to be extended to data for Black Ducks from the range in the US before there is much chance of seeing whether it is possible to identify a threshold point or, more probably, a zone of increasing intensity of kill, beyond which the hunting kill is heavy enough seriously to influence the survival of young Black Ducks.

4. DISCUSSION

Having shown that the evidence available from recent ringing in eastern Canada supports Blandin's (1982a) conclusion that it is not possible to demonstrate that Black Duck hunting at the prevailing levels has affected survival, we find that the practical questions to be addressed are the inconvenient ones: should Canada nevertheless proceed to introduce additional restrictions on hunting of Black Ducks; and, if so, how and where? Two lines of attack seem possible. First, to bring about a major reduction in the Canadian kill and see whether this does lead to an increase in breeding Black Ducks. That would require a new scheme for monitoring the size of the breeding population, not hitherto thought practicable, after expensive and unsatisfactory efforts at aerial transect sampling of the boreal forest region

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Table 7

Estimates of the slope b in the relationship between non-hunting mortality (V^1) and hunting mortality (K^1) for young Black Ducks ringed pre-season in Ontario, Quebec and the Atlantic Provinces and young Mallard ringed in Ontario and Quebec. These reflect losses of ducks hatched in year t suffered prior to August in year $t+1$.

	Ontario	Quebec	Atlantic Provinces
(1) hunting and other losses compensatory			
Black Duck	-0.8236	-0.5712	-0.8213
Mallard	-1.0	-1.0	
(2) hunting and other losses additive			
Black Duck	-0.4096	-0.3889	-0.4415
Mallard	-0.3247	-0.4264	

in the 1950s and 1960s (Chamberlain and Kaczynski, 1968). Fortunately, recent studies inspired by concern about the possible effects of "acid rain" on biological productivity in areas underlain by the Canadian Shield, which includes most of the Canadian range of the Black Duck, have shown that it is now possible to carry out a sufficiently accurate sampling scheme, using low-level helicopter surveys to detect Black Ducks and other waterfowl (CWS, unpublished progress reports). Such helicopter surveys are expensive and somewhat risky, as they require the aircraft to be operated at a height from which safe descent is difficult should mechanical troubles develop. So a decision to embark on annual aerial sampling surveys of ducks breeding in the eastern boreal region will not be made solely on the ground that it might help to determine whether Black Duck numbers are increasing.

An alternative cheaper and safer approach might be to continue to rely on harvest surveys to monitor the size and age-composition of the Black Duck population, using some simplifying assumptions about the relationship between population size and availability to hunters. Such an approach shows most promise if the existing harvest surveys can be intensified in those parts of the northern Black Duck range where local hunting is most heavy and if the data can be related to ecological regions, rather than the political regions used so far. Preliminary work suggests that the output

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of young per unit of breeding population varies importantly between wetland regions. Using the major wetland categories identified in eastern Canada by the Canada Committee on Ecological Land Classification (1981), the production of young seems since 1968 to have been highest in the Low Boreal region, a little less in the Mid-Boreal (above 48°N in western Quebec and Ontario), substantially less in the Atlantic Boreal (most of the Maritime Provinces and the north shore of the Gulf of St. Lawrence) and least of all in the Eastern Temperate region (southwestern Ontario, where few breeding Black Ducks now remain, and along the St. Lawrence Valley) where land use changes have been greatest (Boyd, unpublished). Even though the harvest surveys would remain, for reasons of economy, the principal source of data, the emphasis could profitably be shifted from the size of the kill to the size of the supply, quite probably more important.

Meanwhile the central anomaly remains. Despite the lack of evidence that recent harvest rates have been hurtful, the responsible administrators judge it more prudent to annoy hunters by cutting down their opportunities to take Black Ducks and hence reducing their kill than to risk further damage to Black Duck stocks by allowing the kill to remain at 20-40 percent of the fall flight. This precautionary approach contrasts strongly with that more commonly used in the exploitation of marine fish stocks and other renewable resources with an immediately determinable market value, in which the standard approach has been to deplete stocks until a "crash" has occurred before embarking on protective or remedial measures. Should Black Ducks be grateful?

ACKNOWLEDGEMENTS

We have benefited greatly from access to the unpublished work of Warren Blandin, whose recent early death deprives North American waterfowl management of a popular and respected biologist who had made the Black Duck his own. We are indebted to Maurice Gratton of the Computing and Applied Statistics Directorate, Environment Canada, for help in computing; and to Dianne Saliga for expert preparation of the final typescript.

THE ESTIMATION OF SURVIVAL IN BIRD POPULATIONS
BY RECAPTURES OR SIGHTINGS OF MARKED INDIVIDUALS

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SUMMARY

To estimate bird survival rates, the shortcomings of methods based on recoveries (of dead birds) make it logical to use recapture information (of live birds) in specific statistical models. In this paper, the basic model of Cormack (1964) and some recent developments allowing equality constraints between parameters are reviewed. Applications to Fulmar, Starling, and Coot data are presented, with the emphasis on model selection. For Swallow data, these models designed to estimate survival are compared to more general recapture models. In conclusion, using the Cormack model and its generalisations in the course of population studies on a local scale is recommended.

Keywords: CAPTURE-RECAPTURE; SURVIVAL; BIRDS; MAXIMUM LIKELIHOOD

1. INTRODUCTION

In the management of animal populations and in fundamental research in population dynamics, the emphasis is now on mechanisms - and as a consequence on parameters - of population changes, rather than on changes in numbers by themselves. Survival rates are as such major components of animal population dynamics. To estimate survival rates in birds, ringing provides numerous data that are a real

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challenge to statisticians.

Recoveries (i.e. records of time of death by people) have been widely used to estimate survival: good statistical models have been developed (Haldane, 1955; Cormack, 1970; see reviews by Seber, 1973; Brownie *et al.*, 1978) while the statistical shortcomings of some widely used methods have been demonstrated (Anderson *et al.*, 1981). Nevertheless, the number of recoveries available, various sources of bias (e.g. Anderson and Burnham, 1980; Nelson *et al.*, 1980) and problems in the identifiability of the models (Lakhani and Newton, 1983) generally impose severe limitations on the quality of the estimates obtainable. Thus, to estimate survival, it seems logical to use other kinds of information, in particular that based on recaptures of live animals over the years (or sightings when the animals are not actually captured). See also Cormack (1985).

Besides general recapture models, some specific approaches have been developed (Chapman and Robson, 1960; Cormack, 1964; Clobert, 1981; Sandland and Kirkwood, 1981). While Chapman's and Robson's model is based on transversal data (recaptures in the same year of birds ringed for several years), the other models cited use longitudinal data, namely individual recapture histories over the years.

The purpose of this paper is to present various longitudinal models available, which seem to provide the most efficient way to estimate survival rates, while being rarely used. We apply the models to the Fulmar (*Fulmarus glacialis*) (from data in Cormack, 1964), to the Starling (*Sturnus vulgaris*), and to the Coot (*Fulica atra*). Then we compare various recapture models, using data on the Swallow (*Hirundo rustica*). In conclusion, we discuss the efficiency of the longitudinal models, especially when compared with models using recoveries.

2. METHODS

2.1 General Presentation

The parameters used in all the models are (Fig. 1):

- the probability of survival from year i to year $i+1$, s_i ;
- the probability that a survivor in year i comes back to the study area this year, π_i ;
- the probability that a bird present in the study area in year i is captured (prob. of capture), p_i .

When there is permanent emigration ($\pi_i < 1$), the models provide an apparent survival,

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i.e. an estimate of $\pi_i s_i$. The effect of non-permanent absences of birds is included in p_i . From now on, we will suppose $\pi_i = 1$, a reasonable assumption in a lot of cases, but which could depend upon the biology of the species studied. The parameters s_i and p_i are common to all individuals, so that, in particular, no age-specific effects are included in the models. The absence of age-specificity seems reasonable when working on breeding populations.

On the contrary, the parameters can be time-specific (Cormack, 1964), or subject to various constraints of equality to achieve a greater parsimony (Sandland and Kirkwood, 1981; Clobert, 1981).

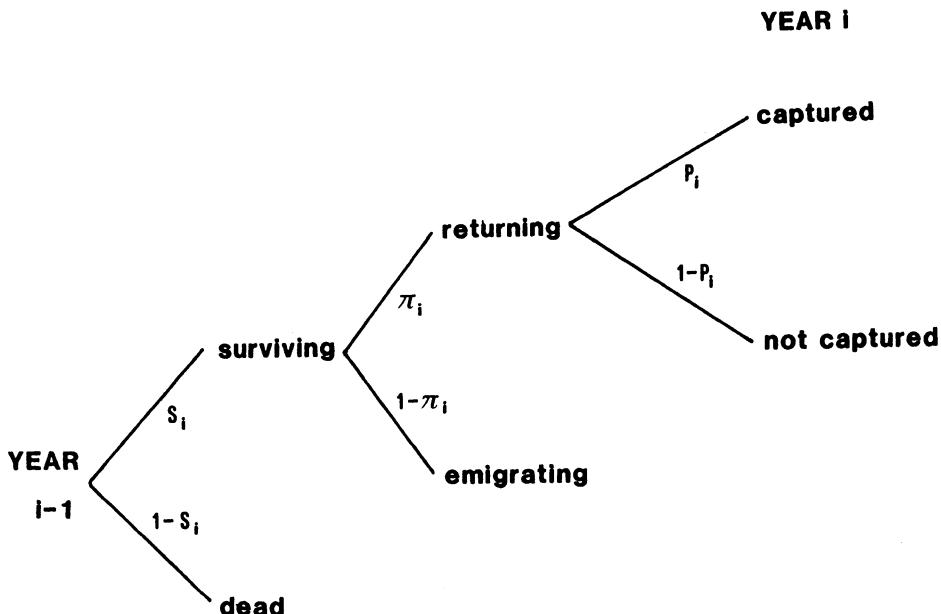


Figure 1 Parameters used in the recapture models to estimate survival.
Recoveries from dead birds are not taken into account.

The data can be presented as dichotomous trees of recapture histories (Fig. 2). The various recapture histories in a tree (= the leaves of each tree) are mutually exclusive events: each individual has one history, and only one. Under the hypothesis of independence of the individuals, the numbers in the histories follow a multinomial distribution. Usually, when there are n years of recapture, there are

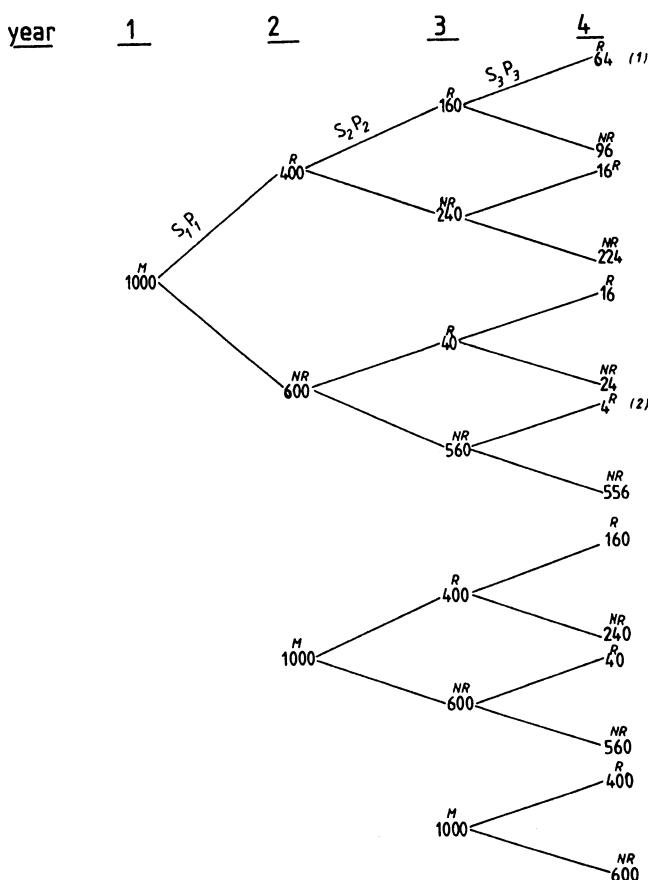
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Figure 2 Recapture trees with survival probabilities $s_1=s_2=s_3=0.5$ and probabilities of captures $p_1=p_2=p_3=0.3$: expected numbers in the various recapture histories. ($M=\text{marked}$, $R=\text{recaptured}$, $NR=\text{not recaptured}$). (1) probability of this event is $s_1 p_1 s_2 p_2 s_3 p_3$. (2) probability of this event is $s_1 (1-p_1) s_2 (1-p_2) s_3 p_3$.

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$n+1$ years of ringing (Fig. 2) and the likelihood of a whole data set is obtained from a product of multinomial densities.

To make the likelihood more compact, it is convenient to use the statistics b_i , a_i , c_i (Cormack, 1964), and v_i defined as follows for $i = 1, \dots, n$:

b_i : number marked in year i ($b_1 = 1000$ in Fig. 2);

a_i : number captured in year $i+1$ ($a_1 = 400$, $a_2 = 160 + 40 + 400 = 600$ in Fig 2);

c_i : number of individuals last seen in year i ($c_3 = 24 + 96 + 240 + 600 = 960$ in Fig. 2);

v_i : $\sum_{j=1}^i (b_j - c_j)$, number of individuals known to be alive after year i .

As an example, the data in Fig. 2 are converted to these statistics in Table 1. With these notations, the likelihood of a data set reduces to (Statistical Appendix):

$$L = \prod_{i=1}^n s_i^{v_i} p_i^{a_i} (1-p_i)^{v_i-a_i} \left(\prod_{k=i+1}^n \left[\prod_{j=i}^k ((1-p_j) s_j) \right] (1-s_{k+1}) \right)^{c_i}$$

(with $\prod_{j=i}^k ((1-p_j) s_j) = 1$ when $k < i$, and $s_{n+1} = 0$).

The Log-likelihood $L_n L$ can be maximized under various constraints on the parameters to provide maximum likelihood estimates (see the Statistical Appendix).

Table 1
Reduction of the recapture histories of Fig. 2 to the statistics b_i , a_i , c_i and v_i

i	b_i	a_i	c_i	v_i
1	1000	400	556	444
2	1000	600	784	660
3	1000	700	960	700

b_i = number marked in year i ;

a_i = number caught in year $i+1$;

c_i = number caught for the last time in year i ;

v_i = number known to be alive after year i .

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2.2 Cormack Model

With the full set of parameters, only $s_1, s_2, \dots, s_{n-1}, p_1, p_2, \dots, p_{n-1}$ and the product $s_n p_n$ are estimable. Cormack (1964) provides explicit maximum likelihood estimates of these quantities, and estimates of their variances and covariances. This model is noted (p_t, s_t) by Sandland and Kirkwood (1981) (2n parameters, 2n-1 estimable).

2.3 Sandland-Kirkwood-Clobert Models

Sandland and Kirkwood (1981) and Clobert (1981) proposed independently several kinds of equality constraints between parameters, to enhance parsimony, resulting in (in Sandland's and Kirkwood's notations):

- model (p_t, s) ($s_i = s$, for all i) (n+1 parameters)
- model (p, s_t) ($p_i = p$, for all i) (n+1 parameters)
- model (p, s) ($p_i = p$, $s_i = s$, for all i) (2 parameters).

Sandland and Kirkwood propose also a (pm, s_t) model with a Markov-type dependence in the probability of capture. Clobert uses also any kind of equality constraints between the survival rates, and between the probabilities of capture, that can be used for example when some years are known as "poor" *a priori*.

In all these cases, numerical methods are required to maximise the likelihood. Likelihood ratio tests help to choose an adequate model for any particular data set (Sandland and Kirkwood, 1981; Clobert, 1981), or to compare data sets (males and females within the same population; separate populations of the same species; populations of different species...).

Numerical estimates of the asymptotic variances and covariances of parameter estimates can be obtained from the second-order derivatives of the likelihood (see statistical appendix).

3. APPLICATIONS

3.1 Fulmar (*Fulmarus glacialis*)

This is Cormack's (1964) original example (Table 2). Comparisons between models (Table 3) do not show any significant variation in survival over the years: when compared with model (p_t, s_t) , the model (p_t, s) is the only model with constraints

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accepted (likelihood ratio test: $\chi^2 = 11.5 < \chi^2_{10}(0.05) = 18.3$; Table 3).

The overall survival $\hat{s} = 0.939$ obtained from model (p_t, s) is very close to the weighted mean of the \hat{s}_i in Cormack's model: $\tilde{s} = 0.942$. The standard-deviations (0.02 and 0.01 respectively) are close. The variation in the probabilities of capture (model (p, s) is rejected) is probably more related to the sighting pressure than to any biological phenomenon.

Table 2
Recapture data of Fulmars (from Cormack, 1964)

Year	i	b _i	a _i	c _i	\hat{s}_i	\hat{p}_i	$\hat{\sigma}(\hat{s}_i)$	$\tilde{\sigma}(\hat{s}_i)$
1950	1	11	4	1	0.97	0.37	0.097	0.097
1951	2	66	36	7	0.93	0.51	0.040	0.040
1952	3	28	43	4	0.97	0.45	0.039	0.039
1953	4	2	54	3	0.96	0.57	0.041	0.043
1954	5	4	63	4	0.96	0.66	0.036	0.037
1955	6	51	69	10	0.97	0.49	0.035	0.037
1956	7	13	99	9	0.94	0.68	0.040	0.042
1957	8	5	85	18	0.85	0.66	0.040	0.042
1958	9	19	51	10	0.94	0.37	0.037	0.038
1959	10	8	102	4	0.97	0.72	0.036	0.036
1960	11	26	133	16	0.90	0.88	0.032	0.032
1961	12	3	116	34	-	-	-	-

b_i = number marked in year i;

a_i = number of animals caught in year $i+1$;

c_i = number of animals caught for the last time in year i;

\hat{s}_i = estimate of survival rate from year $i-1$ to i;

\hat{p}_i = estimate of the probability of capture in year i;

$\hat{\sigma}(\hat{s}_i)$ = estimated standard-deviation of \hat{s}_i , by Cormack's (1964, p.435)
formula number 9;

$\tilde{\sigma}(\hat{s}_i)$ = *idem*, obtained from an iterative method (see Appendix).

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*Likelihood ratio tests between recapture models
on the Fulmar data of Table 2*

Model (*)	Number of parameters estimated	- 2Ln L	Null hypothesis	Test	Conclusion
$p_t s_t$	23	2100.6			
$p s_t$	13	2206.6	$p_i = p$, for all i	$\chi^2 = 2206.6 - 2100.6$ $= 106.0 > \chi^2_{10}(0.05)$ $= 18.3$	model rejected
$p_t s$	13	2112.1	$s_j = s$, for all i	$\chi^2 = 2112.1 - 2100.6$ $= 11.5 < \chi^2_{10}(0.05)$ $= 18.3$	model not rejected
$p s$	2	2235.6	$p_i = p$, for all i (under $s_j = s$, for all i)	$\chi^2 = 2235.6 - 2112.1$ $= 23.5 > \chi^2_{11}(0.05)$ $= 19.7$	model rejected

(*) in Sandland's and Kirkwood's (1981) notations:

- (p_t, s_t) = probability of capture and survival time-dependent;
- (p, s_t) = probability of capture constant over the years, survival time-dependent;
- (p_t, s) = probability of capture time-dependent, survival constant over the years;
- (p, s) = probability of capture and survival constant over the years.

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3.2 Starling (*Sturnus vulgaris*)

Clobert (1981) put 360 nest boxes in a 100 Ha farmland area in Belgium, and studied the breeding population of Starlings for 7 years ($n=6$ years of recaptures; Table 4). Only the females are studied, by nocturnal capture (the males do not spend the night at the nest during the breeding season). Comparisons between models (Table 5) indicate significant differences between survival rates while the probability of capture can be considered constant: model (p, s_t) , when compared with model (p_t, s_t) by a likelihood ratio test, is accepted ($\chi^2 = 4.0 < \chi^2_{\alpha/2}(0.05) = 9.49$). This is obviously related to the experimental design, all the nest-boxes being visited once, and only once, to limit the impact on breeders, each spring. The constraint $p_i = p$, for all i , in model (p, s_t) makes it possible to estimate s_n (last column of Table 4). The standard deviations of survival rates (Table 4) are slightly smaller in model (p, s_t) than in model (p_t, s_t) because of the greater parsimony. The variations in survival are obviously related to weather conditions, the low $\hat{s}_3 = 0.37$ in 1978-1979 resulting from a particularly cold winter (Fig. 3, and Clobert and Leruth, 1983). Correlations between the estimates \hat{s}_i prevent the direct calculation coefficient between a weather variable and survival estimates.

Table 4
Recapture data for Starlings (Clobert, 1981)
Same notations as in Table 3

Year	i	b_i	a_i	c_i	\hat{s}_i	$\hat{\sigma}(\hat{s}_i)$	\hat{p}_i	\tilde{s}_i	$\tilde{\sigma}(\tilde{s}_i)$
1977	1	52	27	21	0.66	.079	0.79	0.67	.079
1978	2	204	122	102	0.65	.049	0.78	0.67	.043
1979	3	102	74	151	0.37	.037	0.79	0.37	.035
1980	4	126	95	101	0.59	.052	0.73	0.58	.050
1981	5	73	67	102	0.53	.068	0.62	0.48	.044
1982	6	43	48	75	-	-	-	0.46	.058

\tilde{s}_i : estimation of s_i in model (p, s_t) , $\tilde{\sigma}$: standard-deviation estimated numerically.

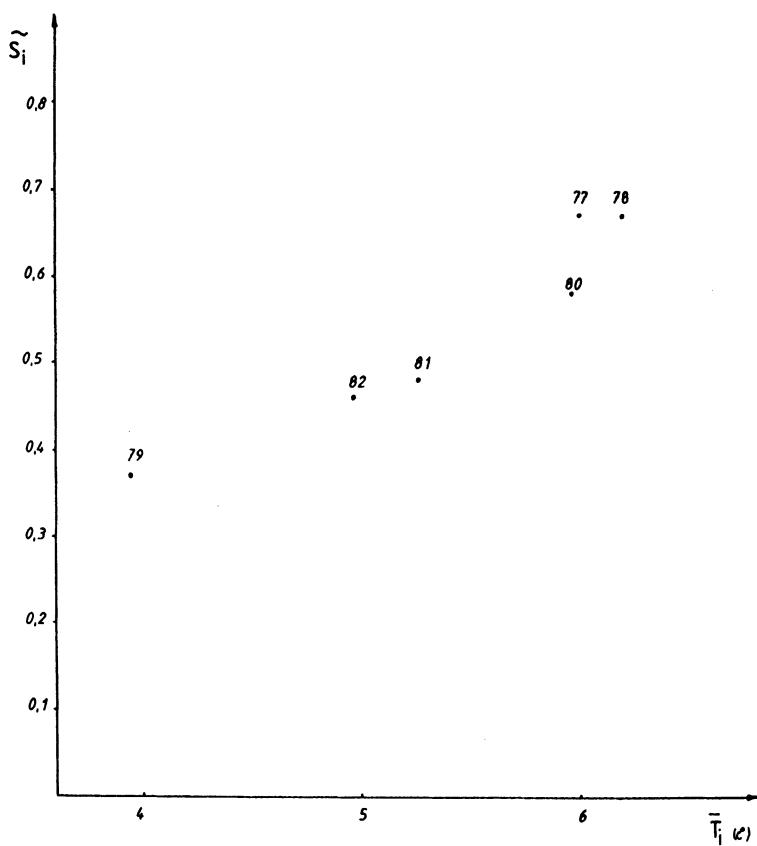
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Figure 3 Relationships between average October-March temperature \bar{T}_i and survival \bar{S}_i in a Belgian population of Starling (*Sturnus vulgaris*).

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Table 5

*Likelihood ratio tests between recapture models
on the Starling data of Table 4*

Model (*)	Number of parameters estimated	- 2LnL	Null hypothesis	Test	Conclusion
$p_t s_t$	11	1625.6	$p_t = p$, for all t		
$p s_t$	7	1629.6	$p_t = p$, for all t	$\chi^2 = 1629.6 - 1625.6$ $= 4.0 < \chi^2_{4(0.05)}$ $= 9.49$	model not rejected
$p s$	2	1665.8	$s_t = s$, for all t	$\chi^2 = 1665.8 - 1629.9$ $= 36.2 > \chi^2_{5(0.05)}$ $= 11.07$	model rejected

(*) in Sandland's and Kirkwood's (1981) notations (see Table 3)

However, a linear relationship between survival and an environmental variable can be built into the model (Clobert and Lebreton, in prep.), in the way used by North and Morgan (1979) in a model based on recoveries.

3.3 Coot (*Fulica atra*)

The quality of the results in the previous examples may be attributed to a high recapture rate (see \hat{p}_i in Tables 2 and 4). Data on Coots in the Dombes area (France) (Table 6, Cordonnier, unpubl.) have been obtained with a much lower recapture probability. The model (p, s_t) is preferable to the model (p, s) for females, but both models are acceptable for males (Table 7). This probably results from fewer data being available for males (Table 6). The comparison between males and females is thus based on model (p, s_t) . The χ^2 used in the likelihood ratio test is the difference between the likelihood of the sum of the data (1170.77) and the likelihoods obtained separately for males (420.99) and females (745.66) (last column of Table 7). The number of degrees of freedom (5) results from the number of constraints in the null hypothesis $(p(\delta) = p(\varphi); s_i(\delta) = s_i(\varphi), i = 1, \dots, 4)$. No significant difference exists between males and females ($\chi^2 = 1170.77 - 420.99 - 745.66 = 4.32 < \chi^2_{5(0.95)} = 11.1$).

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Once again, variation in survival ($\hat{s}_1 = 0.53$, $\hat{s}_2 = 0.32$, $\hat{s}_3 = 0.30$, $\hat{s}_4 = 0.57$) seems related to winter weather conditions (very cold periods during winters 1978 and 1979 i.e. years 2 and 3; Cordonnier, pers. comm.).

Table 6
Recapture data for Coots (Cordonnier, unpubl.)
Same notations as in Table 3

Year	i	Males						Females					
		b_i	a_i	c_i	\hat{s}_i	\hat{p}_i	$\hat{\sigma}(\hat{s}_i)$	b_i	a_i	c_i	\hat{s}_i	\hat{p}_i	$\hat{\sigma}(\hat{s}_i)$
1977	1	101	12	84	0.52	0.23	0.197	196	21	165	0.77	0.14	0.242
1978	2	126	19	121	0.27	0.40	0.107	278	25	276	0.23	0.25	0.076
1979	3	86	11	94	0.24	0.35	0.101	180	20	183	0.36	0.20	0.110
1980	4	112	21	105	-	-	-	190	36	184	-	-	-

Table 7
*Likelihood ratio tests between recapture models
on the Coot data of Table 6*

Sex	Model(*)	-2Ln L	Conclusion of the test	Comparison of males and females using model (p, s_t) ; results of this model
Males	(p_t, s_t)	420.08	model (p, s_t)	$H_0 : s_i(\delta) = s_i(\varphi) \quad (i=1, \dots, 4)$ $p(\delta) = p(\varphi)$ $\chi^2 = 1170.77 - 745.46 - 420.99 = 4.32 < \chi^2_{5(0.05)} = 11.1$
	(p, s_t)	420.99	and (p, s)	
	(p, s)	424.73	both acceptable	
Females	(p_t, s_t)	744.08	model (p, s_t)	H_0 accepted
	(p, s_t)	745.46	selected	
	(p, s)	757.54		
Total	(p, s_t)	1170.77		\hat{s}_i 0.53 0.32 0.30 0.57 $\hat{p} = 0.23$
				$\tilde{\sigma}(\hat{s}_i)$ 0.094 0.052 0.048 0.103 $\tilde{\sigma}(\hat{p}) = 0.036$

(*) In Sandland's and Kirkwood's (1981) notations (see Table 3)

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4. COMPARISON BETWEEN RECAPTURE MODELS: SWALLOW (*HIRUNDO RUSTICA*)

Coquillart (1981) estimated survival rates from data collected on Swallows in two different areas near Lyon (France) (Table 8), using four different models:

- a Chapman-Robson (1960) model, modified to take account of unequal numbers of birds ringed each year. This model is used with recaptures of 1981 only since it is a transversal model (i.e. it uses captures of animals of various ages done in a same year);
- the Jolly-Seber model (see e.g. Seber, 1973);
- the (p_t, s_t) model;
- the (p, s) model, when accepted.

The results are summarised (Table 9) as a 95% confidence interval for the average survival (the calculated variance takes account of the covariances between the \hat{s}_i). The modified Chapman-Robson and the Jolly-Seber models give very poor results: the former uses only part of the data (the recaptures made in the same year), while the latter has numerous parameters without direct interest in our case (recruitment rates, population sizes). The (p_t, s_t) and (p, s) models, because they are designed to estimate survival only, have a better precision, especially striking in area 2 where there are fewer data (Table 8).

The survival obtained in area 1, ($\hat{s} = 0.480$; $\tilde{\sigma}(\hat{s}) = 0.054$) in 3 years, matches favourably the age-dependent survivals (0.33 for birds in their second year of life; 0.57 thereafter; standard deviations 0.052 and 0.061 respectively) calculated from 365 recoveries of Swallows ringed all over France for 18 years (from Table 2 of Hemery *et al.*, 1979).

5. DISCUSSION

The advantages of the models based on recapture histories over other more general recapture models to estimate survival rates are obvious (Table 9). The recapture histories give a better precision since they provide information entirely restricted to survival and recapture probabilities.

In survival studies, population size as it appears in classical models such as the Jolly-Seber model can even be considered as a nuisance parameter. An even greater parsimony can be achieved by selecting an adequate model using likelihood ratio

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Table 8
Recapture data for Swallows (Coquillart, 1981)
Same notations as in Table 3

Year i	Area 1 (Forez)						Area 2 (Pilat)					
	b_i	a_i	c_i	\hat{s}_i	\hat{p}_i	$\hat{\sigma}(\hat{s}_i)$	b_i	a_i	c_i	\hat{s}_i	\hat{p}_i	$\hat{\sigma}(\hat{s}_i)$
1979 1	281	70	187	0.46	0.54	0.047	46	16	29	0.39	0.89	0.075
1980 2	351	178	254	0.50	0.75	0.041	40	27	27	0.63	0.79	0.024
1981 3	655	193	653	-	-	-	88	40	78	-	-	-

Table 9
*Estimates of survival rates on Swallow data of Table 8 using
four different recapture models (from Coquillart, 1981, modified)*

Model	Area 1 (Forez)		Area 2 (Pilat)	
	Av. survival	95% confidence interval	Av. survival	95% confidence interval
CHAPMAN-ROBSON	0.529	0.417-0.624	0.727	0.437-1.018
JOLLY-SEBER	0.588	0.510-0.666	0.505	0.049-1.058
(p_t , s_t)	0.480	0.426-0.534	0.508	0.385-0.631
(p , s)	model rejected		0.470	0.368-0.572

tests. However, as usual with this kind of model (see North and Cormack, 1981), information on the biology of the population studied and on the experimental design is of primary importance to choose an adequate model when tests are not powerful because of the scarcity of data (see the examples of the Swallow, area 2, in Table 9, or male Coots in Table 7). Although we chose to put the emphasis on likelihood ratio tests, goodness-of-fit tests would also be very useful.

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Time-dependence in survival is in particular easily assessed, a result of great biological interest. It is especially striking in the data analysed that survival appears constant over years precisely in the species with the higher survival, the Fulmar.

With a reasonable capture effort, it is possible - as demonstrated in the applications above - to obtain within a few years as good a precision in survival as in long-term studies using recoveries. The estimates obtained are valid for a clearly defined population, that breeding in the study area, which is not the case in large-scale recovery studies. Moreover, with proper experimental planning, many other phenomena can be studied on such a local scale (breeding success; local movements; influence of age on breeding biology...). At the same time, some hypotheses could be more easily met or at least tested in such conditions. This is particularly the case of the homogeneity hypothesis which leads to the multinomial distributions used, and to which the estimates could be very sensitive (Buckland, 1982a). Commenting on shortcomings of recovery analyses, Lakhani and Newton (1983) wrote: 'if the usual recovery data can be supplemented by additional and independent information about one of the required parameters, the range of possible estimates can be greatly narrowed.' Obviously, survival estimates arising from local studies of the type presented here could be a most valuable source of information in this respect. One can even imagine mixed models using simultaneously sightings/recaptures of live animals and recoveries (see Buckland, 1980).

We thus advocate the use of Cormack's (1964) model and of its recent developments (Sandland and Kirkwood, 1981; Clobert, 1981) (a FORTRAN program is available from the latter). Since its publication in 1964 Cormack's method has obviously not been used as much as it should have been. We hope that the account and applications given here will encourage its use as well as the development of more specific models (Lebreton, 1981; Harris, 1983) and tests of hypotheses.

ACKNOWLEDGEMENTS

We thank P. Cordonnier, who kindly made available the Coot data, P. Berthet, G. Gerard and the editors who criticized earlier versions of this text, and R. Berton, who helped with the English translation.

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STATISTICAL APPENDIX

The data may be presented as dichotomous trees of recapture histories which are mutually exclusive events (Fig. 2). In the upper recapture tree of Fig. 2 (3 years of recapture) two probabilities are given as examples:

- (1) the probability of surviving and being captured each year:

$$\theta_{1,1} = s_1 p_1 s_2 p_2 s_3 p_3$$

- (2) the probability of surviving each year, and of being captured only the last year:

$$\theta_{1,7} = s_1(1-p_1) s_2(1-p_2) s_3 p_3.$$

The probability of never being captured after the initial capture is more complex and is obtained as a difference. For the upper recapture tree of Fig. 2, this probability is

$$\theta_{1,8} = 1 - s_1 + s_1(1-p_1)(1-s_2) + s_1(1-p_1)s_2(1-p_2)(1-s_3) + s_1(1-p_1)s_2(1-p_2)s_3(1-p_3)$$

Under the hypothesis of independence between individuals, the numbers in the various recapture histories of a recapture tree follow a multinomial distribution. For n years of recapture, the likelihood is the product of n multinomial distributions with respectively $2^n, \dots, 2^{n-i}, \dots, 2$ recapture histories:

$$L = \left[\begin{array}{ccc} n & 2^{n-i+1} & n \\ \pi & \pi & \theta_{i,j} \\ i=1 & j=1 & \end{array} \right]$$

s_i , p_i , and $(1-p_i)$ occur in several $\theta_{i,j}$ and can thus be grouped with their related exponent. The new exponents obtained by grouping lead to define a_i , v_i and c_i (see text and Table 1). In this way, the likelihood is made more compact:

$$L = \prod_{i=1}^n s_i^{v_i} p_i^{a_i} (1-p_i)^{v_i-a_i} \left[\prod_{k=i-1}^n \left(\prod_{j=i}^k \frac{(1-p_j)s_j}{\pi} \right) (1-s_{k+1}) \right]^{c_i}$$

with $\prod_{j=i}^k (1-p_j)s_j = 1$ when $k < i$

and $s_{n+1} = 0$.

The last term of this likelihood is the probability of never being seen after year i (whatever the year of first capture). The maximization of this likelihood leads to Cormack's (1964) estimates. When constraints of equality between parameters are applied, numerical methods are required to get maximum likelihood estimates. To be able to get estimates of variances and covariances of the parameters, we applied the Fletcher (1970) method (routine VA09AD of the Harwell library) to the log-likelihood.

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This method requires the first order derivatives which are:

$$\frac{\partial \ln L}{\partial s_i} = \frac{v_i}{s_i} - \sum_{v=1}^i c_v \left[\prod_{w=v}^{i-1} \pi_w (1-p_w) s_w \right] \frac{\sum_{k=v}^{n-i+v} \left[\prod_{z=v}^{k+i-v} \pi_z (1-p_z) s_z \right] / s_i}{\sum_{k=v-1}^n \left[\prod_{z=v}^k \pi_z (1-p_z) s_z \right] (1-s_{k+1})} (1-s_{k+i-v+1})$$

$$\frac{\partial \ln L}{\partial p_i} = \frac{a_i}{p_i} - \frac{(v_i - a_i)}{1-p_i} - \sum_{v=1}^i c_v \left[\prod_{k=v}^{n-i+v} \left(\prod_{z=v}^{k+i-v} \pi_z (1-p_z) s_z \right) / (1-p_i) \right] (1-s_{k+i-v+1})$$

with $\prod_{w=v}^{i-1} \pi_w (1-p_w) s_w = 1$ for $v > i-1$

$\prod_{z=v}^k \pi_z (1-p_z) s_z = 1$ for $v > k$

and $s_{n+1} = 0$.

Derivatives of parameters under constraints of equality are obtained as sums of derivates, e.g. if $s = s_i$, for all i ,

$$\frac{\partial \ln L}{\partial s} = \sum_i \frac{\partial \ln L}{\partial s_i}$$

The Fletcher method converges very rapidly, especially when an approximation of the second-order derivatives at the starting point is provided. We did not meet problems of local optima. The method provides an estimate of the second-order derivatives F calculated at the convergence point. According to standard maximum likelihood theory, $-F^{-1}$ is an estimate of the asymptotic variance-covariance matrix of the parameters, which compares favourably with the explicit estimates provided by Cormack (1964) for the model without constraints (see two last columns of Table 2).

MAXIMUM LIKELIHOOD METHODS FOR INVESTIGATING REPORTING RATES OF RINGS ON HUNTER-SHOT BIRDS

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SUMMARY

It is well known that hunters do not report 100% of the rings that they find on shot birds. Reward studies can be used to estimate what this reporting rate is, by comparison of recoveries of rings offering a monetary reward, to ordinary rings. A reward study of American Black Ducks (*Anas rubripes*) is used to illustrate the design, and to motivate the development of statistical models for estimation and for testing hypotheses of temporal and geographic variation in reporting rates. The method involves indexing the data (recoveries) and parameters (reporting, harvest, and solicitation rates) by geographic and temporal strata. Estimates are obtained under unconstrained (e.g., allowing temporal variability in reporting rates) and constrained (e.g., constant reporting rates) models, and hypotheses are tested by likelihood ratio. A FORTRAN program, available from the author, is used to perform the computations.

Keywords: BANDINGS; MAXIMUM LIKELIHOOD; RECOVERIES; REPORTING RATES; RINGINGS.

1. INTRODUCTION

Ring recoveries are an important source of data for estimating population characteristics such as survival rates and distribution patterns of birds. For North American migratory game birds, hunter reports of rings on birds shot during the hunting season represent the majority of ring recoveries. It has been known for years that not all rings on shot and retrieved birds are reported by hunters (Bellrose, 1945, 1955; Geis and Atwood, 1961; Martinson, 1966; Martinson and McCann, 1966). Thus, ring recovery rates underestimate the proportion of ringed birds which are shot and retrieved by hunters ('harvest rate'). Reward studies, in which the finder of a ring is given a reward (usually \$10-20, but sometimes non-monetary) have been used to estimate the proportion of regular rings on harvested

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birds that is reported (Bellrose, 1955; Henny and Burnham, 1976; Tomlinson, 1968; Reeves, 1979; Conroy and Blandin, 1984). In addition to estimating reporting rates, reward studies may be useful for investigating geographic or temporal variation in these rates. Such variability may itself be of interest to investigators, who may wish to consider means by which the reporting rate (often <40% in the United States) of rings may be increased. More frequently, investigators will wish to consider the possibility that variations in reporting rates will affect statistical inferences made from ring recovery data. The purpose of this paper is to describe maximum likelihood methods for estimating ring reporting rates from a reward study, and for investigating variability in these rates.

2. DEFINITIONS AND NOTATION

In a reward study, birds are divided into 2 groups at the time of ringing: those (N) to which standard (e.g., USFWS aluminium) rings are applied to one leg, and those (N') to which standard rings are applied to one leg and reward rings are applied to the other. Standard rings are applied to the reward-ringed birds for consistency with the numerical sequencing of all bird rings, and as a check on the veracity of ring reports. Reports of rings in general, and of reward rings, are made to the USFWS Bird Banding Laboratory (BBL) and are entered in computer files. Recoveries of rings are often classified as to the year of recovery, those recovered in the first hunting season following the ringing period being termed 'direct' recoveries, and those in all subsequent seasons being termed 'indirect' recoveries. Initially, only direct recoveries of the N standard and N' reward rings will be considered. Following Henny and Burnham (1976) recoveries of standard rings fall into two categories: those which are reported voluntarily by hunters, and those which are obtained from hunters at the request of conservation authorities. Requests are usually made during the course of bag or licence checks by conservation authorities, and typically the hunter will give the ring or its number to the authority, who will then submit it to the BBL. It is assumed that the latter type of recoveries of standard rings, and all recoveries of reward rings, are reported with probability 1 by the finder. The effects of violating these two assumptions were discussed by Conroy and Williams (1981), who concluded that the latter assumption was likely violated, with resulting bias in the reporting rate estimate.

The data for the simplest type of reward study, where only one population of ringings and recoveries is considered, are

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R_h , the number of direct hunter-reported recoveries of standard rings ;
 R_s , the number of direct solicited recoveries of standard rings ;
 R' , the number of direct recoveries of reward rings ;
 N , the number of standard rings applied ;
 N' , the number of reward rings applied .

The parameters used to describe the probabilities of the R_h , R_s , and R' recoveries occurring are

H , the probability that a ringed bird is shot and retrieved by a hunter (harvest rate) ;
 γ , the probability that a ring on a harvested bird is reported due to solicitation efforts (solicitation rate) ;
 λ , the probability that a ring on a harvested bird is reported voluntarily, given that it is not solicited (reporting rate).

In the subsequent consideration of variability in reporting rates, the data (R_h, R_s, R') and parameters (λ, γ, H) will be subscripted to correspond to temporal or geographic strata.

3. GENERAL APPROACH

The data for all of these models consist of N standard-ringed birds and recoveries of two types: hunter reported (R_h) and solicited (R_s); and N' reward-ringed birds and R' reward recoveries. The N and N' ringings can be indexed N_i , N'_i where $i = 1, \dots, I$ may refer to ringing locations, years, etc. The R_h , R_s and R' recoveries can be indexed as R_{hij} , R_{sij} , R_{ij}' where $i = 1, \dots, I$ again may refer to ringing locations or years and $j = 1, \dots, J$ to recovery locations or years. For the present, assign the three types of recovery R_h , R_s , and R' probabilities: π_h , π_s , and π' , recognising that each of the types of recoveries (R_h , R_s and R') and corresponding probabilities may in fact consist of a number of recoveries stratified in time and space. If we make standard assumptions of randomness and independence (cf. Brownie *et al.*, 1978; Pollock and Kavelling, 1982) then the joint probability function of R_h , R_s , R' is

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$$\text{Prob } \{R_h, R_s, R'\} = \binom{N}{R_h, R_s} (\pi_h)^{R_h} (\pi_s)^{R_s} \\ \times (1 - \pi_h - \pi_s)^{(N - R_h - R_s)} \binom{N'}{R'} \pi'^{R'} (1 - \pi')^{(N' - R')} \quad (3.1)$$

which is the product of independent multinomial distributions. If π_h , π_s , and π' are defined as functions of a vector of parameters (e.g., $\pi_h(\theta) = \lambda(1-\gamma)H$, $\pi_s(\theta) = \gamma H$; $\pi'(\theta) = H$, $\theta = [\lambda, \gamma, H]$) then a likelihood function $L(\theta)$ can be written and maximum likelihood estimates (MLEs) for θ obtained. This is exactly the methodology employed by Brownie *et al.* (1978) to estimate survival and recovery rates from ring-recovery data.

Under unconstrained hypotheses (H_a), maximum likelihood estimators can be obtained by the method of moments (Davidson and Solomon, 1974), in which the minimum sufficient statistics (MSS), R_h , R_s , and R' , are equated to their expectations, $N\lambda(1-\gamma)H$, $N\gamma H$, and $N'H$. Under constrained hypotheses (H_0) the number of parameters is less than that of the minimum sufficient statistics, and numerical solution of the likelihood equations is required. The approach in this paper is to index the data and parameters by categories under the alternative hypothesis (e.g., temporal variability), and to obtain MLEs under H_a . The parameter space is then constrained under H_0 , MLEs are obtained by the method of scoring (Kale, 1962; Rao, 1965, pp.302-309), and H_0 is tested by a likelihood ratio statistic

$$T = -2[L(\hat{\theta}_0) - L(\hat{\theta}_a)] \quad (3.2)$$

where $L(\hat{\theta})$ is the log of the likelihood function evaluated at the MLEs under each hypothesis and T is asymptotically distributed as χ^2 with df equal to the difference between the number of parameters in H_0 , and H_a . If H_0 is rejected and the number of degrees of freedom is greater than 1, it may be of interest to perform paired z tests, e.g.:

$$z = \frac{\hat{\lambda}_i - \hat{\lambda}_j}{\sqrt{\text{var}(\hat{\lambda}_i - \hat{\lambda}_j)}} \quad (3.3)$$

The standard normal statistic is used here, because the estimated variances are based on asymptotic theory, as are the likelihood ratio tests described above. Because the denominator of (3.3) may include non-zero covariance terms, and because of the diversity of model forms to be considered, (3.3) is potentially complex. As will be

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described later, a computer algorithm for testing general linear hypotheses about θ simplifies this problem and makes algebraic expressions for covariances unnecessary.

It will be seen that for most of the fully-parameterized models, goodness-of-fit is not an issue, because the number of parameters equals the number of cells in the data set. For example, if the R_h , R_s , and R' are dimensioned by years ($i = 1, \dots, I$), then the data consist of $3I$ cells, and there are $3I$ parameters to be estimated ($\lambda_i, H_i, \gamma_i, i = 1, \dots, I$). On the other hand, for certain data structures, and for reduced parameter models, it is advisable to compute goodness-of-fit statistics. A commonly used procedure is the chi-square goodness-of-fit test (made on appropriate degrees of freedom):

$$\chi^2 = \sum_i^I \left\{ \frac{[R_{hi} - E(R_{hi})]^2}{E(R_{hi})} + \frac{[R_{si} - E(R_{si})]^2}{E(R_{si})} + \frac{[R_i' - E(R_i')]^2}{E(R_i')} \right\}$$

$$\text{where } E(R_{hi}) = N_i \pi_{hi} (\hat{\theta})$$

$$E(R_{si}) = N_i \pi_{si} (\hat{\theta})$$

$$E(R_i') = N_i' \pi_i' (\hat{\theta}) ,$$

and $\pi_i(\hat{\theta})$ denotes the respective cell probabilities evaluated at the parameter estimates, and I denotes the total number of cells (i.e., categories) of recoveries.

4. CASE STUDY: ANALYSIS OF RING REPORTING RATES FOR AMERICAN BLACK DUCKS

Conroy and Blandin (in press) used the general procedure outlined above to analyse reporting rates of rings applied to American Black Ducks (*Anas rubripes*). Black Ducks primarily breed in Canada and the northeast United States, and migrate to wintering areas along the Atlantic coast of the United States (Atlantic Flyway, cf. Lincoln, 1935) and along the Mississippi and Ohio Rivers (Mississippi Flyway) during September and November. During migration, birds are subject to hunting in both countries, and hunting continues in the southern United States until mid-February. Thus, the period during which most rings are recovered is September to February, and in the analyses to follow, only hunting season recoveries of rings are considered.

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A total of 51,098 birds was ringed between 1978 and 1980, 43,078 with standard USFWS rings only, and 8,020 with standard USFWS rings plus reward rings. Birds were ringed at 252 sites in the United States and Canada, during two periods: July-September (prior to the hunting season, or "preseason") and December-February (after the hunting season, or "postseason"). The objectives of this reward experiment were first, to estimate overall reporting rates of rings on Black Ducks, and second, to investigate geographic and temporal variability in reporting rates occurring over the course of the study. The conclusions of this study are reported in detail in Conroy and Blandin (1984), but several representative data examples are presented here to enable motivation of specific statistical models.

4.1 No Stratification of Recoveries

This section is primarily provided to familiarise readers with the general approach, and to motivate the analyses to follow. In this case the data consist of R_h and R_s direct recoveries of N control-ringed birds, and R' direct recoveries of N' reward-ringed birds. The data for Black Ducks ringed in Canada during the pre-season, 1978, are used to illustrate this model (Table 1). Because these data are

Table 1

*Estimates of reporting, solicitation and harvest rates for American Black Ducks ringed in Canada during the preseason period, 1978
(no stratification of recoveries)*

	Rates					
	Reporting		Solicitation		Harvest	
Standard rings ($N = 5765$)	$\hat{\lambda}$	\hat{SE}	$\hat{\gamma}$	\hat{SE}	\hat{H}	\hat{SE}
Hunter reports (R_h) 409*	0.38	0.04	0.12	0.01	0.21	0.02
Solicited (R_s) 151						
 <u>Reward plus standard rings ($N' = 712$)</u>						
Reward reports R' 150						

*All recoveries are direct (1st year) recoveries

not stratified, either spatially or temporally, there are just three observations: the numbers of hunter-reported standard rings (R_h), solicited standard rings (R_s), and hunter-reward rings (R'). These three types of ring recoveries have expectations

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$$E[R_h] = N\lambda(1-\gamma)H ,$$

$$E[R_s] = NyH ,$$

$$E[R'] = N'H ,$$

where λ , γ , and H are respectively the reporting, solicitation, and harvest rates. The MSS for this parameterisation are R_h , R_s , and R' ; setting these equal to their expectations we obtain

$$H = R'/N' \quad (4.1.1)$$

$$\hat{\gamma} = \frac{R_s}{\hat{H}N} = \frac{R_s}{N} \frac{N'}{R'} , \quad (4.1.2)$$

$$\hat{\lambda} = \frac{R_h/N}{\hat{H}(1-\hat{\gamma})} = \frac{R_h/N}{R'/N' - R_s/N} . \quad (4.1.3)$$

Variance estimators of \hat{H} , $\hat{\gamma}$, and $\hat{\lambda}$ are presented in Appendix 1. These expressions were used to estimate λ , γ , and H for Black Ducks ringed in Canada during 1978 (Table 1). This analysis suggests that reporting rates of standard rings by hunters were approximately 0.38 ($\hat{SE} = 0.04$). Note that for this simple data structure, the number of parameters estimated equals the number of data cells (3), so that there is no need for a test of goodness-of-fit.

4.2 Geographic Variations in Reporting Rates

Henny and Burnham (1976) investigated variations in ring reporting rates for Mallards (*Anas platyrhynchos*) and concluded that reporting rates were subject to geographic variability consisting of two components: differences between major regions (e.g., Flyways, United States and Canada), and a tendency for rings encountered near ringing sites to be reported at a depressed rate. The hypothesis of constant reporting rates by regions or distances from ringing sites can be tested by indexing the data and parameters by geographic locations of the recoveries. A total of 6477 Black Ducks was ringed, 5765 (N) with standard rings only and 712 (N') with standard plus reward rings during the preseason, 1978 in the United States and Canada. The recoveries from these ringed birds were stratified by three major geographic regions: Canada, United States - Atlantic Flyway, and United States - Mississippi Flyway (Table 2). The data in Table 2 correspond to the matrix of expected values:

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<u>Recovery Area</u>	<u>Standard Rings (N)</u>		<u>Reward Rings (N')</u>
	<u>Hunter-Reported</u>	<u>Solicited</u>	
Canada	$N\lambda_1(1-\gamma_1)H_1$	$N\gamma_1 H_1$	$N'H_1$
US-Atlantic	$N\lambda_2(1-\gamma_2)H_2$	$N\gamma_2 H_2$	$N'H_2$
US-Mississippi	$N\lambda_3(1-\gamma_3)H_3$	$N\gamma_3 H_3$	$N'H_3$

The null hypotheses (H_0) of no effect of geographic region on reporting rate is tested by a likelihood ratio test of the above model (H_a) versus a model in which λ_j are constrained to be equal. Under both models, solicitation (γ) and harvest (H) rates are allowed to vary with geographic area.

Table 2

Tests of geographic variability in reporting rates of American Black Ducks ringed in the US and Canada in the preseason period, 1978

N = 5765, N' = 712				Estimates under $H_a: \lambda_j \neq \lambda_k$					
Recovery Area	R _h	R _s	R'	$\hat{\lambda}_j$	SE	$\hat{\gamma}_j$	SE	\hat{H}_j	SE
Canada	189	91	81	0.33	0.05	0.14	0.02	0.11	0.01
US-Atlantic Flyway	195	57	63	0.43	0.07	0.11	0.02	0.09	0.01
US-Mississippi Flyway	25	3	6	0.55	0.26	0.06	0.04	0.01	0.003

	Estimates Under $H_0: \lambda_j = \lambda$				Goodness-of-Fit				
	$\hat{\lambda}$	SE	$\hat{\gamma}_j$	SE	\hat{H}_j	SE	χ^2	df	P
Canada	0.39	0.04	0.15	0.02	0.10	0.01	1.92	2	0.38
US-Atlantic			0.10	0.02	0.10	0.01			
US-Mississippi			0.05	0.03	0.01	0.002			

Test of $H_0: \lambda_j = \lambda$

χ^2	df	P ^a
1.96	2	0.38

^aLikelihood ratio test of $H_0: \lambda_{CANADA} = \lambda_{ATLANTIC} = \lambda_{MISSISSIPPI}$

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Moment-type estimators under H_a are

$$\hat{H}_j = R_j'/N' , \quad (4.2.1)$$

$$\hat{\gamma}_j = (R_{sj}/N)/\hat{H}_j , \quad (4.2.2)$$

$$\hat{\lambda}_j = \frac{(R_{hj}/N)}{\hat{H}_j(1-\hat{\gamma}_j)} , \quad (4.2.3)$$

where $j = 1, \dots, J$ geographic areas under consideration. In the above example $J = 3$ variances for \hat{H}_j , $\hat{\gamma}_j$, and $\hat{\lambda}_j$ are described in Appendix 2. Estimates under H_0 : $\lambda_1 = \lambda_2 = \lambda_3$ cannot be obtained in closed-form, and are obtained by the method of scoring. These estimates, the goodness-of-fit under H_0 , and the test of H_0 versus H_a , are presented in Table 2. The test of $H_0: \lambda_j = \lambda$ was not rejected ($P > 0.10$), and it was concluded that in 1978 there was no evidence of variations in λ among these three regions ($\hat{\lambda} = 0.39$, $SE(\lambda) = 0.04$).

4.3 Temporal Variation in Reporting Rates

Besides testing for geographic variability in ring-reporting rates of Black Ducks, Conroy and Blandin (1984) were also interested in examining temporal variations. Short term variability in ring reporting rate might be expected, perhaps due to the increased prevalence of rings in hunters' bags following an intensive ringing study (cf. Henny and Burnham, 1976). However, if such variability were not pronounced, then we would like to be able to reduce the number of parameters to be estimated, hence increasing the precision of the estimates and the power of other tests. In the Black Duck reward study, two approaches to this problem were taken: in the first, only direct (first year) recoveries were used to test $H_0: \lambda_i = \lambda$ ($i = 1, \dots, I$ years), whereas in the second case all recoveries (direct plus second through K^{th} year) were used to test H_0 . It will be seen that the latter case requires the addition of some parameters which we have not yet considered. Hence, the simple case of direct recoveries only will be considered first.

4.3.1 Direct recoveries

Direct recoveries of Black Ducks ringed in the US and Canada and recovered in

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Canada were examined for 1978-80 (Table 3). Thus, in this model we did not consider geographic variability in λ , H , or γ . In the following, the ringings for each year, and the direct recoveries of these, are subscripted by i to denote calendar year.

R_{hi} , the number of hunter-reported direct recoveries of standard rings in year i ;

R_{si} , the number of solicited direct recoveries of standard rings in year i ;

R_i' , the number of reward direct recoveries in year i ;

N_i , the number of standard rings applied in year i ; and

N_i' , the number of reward rings applied in year i ,

$i = 1, \dots, I$ years of ringing.

Moment-type estimators of H_i , γ_i , and λ_i , are

$$\hat{H}_i = R_i' / N_i' , \quad (4.3.1.1)$$

$$\hat{\gamma}_i = (R_{si} / N_i) / \hat{H}_i , \quad (4.3.1.2)$$

$$\hat{\lambda}_i = \frac{(R_{hi} / N_i)}{\hat{H}_i (1 - \hat{\gamma}_i)} , \quad (4.3.1.3)$$

Variance estimators for $\hat{\lambda}_i$, \hat{H}_i and $\hat{\gamma}_i$ are described in Appendix 3. As before, a test of $H_0: \lambda_i = \lambda$ is obtained by constraining the above parameter space and obtaining estimates for λ , γ_i , and H_i by the method of scoring. These estimates are used with those for H_a in (4.3.1.1-4.3.1.3) and (3.2).

The results for the Black Ducks ringed in Canada during 1978-80 are presented in Table 3. Estimates of λ_i , γ_i and H_i ($i = 1, 2, 3$ years) were obtained under the hypothesis (H_a) allowing temporal variability, and for λ , γ_i , and H_i under $H_0: \lambda_1 = \lambda_2 = \lambda_3 = \lambda$. This null hypothesis was rejected ($P < 0.05$), suggesting that reporting rates were different for at least one year of the study. Reporting rates were further examined by paired z tests, and it was concluded that reporting rates were similar ($P > 0.50$) in 1978 and 1979, but were higher ($P < 0.10$) for 1980 than in each of the previous two years. While this particular data set exhibited temporal variation in reporting over the course of the study, Conroy and Blandin (1984)

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examined several data sets, and concluded that, overall, reporting rates did not vary significantly from 1978-80.

Table 3

Test of temporal variability in reporting rates of American Black Ducks ringed in the US and Canada and recovered in Canada

Year	Ringings		Direct Recoveries			Estimates under H_a						
	N_i	N'_i	R_h	R_s	R'	$\hat{\lambda}_i$	$\hat{S}\hat{E}$	$\hat{\gamma}_i$	$\hat{S}\hat{E}$	\hat{H}_i	$\hat{S}\hat{E}$	
1978	5765	712	189	91	81	0.33	0.05	0.14	0.02	0.11	0.01	
1979	5492	962	176	61	109	0.31	0.04	0.10	0.02	0.11	0.01	
1980	6751	1291	249	61	111	0.48	0.06	0.11	0.02	0.09	0.01	
<u>Estimates under $H_0: \lambda_i = \lambda$</u>						<u>Goodness-of-fit</u>			<u>Test of $H_0: \lambda_i = \lambda^a$</u>			
	$\hat{\lambda}$	$\hat{S}\hat{E}$	$\hat{\gamma}_i$	$\hat{S}\hat{E}$	\hat{H}_i	$\hat{S}\hat{E}$	χ^2	df	P	χ^2	df	P
1978	0.38	0.03	0.15	0.02	0.10	0.01	6.98	2	0.03	7.01	2	0.03
1979			0.11	0.02	0.10	0.01						
1980			0.09	0.01	0.10	0.01						
<u>Contrast^b</u>						$ z $		P				
	$H_0: \lambda_{78} - \lambda_{79} = 0$					0.34		0.73				
	$H_0: \lambda_{78} - \lambda_{80} = 0$					1.94		0.05				
	$H_0: \lambda_{79} - \lambda_{80} = 0$					2.38		0.02				

^aLikelihood ratio test of $H_0: \lambda_i = \lambda$ vs. $H_a: \lambda_i$ unconstrained

^bPaired z tests of reporting rates in different years

4.3.2 Direct (first year) and Indirect (after first-year) Recoveries

In the Black Duck study, we had available recoveries for the period 1978-80 from ringings in each of these years. Thus, birds that had been ringed in 1978 and had survived until the hunting season following the 1979 ringing period, could appear in the 1979 recovery sample. We refer to the recoveries of rings in a hunting season subsequent to that immediately following the ringing period, as "indirect" recoveries. In Table 4 we present the direct and indirect recoveries for male Black Ducks ringed during postseason periods, 1978-80, in eastern Canada. Conroy and Blandin

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Table 4

Test of temporal variability in ring reporting rates of adult male Black Ducks ringed after the hunting season in eastern Canada 1978-80, using direct and indirect recoveries

Ringing Year	N	Recovery Years						
		1978	R _h	1979	1980	1978	R _s	1979
1978	925	20	9	17		16	10	2
1979	694		9	10			7	7
1980	758			23				7

N'

1978	208	11	11	6
1979	150		11	8
1980	150			13

Estimates under H_a: λ_i unconstrained

	λ̂ _i	S.E.	γ̂ _i	S.E.	λ̂ _i	S.E.	λ̂ _i	S.E.
1978	0.62	0.31	0.33	0.13	0.05	0.02	0.78	0.15
1979	0.22	0.08	0.17	0.05	0.07	0.02	0.60	0.14
1980	0.44	0.11	0.12	0.04	0.08	0.02		

Goodness-of-Fit

	X ²	df	P		X ²	df	P
1978	8.09	7	0.32		3.75	.2	0.15

Estimates under H₀: λ_i = λ

	λ̂	S.E.	γ̂ _i	S.E.	λ̂ _i	S.E.	λ̂ _i	S.E.
1978	0.39	0.07	0.25	0.07	0.07	0.01	0.78	0.15
1979			0.24	0.06	0.05	0.01	0.60	0.14
1980			0.11	0.03	0.09	0.02		

Goodness-of-Fit

	X ²	df	P
	9.67	9	0.38

^aLikelihood-ratio test of H₀: λ₁₉₇₈ = λ₁₉₇₉ = λ₁₉₈₀.

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(1984) separated males and females in their analyses because, as will be seen, these analyses require the additional parameters of annual survivorship, which are believed to differ for males and females. Further, we used postseason ringings, because birds in this period had all survived one hunting season, were at least six months old, and could be considered adults for the purposes of a one-age class recovery analysis.

To enable readers to understand these analyses it is useful to compare this data structure and model to those considered by Brownie *et al.* (1978). Brownie *et al.* (1978) describe one-age class models where N_i birds are ringed at each of $i = 1, \dots, I$ years and are recovered during $j = i, \dots, K$ subsequent hunting seasons. These models require the additional parameters S_{ij} ($i = 1, \dots, I - 1$), the probability of survival from year i to year $i + 1$. If all recoveries were of the same type (e.g., reward-ringed), a matrix of expected numbers of these recoveries for $I = K = 3$ would be

Ringing Year	Number Ringed	Recovery Year		
		1	2	3
1	N_1'	$N_1'H_1$	$N_1'S_1H_2$	$N_1'S_1S_2H_3$
2	N_2'		$N_2'H_2$	$N_2'S_2H_3$
3	N_3'			$N_3'H_3$

and the estimators for H_i and S_{ij} would be obtained from the ring-recovery models described by Brownie *et al.* (1978). In a reward study we need to consider three types of recoveries:

R_{hij} , the number of standard-ringed birds in year i that are reported by hunters in year j ;

R_{sij} , the number of standard-ringed birds in year i that are obtained by solicitation in year j ; and

R_{ij}' , the number of reward-ringed birds in year i that are reported in year j .

We may represent the expected numbers of R_{hij} , R_{sij} , and R_{ij}' in the case of $I = K = 3$ as

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Ringing Year	Number Ringed	Numbers of Recoveries					
		Hunted-Reported (Recovery Year)			Solicited (Recovery Year)		
		1	2	3	1	2	3
<u>Standard</u>							
1	N_1	$N_1 f_{h1}$	$N_1 S_1 f_{h2}$	$N_1 S_1 S_2 f_{h3}$	$N_1 f_{s1}$	$N_1 S_1 f_{s2}$	$N_1 S_1 S_2 f_{s3}$
2	N_2		$N_2 f_{h2}$	$N_2 S_2 f_{h3}$		$N_2 f_{s2}$	$N_2 S_2 f_{s3}$
3	N_3			$N_3 f_{h3}$			$N_3 f_{s3}$
<u>Reward</u>							
1	N_1'	$N_1' H_1$	$N_1' S_1' H_2$	$N_1' S_1' S_2' H_3$			
2	N_2'		$N_2' H_2$	$N_2' S_2' H_3$			
3	N_3'			$N_3' H_3$			

where

$f_{hi} = \lambda_i(1 - \gamma_i)H_i$ is the probability that a ringed bird that is alive at the ringing period in year i is harvested (H_i) and reported by a hunter ($\lambda_i(1 - \gamma_i)$) during the subsequent hunting season;

$f_{si} = \gamma_i H_i$ is the probability that a ringed bird that is alive at the ringing period in year i is harvested and reported by solicitation (γ_i) during the subsequent hunting season;

H_i = the probability that a bird that is alive at the ringing period in year i is harvested during the subsequent hunting season;

S_i = is the probability of survival from year i to $i + 1$ for standard-ringed birds;

S_i' = is the probability of survival from year i to $i + 1$ for reward-ringed birds.

Note that the matrix of data (Table 4) corresponds in structure to the above matrix of expected values. Under the fully-parameterised model described above, the moment-type estimators for λ_i , γ_i , H_i , S_i , and S_i' are again obtained by equating the MSS to their expectations. Unlike the previously considered models, the MSS are not immediately obvious from the model structure. Interested readers are referred to Brownie *et al.* (1978, pp.209-212) for a detailed discussion of this problem. The moment-type estimators for the above parameterisation are presented in Appendix 4.

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This model is of little practical value, because of the assumption that $S_i \neq S_i'$ (i.e., that survival rates of reward and control-ringed birds are unequal) which was necessary to obtain a fully parameterised model. For this reason, variance estimators for the parameters are not presented, although these can be obtained by the methods described in Brownie *et al.* (1978). A reduced-parameter model is obtained by imposing the constraint $S_i = S_i'$. Maximum likelihood estimates for this may again be obtained by the method of scoring. To test the hypothesis of temporal constancy in reporting rates, the further constraint of $\lambda_i = \lambda$ is imposed and estimates obtained by the method of scoring.

This methodology was used in conjunction with the data in Table 4 to test the hypothesis that reporting rates did not vary between 1978 and 1980. Reporting (λ_i), solicitation (γ_i), and harvest (H_i) were estimated under the hypothesis (H_0) allowing temporal variability in λ . The test of $H_0: \lambda_i = \lambda$ was not rejected ($P > 0.10$). Both models fit the data ($P > 0.30$), but the failure to reject H_0 suggests that reporting rates were not variable over this period, and can be best described by $\hat{\lambda} = 0.39$ ($\hat{SE} = 0.07$).

4.4 Geographic and Temporal Variation in Reporting Rates

In Conroy and Blandin (1984) we were interested in simultaneously investigating temporal and geographic variability in ring reporting rates. That is, it might be that reporting rates varied temporally in some geographic areas but not in others, or that patterns in geographic variation differed over time. In this example, we considered the relationship between reporting rates and the distance from ringing sites at which rings were recovered. As previously noted, Henny and Burnham (1976) suggested that Mallard reporting rates were depressed in hunting areas close to ringing sites, because of the commonness of ringed birds among those shot. Thus, direct recoveries of Black Ducks ringed during preseason, 1978-80 were stratified by year and by distance of the recovery to the ringing site (Table 5).

For this type of data structure, we considered the three types of direct recoveries (R_h , R_s , and R') and indexed them in two dimensions, as R_{hij} , R_{sij} , and R'_{ij} , for $i = 1, \dots, I$ years and $j = 1, \dots, K$ recovery 'areas' (distance classes). Estimates for H_{ij} , γ_{ij} , and λ_{ij} , the year- and area-specific harvest, solicitation and reporting rates, can be obtained by

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Table 5

Tests of geographical and temporal variability in reporting rates of American Black Ducks ringed in eastern Canada, 1978-80. Direct recoveries stratified by distance from the ringing station

Year	Ringings		R_h			R_s		
	N_i	N_{ij}	0-20 km	21-100 km	>100 km	0-20 km	21-100 km	>100 km
1978	2719	374	111	26	61	65	18	6
1979	2809	599	83	28	64	26	15	15
1980	3113	627	142	29	100	34	19	10

Year	R^t		
	0-20 km	21-100 km	>100 km
1978	41	16	34
1979	46	20	52
1980	47	20	74

Year	(i)	Estimates of reporting rate.							
		0-21 km (1)		21-100 km (2)		>100 km (3)		$\hat{\lambda}_i^b$	$\hat{S}\hat{E}$
1978	(1)	0.48	0.10	0.26	0.09	0.25	0.05	0.34	0.04
1979	(2)	0.44	0.09	0.36	0.12	0.28	0.05	0.35	0.04
1980	(3)	0.71	0.13	0.36	0.12	0.28	0.04	0.42	0.04
	$\hat{\lambda}_j^c$	0.55	0.06	0.33	0.06	0.27	0.03		

Goodness-of-fit				Likelihood ratio tests			
Model	χ^2	df	P	Comparison	χ^2	df	P
H_a	-	0	-	H_t vs. H_a	22.73	6	<0.01
H_t : $\lambda_{ij} = \lambda_i$	22.50	6	<0.01	H_d vs. H_a	4.72	6	0.58
H_d : $\lambda_{ij} = \lambda_j$	4.71	6	0.58	H_o vs. H_a	25.02	8	<0.01
H_o : $\lambda_{ij} = \lambda$	24.57	6	<0.01				

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Table 5 (Cont'd.)

Contrast ^d	z	P
$H_0: \lambda_{0-20} = \lambda_{21-100}$	2.42	0.02
$H_0: \lambda_{0-20} = \lambda_{>100}$	3.91	<0.01
$H_0: \lambda_{21-100} = \lambda_{>100}$	0.76	0.45

^aEstimates of reporting rate under H_a : temporal and geographic variation in λ_{ij}

^bEstimates under H_t : $\lambda_{ij} = \lambda_j$ (temporal variability only)

^cEstimates under H_d : $\lambda_{ij} = \lambda_j$ (geographic variability only)

^dPaired z tests for comparison of reporting rates at differing distances from ringing stations

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$$\hat{H}_{ij} = R_{ij}' / N_i' . \quad (4.4.1)$$

$$\hat{\gamma}_{ij} = (R_{sij}/N_i) / \hat{H}_{ij} \quad (4.4.2)$$

$$\hat{\lambda}_{ij} = (R_{hij}/N_i) / [\hat{H}_{ij}(1-\hat{\gamma}_{ij})] \quad (4.4.3)$$

and their variance estimators are presented in Appendix 5. Again, tests of null hypotheses (e.g., $H_0 : \lambda_{ij} = \lambda_j$, $H_0 : \lambda_{ij} = \lambda_i$) were obtained by application of the method of scoring and (3.2.). Using the data in Table 5, estimates were obtained under the alternative hypothesis (H_a) allowing for both temporal and geographic variability, and under two null hypotheses: $H_t : \lambda_{ij} = \lambda_i$, allowing temporal variability but assuming geographically constant rates, and $H_d : \lambda_{ij} = \lambda_j$, allowing geographic but not temporal variability. The test of H_d vs. H_a was not rejected ($P > 0.50$), whereas the test of H_t vs. H_a was rejected ($P < 0.01$), suggesting that variation in reporting rates was mainly associated with distance of the recovery from ringing sites. However, the paired z tests suggest that reporting rates were higher ($P < 0.05$) close to (0-20 km) ringing sites than farther from (>20 km), which is opposite to the conclusion reached by Henny and Burnham (1976) for Mallards. We have no explanation for these different results, but note (Conroy and Blandin, 1984) that for the majority of data sets examined, no difference due to distance from ringing sites was observed. However, in all cases where such a difference was observed, it was consistent with the results above. Henny and Burnham (1976) suggested that in certain types of analyses, recoveries should be weighted by distance from ringing sites, to reflect the apparent effect of proximity to these sites on reporting rates. Conroy and Williams (1981) caution against the use of weightings in survival analyses of ringing data, and Conroy and Blandin (1984) suggest additional reasons why such weightings may give spurious results for Black Duck ring recoveries.

5. COMPUTING ALGORITHM

An algorithm has been written in FORTRAN for the HP-3000 computer, to perform the computations described above. Briefly, this algorithm numerically maximises the likelihood function for θ as a function of π_h , π_s , π' . The method of scoring can be used for any identifiable parameter space, and is the iterative solution to

$$\hat{\theta}_{i+1} = \hat{\theta}_i + g(\hat{\theta}_i) I^{-1}(\hat{\theta}_i) \quad (5.1)$$

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where $I(\hat{\theta})$ is the Fisher Information Matrix, and can be shown (Appendix 6) to depend only on $\pi_h(\theta)$, $\pi_s(\theta)$, $\pi'(\theta)$ and the first derivatives of these expressions with respect to θ . In practice, moment-type MLEs can be used for fully parameterised models, in which case $I^{-1}(\hat{\theta})$ from the computing algorithm will provide numerical estimates of the variance-covariance matrix. Estimates from a fully parameterised model can be used as starting values (θ_0) in (5.1), in which case convergence to a numerical solution to the likelihood equations follows quickly (usually <5 iterations).

As mentioned earlier, it may be of interest to perform paired z tests on specific contrasts, after rejection of an overall null hypothesis. The algorithm provides a numerical estimate of $I^{-1}(\hat{\theta})$, the variance-covariance matrix under H_A , and allows the user to provide a vector of coefficients for a contrast. The null hypothesis is expressed as $H_0: \sum_{i=1}^P c_i \theta_i = 0$, and is tested by

$$z = \frac{\sum_{i=1}^P c_i \hat{\theta}_i}{\sqrt{\sum_{i=1}^P \sum_{j=1}^P c_i c_j V_{ij}(\hat{\theta})}} \quad (5.2)$$

where

c_i are the coefficients of the contrast;

$\hat{\theta}_i$ are the estimates under H_A , $i = 1, \dots, P$ parameters;

$V_{ij}(\hat{\theta})$ are the elements of the variance-covariance matrix and are obtained from $I^{-1}(\hat{\theta})$.

Expression (5.2) is asymptotically distributed as Normal (0,1) when H_0 is true.

A documented listing of the FORTRAN program, user instructions, and worked examples are available from the author on request.

ACKNOWLEDGEMENTS

I wish to thank J.E. Hines and F. Fiehrer for their assistance in modifying the FORTRAN program, and R.M. Wilcox for her skillful typing of the manuscripts. J.E. Hines, M.A. Howe, J.D. Nichols and the editors provided many useful comments on earlier drafts.

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APPENDIX 1

Approximate asymptotic variances for the parameter estimates of a reward study - no stratification of recoveries. The parameters of this model are λ , γ , and H , and the moment-type estimators were described in 4.1.1-4.1.3.

The variance of \hat{H} is obtained as a binomial variance

$$\widehat{\text{Var}}(H) = \frac{\hat{H}(1-\hat{H})}{N'}$$

and of $\hat{\gamma}$ and $\hat{\lambda}$ by application of the delta method,

$$\begin{aligned} \widehat{\text{Var}}(\gamma) &\approx \hat{\gamma}^2 \left[\frac{1}{R_s} - \frac{1}{N} + \frac{1}{R'} - \frac{1}{N'} \right] \\ \widehat{\text{Var}}(\lambda) &\approx \hat{\lambda}^2 \left\{ \frac{1}{R_h} - \frac{1}{N} + \left(\frac{\hat{\lambda}}{R_h} \right)^2 \left[\left(\frac{N}{N'} \right)^2 R'^2 \left(\frac{1}{R'} - \frac{1}{N'} \right) \right. \right. \\ &\quad \left. \left. + \left(\frac{1}{R_s} - \frac{1}{N} \right) R_s^2 \right] + \frac{\hat{\lambda}}{N} \frac{R_s}{R_h} \right\} \end{aligned}$$

which, as $N, N' \rightarrow \infty$ ($N > N'$), converges to

$$\widehat{\text{Var}}(\lambda) \approx \hat{\lambda}^2 \left\{ \frac{1}{R_h} + \left(\frac{\hat{\lambda}}{R_h} \right)^2 \left[\left(\frac{N}{N'} \right)^2 R'^2 + R_s \right] \right\} .$$

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APPENDIX 2

Approximate asymptotic variances for λ , H , and γ when recoveries are stratified by the geographic location of recovery.

The parameters of this model are λ_j , γ_j , and H_j ($j = 1, \dots, J$ geographic areas or categories). The moment-type estimators for these parameters were described in 4.2.1.-4.2.3.

Approximate variances for these parameters are obtained as in Appendix 1, except that the data and parameters are indexed by geographic stratum.

$$\widehat{\text{Var}}(H_j) = \frac{\hat{H}_j(1-\hat{H}_j)}{N'}$$

$$\widehat{\text{Var}}(\gamma_j) \approx \hat{\gamma}_j^2 \left[\frac{1}{R_{sj}} - \frac{1}{N} + \frac{1}{R'_j} - \frac{1}{N'} \right]$$

$$\widehat{\text{Var}}(\lambda_j) \approx \lambda_j^2 \left\{ \frac{1}{R_{hj}} + \left(\frac{\hat{\lambda}_j}{R_{hj}} \right)^2 \left[\left(\frac{N}{N'} \right)^2 R'_j + R_{sj} \right] \right\},$$

($j = 1, \dots, J$)

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APPENDIX 3

Approximate asymptotic variances for the parameter estimates of a reward study
 - ringings and recoveries stratified by year.

The parameters of this model are λ_i , γ_i , and H_i , ($i = 1, \dots, I$ years). The moment-type estimators for these parameters were described in 4.3.1.1-4.3.1.3. Again, approximate variances for the parameters are obtained as in Appendix 1-2 but with ringings and recoveries stratified by year.

$$\widehat{\text{Var}}(H_i) = \frac{\widehat{H}_i(1-\widehat{H}_i)}{N_i'}$$

$$\widehat{\text{Var}}(\gamma) \approx \widehat{\gamma}_i^2 \left[\frac{1}{R_{si}} - \frac{1}{N_i} + \frac{1}{R_i'} - \frac{1}{N_i'} \right]$$

$$\widehat{\text{Var}}(\lambda_i) \approx \widehat{\lambda}_i^2 \left\{ \frac{1}{R_{hi}} + \left(\frac{\widehat{\lambda}_i}{R_{hi}} \right)^2 \left[\left(\frac{N_i}{N_i'} \right)^2 R_i' + R_{si} \right] \right\}.$$

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APPENDIX 4

Moment-type estimators for the reward model where both direct and indirect recoveries of standard and reward rings are employed.

The parameters of this model are λ_i , γ_i , H_i , $i = 1, \dots, I$, and s_i , s'_i , $i = 1, \dots, I - 1$. Moment-type estimators of these parameters are:

$$\hat{H}_i = \left(\frac{R_i'}{N_i'} \right) \left(\begin{array}{l} C_i' \\ B_i' \end{array} \right), \quad i = 1, \dots, I$$

$$\hat{\gamma}_i = \left(\frac{R_i}{N_i} \right) \left(\begin{array}{l} C_{si} \\ B_i \end{array} \right) / \hat{H}_i, \quad i = 1, \dots, I$$

$$\hat{\lambda}_i = \left(\frac{R_i}{N_i} \right) \left(\begin{array}{l} C_{hi} \\ B_i \end{array} \right) / [\hat{H}_i(1 - \hat{\gamma}_i)], \quad i = 1, \dots, I$$

$$\hat{s}_i = \left(\frac{R_i}{N_i} \right) \left(1 - \frac{C_i}{B_i} \right) / \left(\frac{R_{i+1}}{N_{i+1}} \right), \quad i = 1, \dots, I - 1$$

$$\hat{s}'_i = \left(\frac{R'_i}{N'_i} \right) \left(1 - \frac{C'_i}{B'_i} \right) / \left(\frac{R'_{i+1}}{N'_{i+1}} \right), \quad i = 1, \dots, I - 1$$

where

$$R_i = \sum_{j=1}^I (R_{hij} + R_{sij})$$

$$C_{hj} = \sum_{i=1}^I R_{hij}$$

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$$C_{sj} = \sum_{i=1}^I R_{sij}$$

$$C_j = C_{hj} + C_{sj}$$

$$B_1 = R_1$$

$$B_i = R_i + B_{i-1} - C_{i-1}, \quad i = 2, \dots, I$$

$$R_i' = \sum_{j=i}^I R_{ij}'$$

$$C_i' = \sum_{j=1}^I R_{ij}'$$

$$B_1' = R_1'$$

$$B_i' = R_i' + B_{i-1}' - C_{i-1}', \quad i = 2, \dots, I$$

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APPENDIX 5

Approximate asymptotic variances for parameter estimates of a reward study. Recoveries are stratified by both years (i) and geographic areas (j); ringings are stratified by year.

The parameters of this model are λ_{ij} , γ_{ij} , H_{ij} , ($i = 1, \dots, I$, $j = 1, \dots, J$) for I years and J geographic areas. The approximate variances of these parameters are obtained by the same methods employed in Appendices 1-3:

$$\widehat{\text{Var}}(H_{ij}) = \hat{H}_{ij}(1-\hat{H}_{ij}) / N_i'$$

$$\widehat{\text{Var}}(\gamma_{ij}) \approx \hat{\gamma}_{ij}^2 \left[\frac{1}{R_{sij}} - \frac{1}{N_i} + \frac{1}{R'_i} - \frac{1}{N'_i} \right]$$

$$\widehat{\text{Var}}(\lambda_{ij}) \approx \hat{\lambda}_{ij}^2 \left\{ \frac{1}{R_{hi,i}} + \left(\frac{\hat{\lambda}_{ij}}{R_{hij}} \right)^2 \left[\left(\frac{N_i}{N'_i} \right)^2 R'_{ij} + R_{sij} \right] \right\}.$$

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APPENDIX 6

Expansion of the likelihood function to obtain MLEs for the case where recoveries are stratified in one dimension.

$$\pi_{hj}(\theta) = \lambda_j(1-\gamma_j)H_j$$

$$\pi_{sj}(\theta) = \gamma_j H_j$$

$$\pi_j(\theta) = H_j$$

and (3.1) is indexed by j so that

$$\begin{aligned} & P[\{R_{hj}, R_{sj}, R_j\}] \\ &= \left(\begin{array}{c} N \\ R_{hj}, R_{sj} \end{array} \right) \prod_{j=1}^J \frac{\pi_{hj}^{R_{hj}} \pi_{sj}^{R_{sj}}}{\left[1 - \sum_{j=1}^J (\pi_{hj} + \pi_{sj}) \right]^{[N - \sum_{j=1}^J (R_{hj} + R_{sj})]} } \\ &\times \left(\begin{array}{c} N \\ R_j' \end{array} \right) \prod_{j=1}^J \frac{\pi_j'^{R_j'}}{\left(1 - \sum_{j=1}^J \pi_j' \right)^{(N' - \sum_{j=1}^J R_j')}} \end{aligned}$$

The MLEs are obtained as the solution to

$$\begin{aligned} g(\theta) &= \sum_{j=1}^J \left[\frac{R_{hj}}{\pi_{hj}} \frac{\partial \pi_{hj}}{\partial \theta} + \frac{R_{sj}}{\pi_{sj}} \frac{\partial \pi_{sj}}{\partial \theta} + \frac{R_j'}{\pi_j'} \frac{\partial \pi_j'}{\partial \theta} \right] \\ &+ \frac{R^* \partial \pi^*}{\pi^* \partial \theta} + \frac{Q \partial \rho}{\rho \partial \theta} = 0 \quad , \end{aligned}$$

where

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$$R^* = N - \sum_{j=1}^J (R_{hj} + R_{sj})$$

$$\pi^* = 1 - \sum_{j=1}^J (\pi_{hj} + \pi_{sj})$$

$$Q = N' - \sum_{j=1}^J R' j$$

$$\rho = 1 - \sum_{j=1}^J \pi' j ,$$

and $\frac{\partial}{\partial \theta_j}$ are the first partial derivatives with respect to the elements of θ .

EXAMPLES OF THE USE OF GLIM
TO ANALYSE CAPTURE-RECAPTURE STUDIES

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SUMMARY

The analysis of capture-recapture data from 7 or fewer samples can be easily carried out using the GLIM computer package. A program is given which enables the user to be guided by the data towards selection of an appropriate model. Five examples are discussed in detail to demonstrate how easy and flexible the analysis is. These show how misleading the estimates from unthinking application of a Jolly-Seber analysis can be.

Keywords: ANIMAL POPULATIONS; CAPTURE-RECAPTURE; GLIM; LOGLINEAR MODELS;
RESIDUAL PLOTS.

1. INTRODUCTION

Ringing is one of the most widespread sources of information about bird populations. It permits individuals to be uniquely identified, so that repeated observations of a single bird can yield information, perhaps on local behaviour, perhaps on large-scale movement. Most ringing studies provide information from a single recovery of a dead bird. In this paper we are on the other hand concerned with more intensive studies of a population of individuals subjected to repeated capture. Capture need not imply physical handling if the identity of the individual can be established with certainty by sight alone, whether by rings or other markings, natural or man-imposed. Although the method of analysis to be described can be adapted to studies in which initial capture and marking are accomplished by a different procedure from subsequent observations, notably studies initiated by ringing nestlings, the examples described in Section 3 are all concerned with multiple recaptures of individuals in the same stage of life.

The basic assumptions are those of the standard Jolly-Seber analysis (see, for

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example, Seber (1982)): that birds do not lose their marks, all behave independently with respect to the sampling procedure, have the same probability of capture in a particular sample and the same probability of surviving to the next sample period (whatever their age and their history of capture) and are not, during any sampling period, absent from a population to which they later return.

The Jolly-Seber method, though both powerful and elegant, has been criticised on various grounds. One set of criticisms attack the results:

- i) for having standard errors that are too large to be of practical value, and which are correlated with the estimated values;
- ii) for permitting nonsensical estimates, such as survival probabilities greater than unity or negative birth rates.

One reason for the large standard errors is the apparent lack of parsimony in the Jolly-Seber method in which simple explicit expressions for parameter estimates are available only if different survival and capture parameters are defined for each sample. The method has always been more general than this (Jolly, 1965) although simplicity is lost in other cases. A very important recent paper by Jolly (1982) goes a long way to overcome this difficulty by developing fairly simple equations for estimates of the parameters in models with constant survival or constant capture probability, together with tests of the constancy of these parameters. The second problem is wholly overcome by modifications of the Jolly-Seber estimators either as developed by Buckland (1980) or as shown later in this paper. See also Clobert *et al.*, (1985)

The other line of criticism attacks the restrictive nature of the assumptions, particularly:

- i) that all individuals are independent with the same capture probability;
- ii) that an individual's behaviour is unaffected by its capture history;
- iii) that there can be no temporary emigration from the study population.

For closed populations, the need for the first and to some extent the second restriction has been removed by various models, with associated methods of estimation, developed by Otis *et al.* (1978), and discussed further in White *et al.* (1982). For open populations progress towards removing these restrictions has been achieved by Pollock (1975, 1981a) using hypergeometric models. No statistical model has yet been proposed which does away with the third assumption: it can be made more realistic by careful definition of the population and design of the sampling program. If temporary emigration occurs and there is no subsidiary estimate of its extent from observations on the movements of the species studied, no capture-recapture estimates will be reliable.

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An alternative approach to the analysis of a closed population was proposed by Fienberg, and later adapted for open populations by Cormack (1979, 1981): the statistical theory underlying the relationship between this adaptation, which is the approach used in this paper, and the classical multinomial approach is discussed by Sandland and Cormack (1984). Since this new method makes many of the same assumptions as the Jolly-Seber method, and yields identical estimates when the same model is chosen, the question may be asked why the biologist should be interested. I offer four reasons:

- i) the method provides statistical tests of some of the assumptions and, within limits, offers the adoption of a suitable model in response to the outcome of the tests;
- ii) it sheds new light on the inter-relationships of some of the assumptions;
- iii) it switches attention back firmly on to the individual animal, and, by so doing, can reveal how particular behaviour (as defined by patterns of capture histories) of one or two individuals can have great influence on the estimates;
- iv) it is readily available to most biologists with access to a mainframe computer, and straightforward to use in an interactive mode which allows the biologist to modify the analysis in the light of what the data reveal.

The method is currently incomplete. No model with constant survival rate is available, and, although estimates of the usual biological parameters are provided, no measure of their variability is given. The method will always remain limited in the number of samples that can be analysed: seven is the limit in the program given in Appendix 2, although an experiment with eight sampling periods has been analysed with some success. The reasons for these limitations should become clear later in the paper.

The aim of the paper is to show by examples exactly how the method works and what insights it provides, to make it available to others and encourage them to use it. The principles of an interactive analysis, and explanation of the symbols adopted in this application of the GLIM computer package, are given in Section 2, while the complete program is listed in Appendix 2. The core of this paper is the detailed case studies in Section 3. Ornithological data have been used where available, but some features of the analysis have not been revealed by any such data so far considered: to see the full flexibility of the approach, the ornithological reader will have to demean himself to look at data on lesser species.

The descriptions concentrate on what the statistical analysis can reveal, and

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the questions it poses to the biologist, rather than on the biological interpretation of each study. Although provisional estimates of population parameters are given at the end of some of the examples, the importance of the approach lies more in its ability to select an acceptable description of the behaviour of the individuals in the population.

2. PRINCIPLES

2.1 The Data

Since we want to focus attention on the individual we require observations on the complete capture history of each individual over the period of study. If the study consists of field samples on 3 occasions there are 8 possible capture histories for each individual.

Occasion			Notation		
1	2	3			
Seen	Seen	Seen	1	1	1
Not seen	Seen	Seen	2	1	1
Seen	Not seen	Seen	1	2	1
Not seen	Not seen	Seen	2	2	1
Seen	Seen	Not seen	1	1	2
Not seen	Seen	Not seen	2	1	2
Seen	Not seen	Not seen	1	2	2
Not seen	Not seen	Not seen	2	2	2

Of course no animals are observed to have the last of these capture histories. Individuals with identical capture histories are behaviourally identical in respect of any aspect of the population study, so that the above records can be condensed into the observed number of animals $n_{ijk\dots}$ with a particular capture history, where there are s suffices, one for each of the s samples taken, each taking the value 1 or 2 according as the animals are or are not seen in that sample.

To facilitate analysis, these should always be listed in the standard order, illustrated above for the three sample study: $n_{111}, n_{211}, n_{121}, n_{221}, n_{112}, n_{212}, n_{122}$. With s samples there are $(2^s - 1)$ possible observable capture histories, a number which gets out of hand rapidly with increasing s . The program is limited to

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a maximum of $s=7$ sample periods, for which study there are 127 possible observable capture histories. Many of these will be unrecorded and this raises some technical problems for the statistical theory and consequently for the interpretation of the analysis.

The data in the examples, given in Tables 1, 3, 6, 9 and 11, are the frequencies of the different possible capture histories in this standard order when read (as the computer reads) by row. Thus in Table 1, with 5 sample periods, there are $31=2^5-1$ possible capture histories (or UNITS). The first 0 represents the fact that no birds were seen in all samples, the 1 following represents the one bird which was seen in all samples except the first, and so on. The first eight units are all frequencies of birds caught in both of the last two samples, their capture histories in the first three samples being in order those listed above for the 3-sample study.

2.2 The Parameters

The nature and the order of the data having been established, the next aspect of the analysis which needs explanation is the interpretation of the parameters used in the GLIM formulation. These are related directly to the classical parameters of capture probabilities, survival rate, birth rate and population size: the exact correspondence is to be found in Appendix 1.

There are four sets of parameters.

- 1 Capture probabilities: P_1, P_2, \dots, P_s for the s sample periods in order, are related to the probabilities p_1, \dots, p_s that a live animal is observed in samples 1, ..., s respectively.

In the classical Jolly-Seber approach it is well known that p_s cannot be estimated if death is occurring, nor can p_1 be estimated in the presence of birth. In the GLIM model P_1 and P_s can always be estimated but estimates of p_1 and p_s can be deduced from these only in the absence respectively of birth and of death.

A model in which each bird has the same probability of being seen on each sampling occasion is obtained by replacing all equivalent parameters by the same one. Thus in a closed population, all of $P_1 \dots P_s$ are replaced by a single PC ; with birth P_1 must remain separate, while $P_2 \dots P(s-1)$ are replaced by PB ; with death P_s remains separate, while $P_1 \dots P(s-1)$ are replaced by PD ; with both birth and death $P_2 \dots P(s-1)$ are replaced by

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PBD while P1 and PS remain separate.

If any of these parameters representing the probability of capture were to be omitted from the model the effect would be that of fixing the probability of capture of an individual in that sample at $\frac{1}{2}$ - most unlikely to be sensible.

- 2 Death rates: D1, D2 ..., D(s-2), are related to the probabilities $\phi_1, \dots, \phi_{s-2}$ that an animal alive in the population at any one sample is still alive in the population at the time of the next sample. Information on ϕ_{s-1} can be retrieved from the final sampling intensity parameter PS only if constant sampling intensity is assumed.

Omission of any death parameter fixes the death rate at zero for the particular period. A negative estimate for any GLIM death parameter indicates a survival rate estimated to be greater than 1. This can occur because of sampling variability, in which case the survival rate can be set equal to 1 by the very simple procedure of omitting the corresponding parameter from the model.

An alternative explanation for out-of-range estimates is that the model has been wrongly formulated - perhaps that individual birds do not have the same probability of being captured in a sample independent of their previous capture history. Evidence for this must be sought elsewhere in the analysis, as described below.

- 3 Birth rates: B2, B3, ..., B(s-1), represent the arrival of new animals in the population between one sample and the next. Information on births between the first and second samples can be retrieved from the parameter P1 only if constant sampling intensity is assumed.

As with the death rates any birth parameter can be set to zero by omitting the parameter from the model. Any parameter whose estimate is negative should be set to zero to bring it within range. The same warning applies about alternative explanations for this phenomenon.

- 4 Interaction parameters: I1, I2, ..., I(s-1), represent the immediate effect that being captured may have on an individual's behaviour in the next sampling period. This is a limited model for trap-independence, in that it is not concerned with effects which last for more than one sampling period and

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also it assumes that the effect is the same for each animal caught in a sample, irrespective of the animal's previous history of capture. However, we are concerned in these analyses only with establishing whether it is safe to proceed with an analysis which assumes that trap-dependence is not serious. It is plausible that any such dependence will have its greatest effect in the immediately succeeding period - what the parameters are designed to discover.

The first and last of these parameters are unidentifiable if birth and death occur, I_1 being identical to B_2 and $I_{(s-1)}$ to $D_{(s-2)}$. This means that in a 3-sample study there is no statistical method of distinguishing between birth and death on the one hand and trap-dependence on the other. A 3-sample study can yield information only if the biologist is willing to assert categorically either that trap-dependence or that demographic change does not exist. With a 4-sample study, only one parameter, I_2 , unequivocally represents trap-dependence: with such limited information, any statistical test has limited power to discover trap-dependence.

We may note in passing that an alternative model has been proposed by Otis *et al.* (1978) in which trap-dependence affects an animal only as a consequence of its first capture. The GLIM parameterisation reveals that the parameters needed to describe such behaviour are identical to $B_2, B_3, \dots, B_{(s-1)}$ respectively so that this type of trap-dependence is completely indistinguishable from birth, unless some further condition is placed on the way in which animals first captured in different samples react to the capture. Different GLIM parameters can be constructed to represent such behaviour.

2.3 The Program

GLIM is a widely available and extremely flexible statistical package for general linear interactive modelling. Its use for capture-recapture models is demonstrated in the next section. The instruction '\$FIT Model' where the Model contains a set of parameters written, using the model for a closed population as example, $P_1+P_2+\dots+P_S$, elicits as response a measure, called the deviance, of the extent to which the Model fails to explain the set of observations, together with the degrees of freedom for assessment of the lack of fit. When a satisfactory model has been established, estimates and residuals can be displayed.

To facilitate the use of the GLIM package to analyse capture-recapture data,

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a program of subsidiary GLIM instructions is given in Appendix 2. Its use should become clear from the examples. It contains several sub-files. One group of these, CR3 to CR7, define the parameters appropriate to a study with the particular number of sample periods designated by the number in the file name. The other, CR1, performs the calculations common to all data sets, and makes available two further routines.

One of these, PLOT, assists assessment of the validity of a chosen model by plotting two graphs. The first of these plots on the vertical axis the residual for each capture history - the difference between the observed number of individuals with a given capture-history (the basic data of the analysis) and the corresponding number predicted by the model, standardised so that the residuals should be roughly normally distributed with the same variance - against the number of occasions on which these individuals were captured, on the horizontal axis. This may reveal evidence of heterogeneity, of some individuals being inherently more catchable than others. If heterogeneity occurs, we would expect too many individuals to be caught only once and too many to be caught either s or $(s-1)$ times - giving positive residuals for these capture histories - and too few to be caught an intermediate number of times. Thus with heterogeneity one expects a plot which is higher at both ends than in the middle. The second plot is a standard plot of these same residuals on Normal probability paper. Particularly with sparse data this is far from the straight line that we might expect well-behaved data to show: instead, as in Example 1, it characteristically takes on a broken stick form, the slope of the line for negative residuals being markedly less than that for positive residuals. The difficulty is that no amount of standardisation can eliminate the facts that:

- a zero observation must have a negative residual;
- when the number expected to have a particular capture history is less than one, only a zero observation has a negative residual;
- when the expected number is much less than one, an observation of 1 is the only plausible observation with a positive residual.

In these circumstances, such observations dominate both the analysis and the plot. The plot will however still reveal marked outliers: capture histories which are highly unexpectedly rare or very common. The help provided by PLOT is however limited. General discussion of the limitations of visual displays for the acceptability of a generalized linear model is given by McCullagh and Nelder (1983). They also list a number of alternative forms of standardised residuals: the one incorporated in this program is due to Haberman (1974), with GLIM formulation given by Defize (1980).

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The other routine, USE, uses the relationships given in Appendix 1 to convert estimates of the GLIM parameters to estimates of the more usual biological parameters: the population size at each sample period, the survival rate between samples, and the number of births or immigrants between samples. These estimates are not valid if either trap dependence or heterogeneity is present. USE is fairly expensive in computer time and should only be implemented when a satisfactory model has been found. Conditions for the validity of the estimates under different models are output along with the table of estimates.

2.4 Model Selection

For all the models described in this paper the deviance from the true model should theoretically approximate to a χ^2 distribution with the stated number of degrees of freedom, provided that the number of individuals expected to have any of the possible capture histories is not too small. With many sets of capture-recapture data this proviso is not satisfied. The more sampling periods there are, the more possible capture histories there are, many of which will have a zero observed count and an extremely small expected count. This places a serious restriction on the number of sample periods that it is worth analysing. Some examples in the next section show a deviance which is far too small for the χ^2 distribution it is supposed to follow. Research into alternative approximations for the deviance of sparse data sets is currently active, but has so far produced no consensus on a practical method. Fortunately there is consensus that the χ^2 approximation for the difference in deviances between two models, one a special case of the other, will be much better satisfied than that for the deviance from a single model. See, for example, McCullagh and Nelder (1983, p.28). Thus having obtained a deviance which suggests that a model with death only is satisfactory, we can fit another model with the birth parameters incorporated and may find significant reduction in the deviance.

There remains the problem of how to test whether any of the formulated models are satisfactory. If the deviance from a model incorporating all the parameters described earlier is significantly larger than the appropriate χ^2 value, we may be sure that some further dependence or heterogeneity of animals remains which renders invalid any of the estimates of standard classical analyses. Experience with data generated to have such heterogeneity or dependence shows that with sparse data we are very unlikely to find such a large χ^2 and there is currently no statistical test for the validity of our model. As will be shown in one example, simulation provides one possible approach, but it cannot be described as highly sensitive. It is only

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for a study with few unobserved capture histories that a realistic chance of discovering heterogeneity by this approach exists. This restricts the number of sample periods that can usefully be included in an analysis.

The chosen model may be misspecified in either of two ways. We may omit terms which should be included, for example by deciding to omit birth parameters $B_2, \dots, B_{(s-1)}$ when birth took place. This gives biased estimates. Or we may include terms which need not have been included, for example by allowing different capture probabilities in different samples. This increases the variability of estimates, and may render us unable to estimate some parameter. In choosing between models it is wise to lean towards inclusion of a doubtful parameter: the rough use of a 10% significance level in the examples is in line with this, but its application should always be guided by biological insight.

3. EXAMPLES

The examples demonstrate the flexibility and ease of use of the GLIM program. In Example 1 the complete record of the main analysis is given in Table 1 exactly as it would appear on the computer terminal while being carried out. Only the lines starting with \$ (the GLIM directive symbol) and the data are entered at the terminal by the analyst, the other lines being the response of the program. Readers interested in using the methods on their own data should carry out the corresponding basic analyses of the other examples. Since the procedure is identical, details are not given in the paper so that attention can be concentrated on those aspects of the results which lead to the choice of further analyses.

This first data set is moderately sparse even with only 5 sample periods: for eight of the thirty-one observable capture histories the expected number of birds having that capture history is less than 0.1; for twenty of them the expected number is less than 1. The problem of assessing whether a model is or is not satisfactory, when the validity of the asymptotic χ^2 distribution is questionable, is revealed by these data. The model selected - one with constant effort - has to be justified on biological grounds, and the crucial nature of this choice for the resulting estimates is shown by repeating the analysis with a different model.

The data in Example 2 are even more sparse so that the reliability of the chosen model is open to question. Despite this sparseness one observation is shown to be extremely unlikely, and the dependence of the interpretation on the reliability of

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that observation can be easily seen by repeating the analysis as if that observation had not been made.

The third example shows how, with less sparse data, the analysis can demonstrate that the usual Jolly-Seber assumptions do not hold, and how easy it is to carry out subsidiary analyses which suggest that the difficulty is caused by temporary emigration. If the difficulty appears to be a consequence of one particular sampling period, the data can easily be reanalysed as if that sample had not taken place.

The fourth set of data arise from a population asserted to be closed. The GLIM analysis selects this model, and reveals the heterogeneity demonstrated by Burnham, who collected and analysed the data. However the GLIM analysis suggests an alternative explanation of the heterogeneity to that proposed by Burnham. Again the data are extremely sparse (30 of the 63 observable capture histories are not observed) so that the χ^2 distribution is inappropriate. The use of Monte Carlo simulation to justify a chosen model is indicated.

The final example considers a set of data used by Blower, Cook and Bishop (1981) to illustrate the Jolly-Seber and other capture-recapture methods. These methods result in many out-of-range estimates. The ease with which the GLIM analysis can obtain the correct maximum likelihood estimates is demonstrated, while the possibility that the out-of-range estimates are caused by a failure of the assumptions is explored.

Example 1. A winter population of Dunnocks (*Prunella modularis*)

The data in Table 1 summarise in the appropriate form observations, described elsewhere in this volume by Cheke (1985), on a population of Dunnocks exploiting a localised abundance of food at a site in Yorkshire during the 1972-73 winter. Records were made on 5 sampling occasions, 7th October, 18th February, 25th February, 17th March and 14th April, 80 different birds being observed. The 31 observed frequencies are the numbers of birds having each of the 31 observable capture histories in the standard order described earlier.

As a demonstration of how easy it is to carry out such an analysis the complete procedure is shown in Table 1, exactly as performed at the computer terminal. Note the use of the repeater symbol: in the \$FIT statements, and the method of changing models by addition or subtraction of terms instead of specifying each model *ab*

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Table 1

*Complete GLIM analysis of Dunnock
(Prunella modularis) data*

```
$ ASSIGN RECAP.GLM FOR007
$ GLIM
GLIM 3.12 (C)1977 ROYAL STATISTICAL SOCIETY, LONDON

$UNITS 31   $DATA R   $READ
 0 1 0 0 0 1 0 1 0 0 0 1 0 0 0 0 14
 1 1 0 2 1 2 1 16 0 2 0 11 2 13 10
$INPUT 7 CR1 CR5 $
*FIT P1+P2+P3+P4+P5 : +D1+D2+D3 : -D1-D2-D3+B2+B3+B4 $
      SCALED
CYCLE  DEVIANCE    DF
 5      25.51       25

      SCALED
CYCLE  DEVIANCE    DF
 5      24.34       22

      SCALED
CYCLE  DEVIANCE    DF
 5      19.89       22

$FIT +D1+D2+D3 : +I2+I3 : P1+PBD+P5+D1+D2+D3+B2+B3+B4 $
      SCALED
CYCLE  DEVIANCE    DF
 5      12.97       19

      SCALED
CYCLE  DEVIANCE    DF
 10     10.18       17

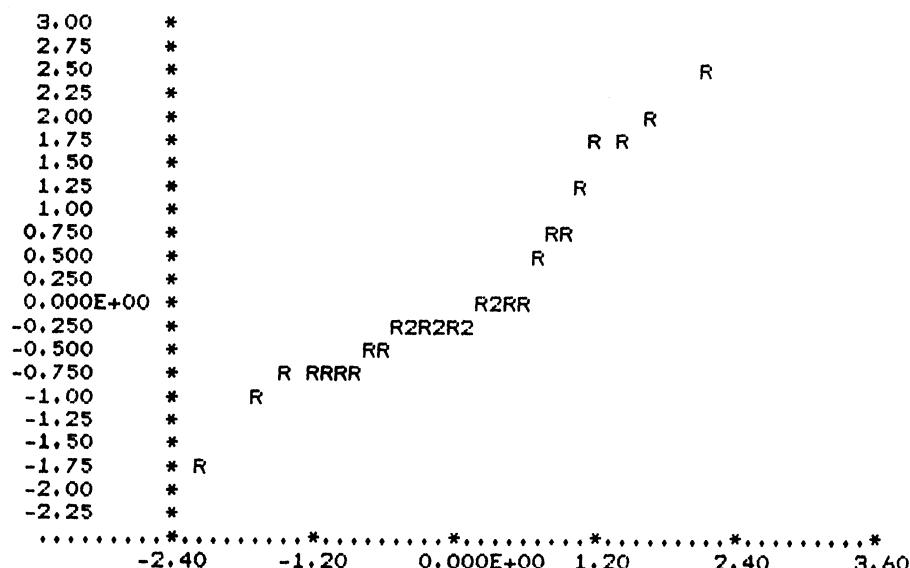
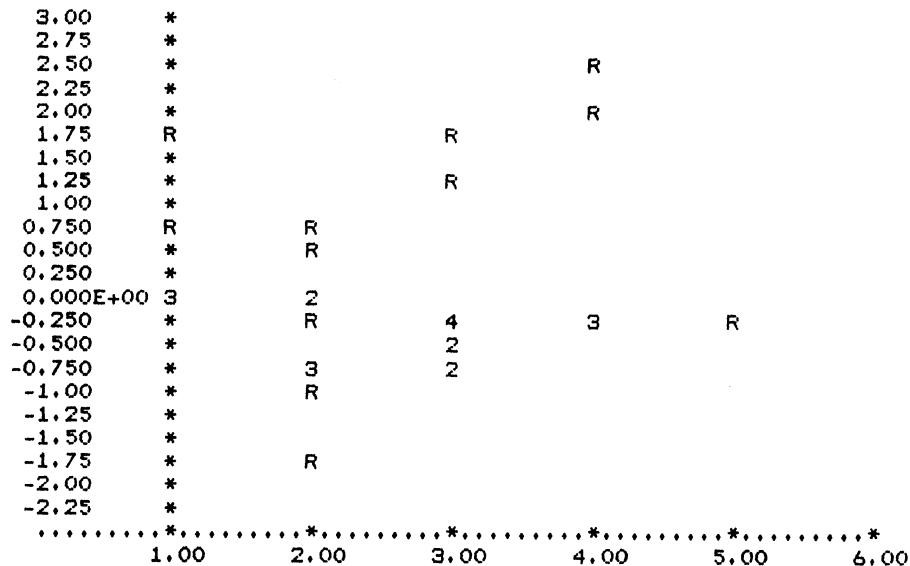
      SCALED
CYCLE  DEVIANCE    DF
 5      14.81       21

$DIS E $
      ESTIMATE    S.E.    PARAMETER
 1    -3.868    0.9379    XGM
 2     1.841    0.5371    P1
 3     0.4890   0.5081    PBD
 4     2.253    0.5757    P5
 5     1.094    0.7005    D1
 6     1.025    0.5901    D2
 7     0.3318   0.5565    D3
 8     0.6579   0.5474    B2
 9     0.8718   0.5901    B3
10     1.669    0.7053    B4
SCALE PARAMETER TAKEN AS    1.000
```

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Table 1 Continued

\$USE PLOT \$



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Table 1 Continued

\$DIS R \$	UNIT	OBSERVED	FITTED	RESIDUAL
	1	0	0.2090E-01	-0.1446
	2	1	0.1317	2.393
	3	0	0.3409E-01	-0.1846
	4	0	0.4147	-0.6440
	5	0	0.3409E-01	-0.1846
	6	1	0.2148	1.694
	7	0	0.5559E-01	-0.2358
	8	1	1.617	-0.4852
	9	0	0.3409E-01	-0.1846
	10	0	0.2148	-0.4634
	11	0	0.5559E-01	-0.2358
	12	1	0.6762	0.3937
	13	0	0.5559E-01	-0.2358
	14	0	0.3502	-0.5918
	15	0	0.9064E-01	-0.3011
	16	14	14.00	0.0000E+00
	17	1	0.1988	1.797
	18	1	1.253	-0.2259
	19	0	0.3243	-0.5694
	20	2	3.945	-0.9792
	21	1	0.3243	1.187
	22	2	2.043	-0.3017E-01
	23	1	0.5288	0.6480
	24	16	15.38	0.1573
	25	0	0.4519	-0.6722
	26	2	2.847	-0.5020
	27	0	0.7369	-0.8584
	28	11	8.964	0.6799
	29	2	2.055	-0.3807E-01
	30	13	12.95	0.1517E-01
	31	10	10.00	0.0000E+00

\$USE USE *

I	N(I)	PHI(I-1)	P(I)	B(I-1)
1	39.46	1.000	0.3801	39.46
2	60.96	0.5567	0.3801	39.00
3	53.41	0.5849	0.3801	17.76
4	69.77	0.8192	0.3801	26.02
5	47.35	0.2502	0.3801	29.90

IF CONSTANT EFFORT THEN ALL ESTIMATES TRUE. OTHERWISE:
 N(1),P(1),B(1) TRUE ONLY IF NO BIRTH IN PERIOD 1
 N(S),P(S) TRUE ONLY IF NO DEATH IN LAST PERIOD
 PHI(S-1) TRUE ONLY IF EFFORT CONSTANT IN (S-1),S
 B(S-1) TRUE ONLY IF N(S),PHI(S-1) BOTH ARE

\$STOP

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initio - the latter is demonstrated for the sixth and final model. The only part of this procedure which may require modification on a different computer is the form of the initial instruction to assign the main program (given in Appendix 2) to an input channel on the computer, channel 7, where the INPUT instruction in GLIM, in line 7 of the Table, makes use of it.

Given the duration of the survey it is likely that death or emigration is occurring, and possible that immigration also is, although genuine birth clearly is not. The first models considered are in turn a closed population, then death only, and then birth only. Despite the fact that these deviances are acceptable values from χ^2 distributions with the indicated degrees of freedom, the fourth model, allowing both birth and death, seems a clear improvement over birth alone although the difference of $19.89 - 12.97 = 6.92$ is significant only at 10% when assessed against a χ^2_3 . Subsequent introduction of trap-dependence seems unnecessary (a χ^2_2 of 2.79). The final model fixes a constant capture probability in each sample, and is quite acceptable (a χ^2_2 of 1.84 compared with the model with unequal capture probability).

Having found an acceptable model, with birth, death and constant capture probability, we ask for a DISplay of the estimates of the GLIM parameters. This checks that no birth or death parameters are out of range: D1, D2, D3, B2, B3, B4 are all positive and PBD is less than either A or E. If the latter condition did not hold then either there would be a negative estimate of birth between the first two samples or of death between the last two samples, or we would have to conclude that the sampling intensity, though constant in the central three samples, was very different in the first or the last.

We then use PLOT to check further on the validity of the chosen model. The plots are typical of moderately sparse data. To examine which capture histories are giving the pattern of the residuals, we DISplay the residuals in order, and observe that the four largest positive residuals are all from single birds with a particular capture history (Units 2,6,17,21). The second, Normal probability, plot, with residuals on the y-axis, gives no suggestion that these positive residuals are larger than would be expected. On the other hand the first plot does give some indication of there being on average too many birds caught once or four times, too few caught twice or three times. The bugbear of heterogeneity casts a slight cloud over our inferences.

Finally USE is invoked to convert the estimates of the GLIM parameters into estimates at each sample of population size N_i , survival rate ϕ_i , capture

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probability p_i , and births/immigrants B_i . We find that the population remains fairly constant in size but with considerable changes in personnel. Thus for example between the second and third sampling periods (18th February and 25th February) only 58.5% of the 61 birds estimated to be present on 18th February remain alive in the population (having neither died nor emigrated) while the population is restored by the arrival of 18 immigrants.

Since a model with constant sampling intensity has been selected, the estimates for the first and last samples are valid provided that the sampling in these periods was effected in the same way as the sampling in the three intervening periods. What has been established is that the capture probabilities in these three periods are not significantly different. The common estimate for these periods is then extrapolated to the first and last periods. There is and can be no statistical evidence for the validity of this extrapolation. The justification, if any, must be given by the biologist. In fact there is no such justification in this case, since the nets were in operation for different lengths of times on the different sampling days - for 3.25, 6.5, 6, 9 and 8 hours respectively. It may not be too surprising that the data were consistent with constant effort on the central three days, and it may be justified to extrapolate that effort to the final sample, but not to the first. The estimates of N_1 and B_1 should therefore be discarded.

To determine whether the estimates which remain available if we do not make the assumption of constant sampling effort remain more or less the same, we may return to the model:

$$P_1 + P_2 + P_3 + P_4 + P_5 + D_1 + D_2 + D_3 + B_2 + B_3 + B_4,$$

fit it to the data, display estimates and residuals, and use the routine USE. The result, in Table 2, shows how critical the assumption of constant effort is in the interpretation of this example. As indicated by the caveats printed with the table, parameters pertaining to the first and last samples can not now be estimated: meaningless values have been scored through in the table. Since the model is now identical with that of Jolly and Seber, the estimates are precisely the same as would have been obtained by their method. We may note that the differences between the estimates of capture probability - successively 0.60, 0.24, 0.53 - do not correspond to the slight changes in the hours of sampling effort - successively 6.5, 6, 9.

The biological interpretation is given by Dr Cheke on pages 13 to 24.

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Table 2

*Estimates of Dunnock (*Prunella modularis*) populations from model with capture probability allowed to vary between samples*

I	N(I)	PHI(I-1)	P(I)	B(I-1)
1	70.00	1.000	0.1667	70.00
2	40.00	0.4444	0.6000	-0.0000E+00
3	79.17	0.7813	0.2400	47.92
4	51.30	0.5455	0.5263	8.118
5	162.0	0.9999	0.1111	110.7

IF CONSTANT EFFORT THEN ALL ESTIMATES TRUE. OTHERWISE:
 N(1),P(1),B(1) TRUE ONLY IF NO BIRTH IN PERIOD 1
 N(S),P(S) TRUE ONLY IF NO DEATH IN LAST PERIOD
 PHI(S-1) TRUE ONLY IF EFFORT CONSTANT IN (S-1),S
 B(S-1) TRUE ONLY IF N(S),PHI(S-1) BOTH ARE

Example 2. Sparrow hawks (*Accipiter nisus*) in Eskdale (Newton, Marquiss and Rothery, 1983)

The recapture data from the Eskdale part of a major long-term study of sparrow-hawks in the South of Scotland have been analysed. Although one of the biologists' main interests was demographic and behavioural differences between the sexes, sex has been ignored in the GLIM analysis reported here. With seven years of observations and a total of 74 different birds observed, the data in Table 3 are already extremely sparse - and would be even sparser if sexes were analysed separately, as they could easily be. Over seven years birth and death must occur so that we would not seriously consider a closed model or models with birth only or with death only. For comparison their deviances are given in Table 4. The analysis rejects these in favour of a model with birth and death, trap-dependence being found to be unnecessary while constant sampling intensity appears unacceptable, the difference between its deviance and that of the model with unequal capture probability being assessed as a χ^2 of 9.0. All estimates are within range.

The deviances can be seen to be ridiculously small, relative to a χ^2 distribution.

One technical point worthy of note is the ability of the program to cope with data for which the classical Jolly-Seber estimate of capture probability p_4 in the fourth sample is exactly 1. Since the GLIM parameter P4 is equal to $\log [(1-p)/p]$

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its estimate ought to be infinity, which might be expected to cause numerical instabilities in the analysis. In the analysis, the estimate of P_4 is obtained as -8.7, which gets converted to an estimate of p_4 of 0.9998.

The use of PLOT and DIS R (not shown here) reveal no evidence of heterogeneity but one gross outlier with a standardised residual of 6.57: the one bird with a capture history 1221211 is far too many! If the model is accepted as applying to all the data, then the estimates of population size and of survival rates - identical with the Jolly-Seber estimates - are as shown in Table 5. One great advantage of GLIM is the ease with which questionable data can be omitted and the analysis repeated to reveal the influence which these data have on the results. A weight vector W is constructed in the program to have value 1 for every capture history. To remove the questionable history, all that is required is \$EDIT 23 W 0. Model selection and estimation can then be repeated. The effect on the estimates is shown in Table 5.

It is therefore important for the biologist to check that that particular record is correct. The pattern of the capture history does not suggest any plausible biological explanation, unlike some of the later examples. Perhaps the initial 1221... suggest temporary emigration after initial capture. However, none of the corresponding histories 21221..., 221221., etc. are represented at all. The statistical analysis draws attention to important questions for the biologist to consider: it cannot by itself answer them.

Table 3
Sparrowhawk (Accipiter nisus) data (in standard order)

0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	9
1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	8	
1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	5	1	1	0	2	0	1	0	7	1	1	1	5	1	8	3			

Capture-recapture samples using GLIM

Table 4

Deviances from possible Sparrowhawk models

Model	Description	d.f.	Deviance
P1+P2+...+P7	Closed	119	102.9
P1+...+P7+B2+...+B6	Birth only	114	85.6
P1+...+P7+D1+...+D5	Death only	114	91.4
P1+...+P7+B2+...+B6+D1+...+D5 as above +I2+...+I5	Birth and death with dependence	109 105	37.9 36.7
P1+PBD+P7+B2+...+B6+D1+...+D5	Constant capture prob.	113	46.9

Table 5

Parameter estimates from Sparrowhawk data

<u>Population size</u>		<u>Survival rates</u>	
	All data		All data
N ₂	31.5	Without outlier	φ ₁ .93
N ₃	29.5	24.3	φ ₂ .53
N ₄	27.0	25.3	φ ₃ .62
N ₅	36.0	26.0	φ ₄ .74
N ₆	36.0	32.4	φ ₅ .67
		37.1	.79
			.50
			.62
			.69
			.71

Example 3. Six-spot burnet moths (*Zygaena filipendula*): Manly and Parr (1968)

The data set in Table 6, of moths sampled on four successive days and a fifth time two days later, is one of the standard sets of data used as illustration, for example, by Seber (1982, p.226). Of the models in Table 7 the most satisfactory is clearly that including birth and death with varying capture probability but without trap dependence - the standard Jolly-Seber model - but, equally clearly, it does not fit the data. The use of the routine PLOT (Table 8) shows there to be an outlier, and the tabulation of the residuals achieved by the instruction \$DIS R shows it to be Unit 3: the 5 moths with capture history 12111 are far too many.

Reanalysis omitting these moths, achieved by \$EDIT 3 W 0, reduces the deviance to a more acceptable value of 23.0 with 18 df. However, \$DIS E shows that the estimate of B4 is now negative. Since a negative birth rate is impossible this

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parameter should be set at zero and the model refitted without it by the instruction \$FIT-B4. \$DIS R now reveals that the largest positive residual is now shown by Unit 7, which has 2 moths with capture history 12211. This pattern, taken in conjunction with the other, eliminated, pattern 12111, gives a very strong indication of temporary emigration after the first sample. Since such emigration completely invalidates all capture-recapture analyses, it seems advisable not to quote any estimates despite the fact that the Normal plot of the remaining residuals after elimination of both these outliers is acceptable as a straight line.

Table 6

Burnet moth (*Zygaena filipendula*) data (in standard order)

1	0	5	1	0	1	2	5	0	4	2	7	4	2	1	19
1	1	0	3	0	2	0	9	9	4	1	13	10	13	21	

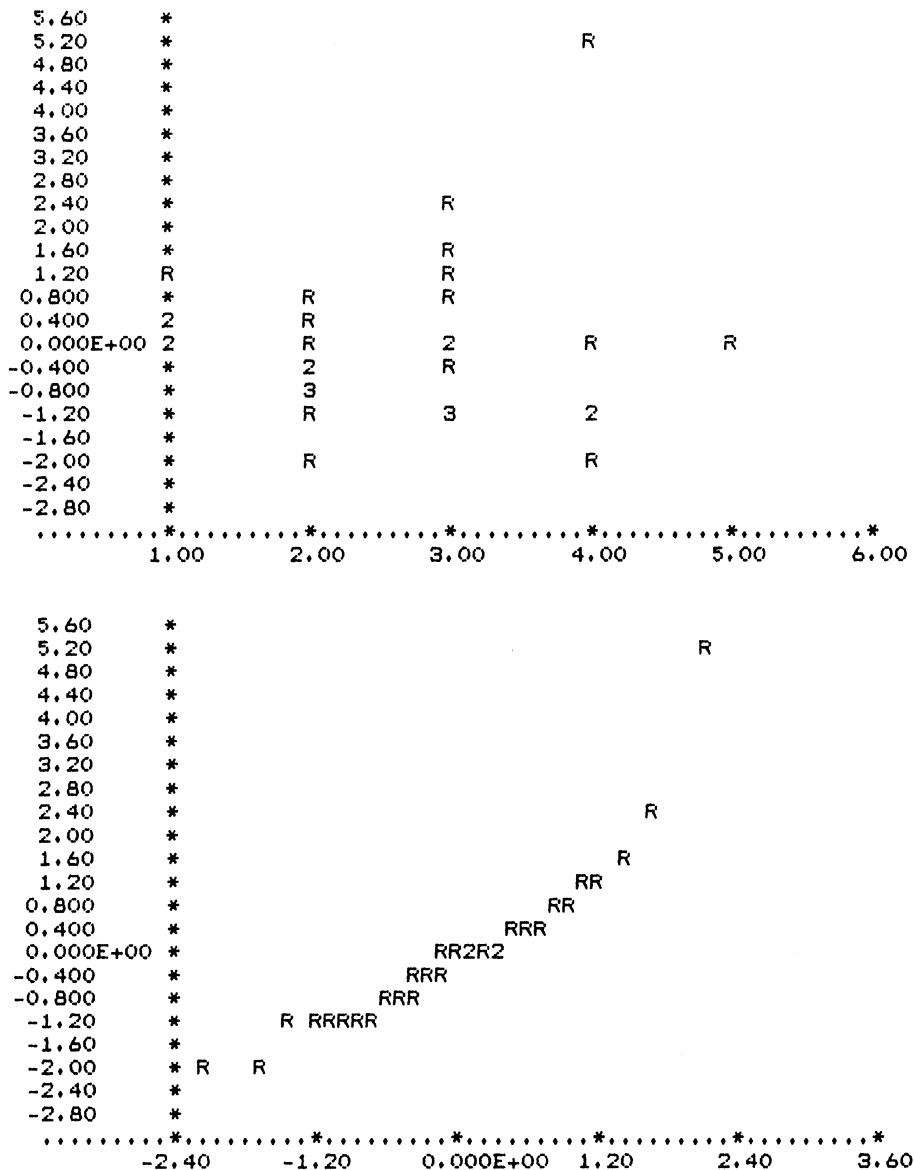
Table 7

Deviances from possible burnet moth models

Method	Description	d.f.	Deviance
P1+P2+P3+P4+P5	Closed	25	67.3
P1+P2+P3+P4+P5+B2+B3+B4	Birth only	22	56.8
P1+P2+P3+P4+P5+D1+D2+D3	Death only	22	59.1
P1+...+P5+B2+B3+B4+D1+D2+D3	Birth and death with dependence	19	37.1
As above +I2+I3		17	36.9
P1+PBD+P5+B2+B3+B4+D1+D2+D3	Constant capture prob.	21	42.6

Strangely, if only the data from the first four samples are analysed - readily calculated by adding together observations in the same column in Table 6, ignoring the 19 moths seen only in the fifth sample - the outliers are much less extreme, and one might be willing to accept a model with birth, death, and constant capture probability: $\chi^2_7 = 11.9$. The acceptance of constant capture probability in this case (the χ^2_6 without it is 11.8), together with its rejection in the full five samples, suggests that the sampling intensity was very different in the fourth sample from what it was in the second and third. If the fifth sample had not been taken we would be tempted on statistical grounds wrongly to extend the constant capture probability to the fourth sample. Any such decision should be taken on biological grounds: was

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Table 8
Residual plots of Burnet Moth data from Jolly-Seber model


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the same effort expended, were weather conditions similar, etc? Any decision on the plausibility of the statistical suggestion that the lack of fit of the usual model is caused by temporary emigration should also be governed by the biologist's knowledge.

Example 4. Heterogeneity in a closed population of Snowshoe hares
(*Lepus americanus*)

Otis *et al.* (1978) use as an example of the jackknife estimator (Burnham and Overton, 1978) of the size of a closed heterogeneous population data on the snowshoe hare collected by Burnham and Cushwa from the last six of nine consecutive trapping days. The GLIM analysis of the data in Table 9 selects the closed model with unequal catchability and no dependence: deviances and estimates are given in Table 10. The usual investigation of residuals shows that the 2 individuals caught in every sample is far too many (the standardised residual is 7.2). The removal of these individuals by \$EDIT 1 W 0 (not the same thing as replacing the first observation by 0) makes little difference to the estimate of population size. Continuing the analysis with these observations removed, we find little evidence of further heterogeneity from the residuals or their plots. The mean values of the standardised residuals in each of the capture frequency groups defined in the first plot show a slight decline for capture frequencies 2 and 3 with a corresponding concavity of the curve joining these means, but the Normal plot shows nothing unusual.

This analysis suggests that the population of hares comprised two subpopulations: one group of two animals whose behaviour was such as to render them liable to capture on every occasion - the other group of 75 animals whose behaviour follows the assumptions required for a valid capture-recapture analysis. This contrasts with the jackknife estimate (Otis *et al.*, 1978) of a heterogeneous population of 87 animals. The numerical difference between estimates of 77 and 87 does not seem large, but it must be remembered that 68 animals had actually been observed: the difference in the estimates is in fact that between 9 and 19 for the number of animals unobserved.

Simulation was adopted to check whether the observed counts, with the exception of the two perpetual captures, are consistent with the selected model. Random observations were generated independently for each of the 63 observable capture histories, to have Poisson distributions with means as predicted by the chosen model - the fitted values shown by \$DIS R. This was repeated 99 times. The same closed model $P_1+P_2+P_3+P_4+P_5+P_6$ was fitted to each of these data sets and the deviance noted.

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Of the 99 deviances, 65 were larger than the 47.9 obtained from the real data with the outlier omitted, providing some comfort for belief in the validity of the chosen model. In only six of the 99 data sets was even 1 individual observed in every sample.

Table 9

Snowshoe hare data (in standard order)

2	1	0	0	0	1	1	1	0	1	0	1	0	2	0	2	0	1	0	3	0	4	0	2	0	2	1	1	4	
0	0	0	0	0	0	1	0	0	1	0	1	3	2	4	0	0	1	0	0	3	2	3	0	0	1	5	0	6	3

Table 10

Deviances from possible snowshoe hare models

Model	Description	Deviance	d.f.	Estimated N
PC	Closed, equal prob.	68.5	61	75.4
P1+P2+P3+P4+P5+P6	Closed	58.3	56	75.1
P1+...+P6+I1+...+I5	with dependence	56.2	51	-
P1+...+P6+B2...+B5	Birth	56.5	52	-
P1+...+P6+D1...+D4	Death	56.7	52	-
P1+...+P6+B2...+D4	Birth and Death	55.3	48	-
with Unit 1 omitted				
PC	Closed, equal prob.	58.6	60	75.3+2
P1+...+P6	Closed	47.9	55	74.8+2

Example 5. Fourth instar nymphs of the grasshopper (*Myrmecotettix maculatus*) (Blower, Cook and Bishop, 1981)

As a final example, let us reanalyse data used by Blower, Cook and Bishop (1981) to exemplify different methods of analysis of capture-recapture data (Table 11).

The standard Jolly-Seber model has a deviance of 51.85 with 48 degrees of freedom, but several estimates of birth and death parameters, B2, D2 and D4, are negative. Immediate use of USE would give the Jolly-Seber estimates obtained by Blower, Cook and Bishop, to which Buckland's (1980) modification might be applied to obtain

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within-range parameter estimates. Since B2 and D2 are not independent, denoting birth and death in the same period between the second and third samples, it may not be necessary to remove both: we must remove each in turn to discover if removing only one will bring the estimate of the other within range. On trying \$FIT-D4-D2 \$DIS E, B2 is still negative and on then trying \$FIT+D2-B2 \$DIS E, D2 remains negative. The final change \$FIT-D2 brings all estimates within range and gives a deviance of 55.38 with 51 degrees of freedom. The difference between the in range and the out of range estimates is shown in Table 12. These in-range estimates differ from those obtained by Buckland's *ad hoc* modification: these estimates are to be preferred since the value attained by the likelihood for these parameter values is greater than is attained for the parameter values selected by Buckland's technique.

The deviance is surprisingly large for a relatively sparse data set. Unit 46, capture history 212212, has the most extreme residual (at a standardised value of 3.65), 6 individuals being observed. However there is no obvious biological reason for the prevalence of such a pattern, nor is any aspect of the pattern shared by other capture histories in which more animals have been observed than were expected: moreover, the residual fits reasonably well with the other points in the probability plot. The plot of residuals against capture frequency shows no sign of concavity, so with some reluctance - because of the high deviance relative to the sparseness of the data - we accept the model and the in-range estimates in Table 12.

If the experimenters were willing to accept that the sampling intensity had been fairly constant throughout the experiment, we can try these more parsimonious models. We find now that both B2 and D2 are out of range and have to be omitted from the model, but D4 is now within range. The resulting model has a deviance of 60.24 with 53 degrees of freedom. The difference of 4.86 is significant at the 10% level as a χ^2_2 , so that it may be safer to adopt the more general model unless the biologists argue strongly that sampling intensity, and hence capture probability, remained constant throughout the experiment. The crucial nature of this choice of model is made clear by inspection of the estimates in Table 12. The more general model suggests a population with a steady increase from the third sample onward: the model with constant capture probability indicates a population which is basically constant in size from the second sample onward, except for a downward hiccup at the fifth sample.

Capture-recapture examples using GLIM

Table 11
Grasshopper nymph data (in standard order)

0	0	0	0	0	1	0	1	0	0	0	0	0	3	0	1	0	0	0	2	0	4	0	0	1	1	0	3	0	12	
0	1	0	0	0	0	1	2	0	0	1	0	0	6	0	5	0	3	2	2	1	2	0	5	0	7	1	6	4	2	9

Table 12
Parameter estimates from grasshopper nymph data

Unmodified Jolly-Seber estimates					In-range estimates			
i	N _i	φ _{i-1}	B _{i-1}	P _i	N _i	φ _{i-1}	B _{i-1}	P _i
2	81	0.62		0.41	65.4	0.63		0.50
3	79	1.28	-25.3	0.33	65.4	1	0	0.40
4	73	0.69	18.7	0.38	75.6	0.87	18.7	0.37
5	102	1.18	16.2	0.21	89.2	1	13.6	0.24

With constant effort ($\hat{\beta}=0.38$)			
i	N _i	φ _{i-1}	B _{i-1}
1	52		
2	73	0.66	38.5
3	73	1	0
4	73	0.83	12.4
5	63	0.79	5.7
6	76	0.88	20.0

4. CONCLUSION

The aim of this paper is missionary: to convince readers that these methods will give them additional insight into the behaviour of a population which they are studying by capture-recapture techniques, and to demonstrate how easy it is to analyse a set of observations in a number of different ways. As a demonstration, the statistician has selected the analyses given in the examples in a fairly routine way.

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By making use of all relevant biological information, the biologist ought to do much better. The flexibility of the method allows the biologist to do so - within limits.

ACKNOWLEDGEMENTS

I am grateful to my colleague C.D. Sinclair for discussions of the analyses and the presentation of the paper, and to A.N. Cormack for provision of the simulation program.

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APPENDIX 1. Jolly-Seber and GLIM models

The classical Jolly-Seber model describes the population and the sampling procedure in terms of four sets of parameters:

N_i : the number of birds alive in the population at the time of the i th sample;

p_i : the probability that any one of the N_i is observed in the i th sample;

ϕ_i : the probability that any one of the N_i remains alive in the population at the time of the $(i+1)$ th sample (i.e. it neither dies nor emigrates);

B_i : the number of new animals joining the population, by birth or immigration, between the i th sample and the $(i+1)$ th sample.

These four sets of parameters are not independent: $N_{i+1} = N_i \phi_i + B_i$. Hence only the initial population size N_i (we call it merely N), together with the sets p_i , ϕ_i and B_i , is needed to define the system completely.

In the development of the Jolly-Seber model, the notation is less clumsy if we also define

x_i : the probability that a bird alive in the population at the time of the i th sample is not seen after that sample.

The x_i are related to the p_i and ϕ_i by the recurrence relation:

$$x_i = 1 - \phi_i + \phi_i(1-p_{i+1})x_{i+1} .$$

For the purpose of describing the correspondence between these parameters and those of the GLIM formulation, it is convenient first to describe birth and death differently. Instead of describing 'birth' as the addition of a certain number of birds to the population, we describe it as the multiplicative increase of the number of unmarked birds by a factor ψ_i . Then $1/\psi_i$ can be interpreted as the probability that an individual alive in the population at the time of the i th sample but not seen prior to that sample was indeed alive in the population at the time of the previous sample. Algebraically the relationship of ψ_i to B_i is given by:

$$\psi_1 = 1 + B_1 / N(1-p_1)\phi_1$$

$$\psi_2 = 1 + B_2 / N(1-p_1)\phi_1\psi_1(1-p_2)\phi_2 \quad \text{etc.}$$

We replace ϕ_i as the 'death' parameter by a parameter λ_i which defines 'death' in the same way as ψ_i defines birth: $1/\lambda_i$ is the probability that an individual alive

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in the population at the time of the i th sample but not seen after that sample is indeed still alive in the population at the time of the next sample. Algebraically:

$$\lambda_i = x_i / \phi_i (1-p_{i+1}) x_{i+1} .$$

The GLIM formulation transforms these parameters further:

1. The s capture probabilities are represented by P_I where,
for all except the first and last samples, $P_I = \log [(1-p_i)/p_i]$.
for the first sample, $P_I = \log [(1-p_1)\psi_1/p_1]$.
for the last sample, $P_S = \log [(1-\phi_{s-1}p_s)/\phi_{s-1}p_s]$.
2. The $(s-2)$ death parameters D_1, D_2, \dots are the logarithms of the corresponding λ parameters:

$$D_I = \log \lambda_i$$

3. The $(s-2)$ birth parameters B_2, B_3, \dots are the logarithms of the corresponding ψ parameters:

$$B_I = \log \psi_i$$

If all p_i are equal (to p) it will be seen that all the P_I except P_I and P_S are equal and hence can be replaced by the single parameter PBD . If the biologist believes that the constant capture probability p applies also to the first sample, then an estimate of the first birth parameter ψ_1 can be obtained from P_I . Similarly if p is believed to apply also to the final sample, an estimate of the final death parameter ϕ_{s-1} can be obtained from P_S . The routine USE is designed to obtain these values whenever it discovers no variation in p_2, \dots, p_{s-1} . There is no statistical justification for this extrapolation: any justification must come from the biologist's knowledge of how the sampling was conducted.

If no birth is occurring then ψ_1 equals 1 and P_I should also be included in this common parameter, then called PD . Likewise if no death is occurring then ϕ_{s-1} equals 1 and P_S also equals the common parameter of capture probability. If one of these models with constant capture probability is selected, and is thought to be extendable to the first or last sample, then the P parameters not included in the constant PBD (or PD or PB) must be not less than the constant value. Thus for example, extension to the first sample means that

$$\begin{aligned} P_I &= \log [(1-p)\psi_1/p] \\ &= \log [(1-p)/p] + \log \psi_1 \\ &= PBD + \log \psi_1 \\ &\geq PBD \end{aligned}$$

since $\psi_1 \geq 1$, $1/\psi_1$ being a probability. Thus, discovery that the estimate of P_I is

Capture-recapture examples using GLIM

less than that of PBD implies either that the constant capture probability cannot be extended to the first sample, or that there is no birth between the first and second samples so that ψ_1 is forced to be 1, and P1 and PBD to be equal, both being replaced by PD.

Standard errors are provided for the estimates of the GLIM parameters by the instruction \$DIS E. Correlations (or covariances) between these estimates can be obtained by instructions \$DIS C (or \$DIS V). From these, by tedious but not inherently difficult algebra, asymptotic standard errors for the biological parameters N_i , ϕ_i etc. could be obtained by standard Taylor series, or δ -technique, approximations. There are two reasons why this has not been included in the program:

- i) The estimates of the biological parameters have highly skew distributions, and the relevance of standard errors for them has often been questioned. It would be better to obtain confidence intervals for the estimates of the GLIM parameters from assumed normal distributions, and to transform these limits appropriately. No way of making this transformation has yet been developed.
- ii) It is arguable whether estimates of variability based on the Poisson distribution used in the GLIM analysis are the ones needed by the biologist. The relationship between these, and estimates of variability based on multinomial models, is discussed by Sandland and Cormack (1984).

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APPENDIX 2. GLIM program RECAP.GLM

```

$SUB CR1
$MAC EST
$CAL XE=2**(%S+%K-1) : XF=2**(-%K) : XJ=%S+%K
$CAL M(XJ)=%FV(1)+%FV(XE+1)
$CAL AFT=AFT*(2-%GL(2,XE))
$CAL AA(XJ)=%CU(AFT*%FV)
$CAL BEF=BEF*(2-%GL(2,XF))
$CAL BB(1-%K)=%CU(BEF*%FV)
$CAL XK=%K+1
$ENDMAC

$MAC USE
$CAL AFT=1 : BEF=1 : XK=1-%S
$VAR %S AA BB M PERM PHIH
$CAL AA=1 : M=1
$WHILE XK EST
$CAL PERM=%GL(%S,1)-1 : PERM(1)=%S : BB(1)=%FV(1)
$CAL AA(%S)=BB(1) : CC=AA(PERM) : M(%S)=CC(%S)
$CAL PH=%FV(1)/M
$CAL TEMP=PH : TEMP(1)=TEMP(2) : TEMP(%S)=TEMP(%S-1)
$SORT TEMP
$CAL %A=TEMP(%S)-TEMP(1) : %C=10**(-4)
$CAL NEST=AA*M*BB/%FV(1)**2
$CAL PHIH=AA*M/(CC*%FV(1))
$CAL %B=%LE(%A,%C)
$SWITCH %B CONST $
$CAL PHIH(1)=1 : %A=M(%S-1)/M(%S) : %B=1-%C
$CAL PHIH(%S)=PHIH(%S)+(%A-1)*(1-%B)*%LE(PHIH(%S-1),%B)
$CAL BH=NEST-PHIH*NEST(PERM)
$CAL BH(1)=NEST(1)
$PRINT
$PRINT ' I N(I) PHI(I-1) P(I) B(I-1) '
$LOOK 1 %S NEST PHIH PH BH
$PRINT
$PRINT ' IF CONSTANT EFFORT THEN ALL ESTIMATES TRUE. OTHERWISE:'
$PRINT ' N(1),P(1),B(1) TRUE ONLY IF NO BIRTH IN PERIOD 1 '
$PRINT ' N(S),P(S) TRUE ONLY IF NO DEATH IN LAST PERIOD '
$PRINT ' PHI(S-1) TRUE ONLY IF EFFORT CONSTANT IN (S-1),S '
$PRINT ' B(S-1) TRUE ONLY IF N(S),PHI(S-1) BOTH ARE ': 
$ENDMAC

$MAC PLOT
$EXTRACT XVL
$CAL FREQ=W*(%S-PC) : QR=%LE((R-%FV)**2,10**(-8))
$CAL RR=W*(R-%FV)/%SQRT(%FV*(1-%FV*XVL)+QR)
$PRINT
$PLOT RR FREQ
$PRINT :
$CAL OR=%ND((%GL(%NU,1)-0.5)/%NU)
$SORT RR $PLOT RR OR
$PRINT
$ENDMAC

```

 Capture-recapture examples using GLIM

```

$MAC CONST
$CAL NEST=NEST*PH/PH(2) :PH(1)=PH(2) :PH(%S)=PH(2)
$CAL PHIH(%S)=%FV(1)/(M(%S)*PH(%S))
$ENDMAC
$RETURN $

$SUB CR3
$CAL P1=%GL(2,1)-1:P2=%GL(2,2)-1:P3=%GL(2,4)-1:W=1:%S=3:
I1=P1*P2:I2=P2*P3:PD=P1+P2:PB=P2+P3:PC=PB+P1:B2=I1:D1=I2
$YVAR R $ERR P $WEI W
$RETURN $

$SUB CR4
$CAL P1=%GL(2,1)-1:P2=%GL(2,2)-1:P3=%GL(2,4)-1:P4=%GL(2,8)-1:
I1=P1*P2:I2=P2*P3:I3=P3*P4:B2=I1:B3=B2*P3:D2=I3:D1=D2*P2:
PBD=P2+P3:PD=PBD+P1:PB=PBD+P4:PC=PB+P1:W=1:%S=4
$YVAR R $ERR P $WEI W
$RETURN $

$SUB CR5
$CAL P1=%GL(2,1)-1:P2=%GL(2,2)-1:P3=%GL(2,4)-1:P4=%GL(2,8)-1:
P5=%GL(2,16)-1:I1=P1*P2:I2=P2*P3:I3=P3*P4:I4=P4*P5:W=1:
B2=I1:B3=B2*P3:B4=B3*P4:D3=I4:D2=D3*P3:D1=D2*P2:
PBD=P2+P3+P4:PD=PBD+P1:PB=PBD+P5:PC=PB+P1:%S=5
$YVAR R $ERR P $WEI W
$RETURN $

$SUB CR6
$CAL P1=%GL(2,1)-1:P2=%GL(2,2)-1:P3=%GL(2,4)-1:P4=%GL(2,8)-1:
P5=%GL(2,16)-1:I1=P1*P2:I2=P2*P3:I3=P3*P4:I4=P4*P5:W=1:
B2=I1:B3=B2*P3:B4=B3*P4:B5=B4*P5:
P6=%GL(2,32)-1:I5=P5*P6:D4=I5:D3=D4*P4:D2=D3*P3:D1=D2*P2:
PBD=P2+P3+P4+P5:PD=PBD+P1:PB=PBD+P6:PC=PB+P1:%S=6
$YVAR R $ERR P $WEI W
$RETURN $

$SUB CR7
$CAL P1=%GL(2,1)-1:P2=%GL(2,2)-1:P3=%GL(2,4)-1:P4=%GL(2,8)-1:
P5=%GL(2,16)-1:I1=P1*P2:I2=P2*P3:I3=P3*P4:I4=P4*P5:W=1:
B2=I1:B3=B2*P3:B4=B3*P4:B5=B4*P5:
P6=%GL(2,32)-1:P7=%GL(2,64)-1:I5=P5*P6:I6=P6*P7:B6=B5*P6:
D5=I6:D4=D5*P5:D3=D4*P4:D2=D3*P3:D1=D2*P2:
PBD=P2+P3+P4+P5+P6:PD=PBD+P1:PB=PBD+P7:PC=PB+P1:%S=7
$YVAR R $ERR P $WEI W
$FINISH $

```

AGE-DEPENDENT MORTALITY RATES OF SOME COMMON BRITISH BIRDS

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SUMMARY

This paper is concerned with the description of a simple model of age-dependent survival that may be applied to data for birds ringed in large numbers as pulli. The biological factors that determine age-dependent mortality rates are briefly discussed and the derivation of the model outlined. The parameters of the model are then estimated using data for six species of common British bird. The utility of the method and some of its drawbacks are then discussed before concluding with a short discussion of the uses and abuses of large data sets in quantitative ornithology.

Keywords: AGE-DEPENDENT MORTALITY RATES, COMMON BRITISH PASSERINES, COMPETING RISK MODELS, RINGING DATA.

1. INTRODUCTION

The ringing schemes operated in different parts of the world have now collected a more comprehensive set of demographic data than is available for any other group of animals, with the possible exception of the Great Whales (Anon, 1976) and, of course, Man. Such a wealth of readily available data should allow us to answer many interesting questions about the way that survival rates and migration vary both between and within different bird species (Dobson, 1983a,c,d). More pragmatically, it could also allow us to develop methods for monitoring populations of a variety of species. Sensibly, this would be done by developing statistical models that predict the expected patterns of recoveries of ringed birds, and mathematical models that illustrate how different species respond to environmental perturbations (Dobson, 1984). Unfortunately, many of the analyses of ringing data undertaken since the seminal work of J.B.S. Haldane (1955), have either been based upon too small a sample size, or have concentrated singlemindedly upon possible sources of bias in the estimated survival rates. Although these considerations are important, too few workers seem to have realised that even the most pure and unbiased estimate of survival is of little

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intrinsic value until the factors that determine variations in that survival rate are identified. The consequences of these variations in survival may then be explored at the population level using simple mathematical models. The development of such models and the calibration of the pertinent biological and environmental factors that tune observed survival rates should be the future aims of quantitative ornithology.

In this paper I would like to describe a simple mathematical model that can be used to compare age-dependent survival rates between different species of birds. The model differs from the more traditional statistical models used to estimate age-dependent mortality rates in that it concentrates upon the instantaneous mortality rates operating upon birds of different ages, rather than upon their annual survival rates. The discrete-time formulation of previous models is consequently replaced by a mathematically more tractable continuous-time framework. Biologically, the model is designed to mimic the different intensities with which different forces interact at successive stages of a bird's life. After briefly describing the essential physiological and ecological factors which are likely to be important in determining any age-dependence in bird survival rates, I have illustrated the model's utility by fitting it to data for six species of common British birds for which large data sets were available: Robins, *Erythacus rubecula*, Chaffinches, *Fringilla coelebs*, Pied Wagtails, *Motacilla alba*, Great Tits, *Parus major*, Jackdaws, *Corvus monedula* and Jays, *Garrulus glandarius*. The same techniques are applied elsewhere to data for some British birds of prey (Dobson, 1983b), where the ability of the model to predict expected numbers of ringed recoveries is also demonstrated.

2. FACTORS DETERMINING AGE DEPENDENCE IN SURVIVAL

The biological factors determining survival rates in birds can be considered under five main headings; genetic and physiological factors, disease, predation and competition for resources. Obviously there are subtle interactions between these factors, however the intensity with which they operate upon birds of different ages is indicated in Figure 1.

The ability to forage efficiently is something that is mainly gained by experience. Although a young bird is physiologically and hence genetically adapted to its main mode of acquiring food, the period of transition from parental dependence to self-sufficiency is crucial in determining the shape of the early part of the species' survival curve. Davies (1976) has described this period in detail for the Spotted Flycatcher, *Muscicapa striata*, (Figure 2) and Tovish (1982) has examined some of the

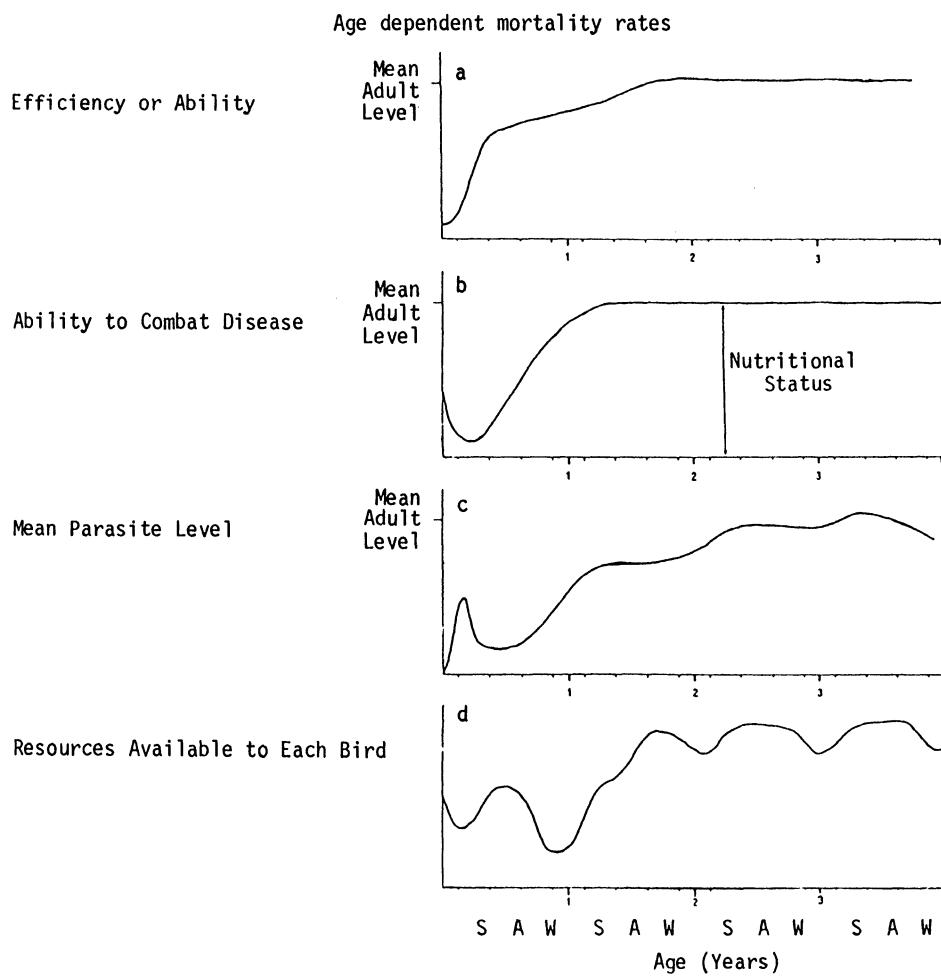


Figure 1 This figure qualitatively illustrates the age-dependence of several factors important in determining survival rates in birds. The relationships plotted are hypothetical examples based upon a number of sources. Some of these are described in detail in the other figures. The graphs assume that the birds hatch in the spring. S, A, and W therefore refer to the successive summers, autumns and winters in the bird's life. (a) Ability to forage or ability to detect and avoid predators; (b) Ability to combat disease; note that the mature bird's ability to mount an effective response to pathogens is dependent upon its nutritional status; (c) Mean population disease level; this curve is produced by the interaction between the transmission properties of the disease, its pathogenicity to the host and the host's ability to contain it; (d) Resources available to each bird; these will be a function of the rate at which resources are renewed, the bird's ability to exploit them and the numbers of potential competitors also seeking to utilise the same resources. It will thus vary both with age and season of the year.

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theoretical consequences of this type of learning behaviour for survival. Similarly, the ability to escape detection and capture by predators is a factor which has both genetic and learnt components. Dunn (1977), Perrins and Geer (1980) and Newton and Marquiss (1982) have all recently detailed the impact that predators have upon nestlings and recently fledged birds. These studies estimate that up to 30% of the initial population may be killed by predators in the first two months of life. The intensity of this force of mortality will again decline as the young birds acquire experience and the predators switch their attention to more readily accessible prey.

Disease, due to the effects of parasites or viral protozoan pathogens is all too rarely considered as a factor likely to be of importance in determining survival in wild animal populations (Hassell *et al.*, 1982). The tables in May (1982) and Dobson (1982) make rough attempts to put disease in its proper perspective when compared to other sources of mortality. The first few months of life are a time when an animal's defences against pathogens are undergoing tremendous development and change (Glick, 1964; Hodges, 1979); it is also a time when the rate of exposure to novel pathogens is at a maximum (Figure 3). This and the interaction between the bird's nutritional status and its steadily increasing quota of helminth and blood parasites (Crompton and Hall, 1981), will further tune the shape of the observed age-dependent survival curve.

Competition with conspecifics for available resources is a problem that is most acute for young birds during their first winter (Jansson, Ekman and Bromsén, 1981; Krebs, 1970). However, the intensity of this source of mortality will fluctuate with both the population density of the species and that of its competitors, as well as with the rates at which the shared resources are renewed. The decoupling and quantifying of these interactions for any group of animals remains an important goal of several different areas of ecology.

Many authors have developed genetic and physiological theories of senescence for biological populations (Medawar, 1952; Hamilton, 1966; Abernethy, 1980; Hirsch, 1982). Unfortunately, estimates of rates of senescent mortality are notoriously hard to make for natural populations, even when the best possible sets of data are available (Dunnet and Ollason, 1978; North and Cormack, 1981). The models described below can be adapted to include a term for senescent mortality (Dobson, 1983b). Although the inclusion of a parameter for senescent mortality does reduce the variation unexplained by the model, the loss of a further degree of freedom means that we remain unable to state categorically that we have been able to identify accurately any senescent effect in the species studied. This would only be possible with inordinately large sets of data, and I have therefore assumed that increased mortality rates with

Age dependent mortality rates

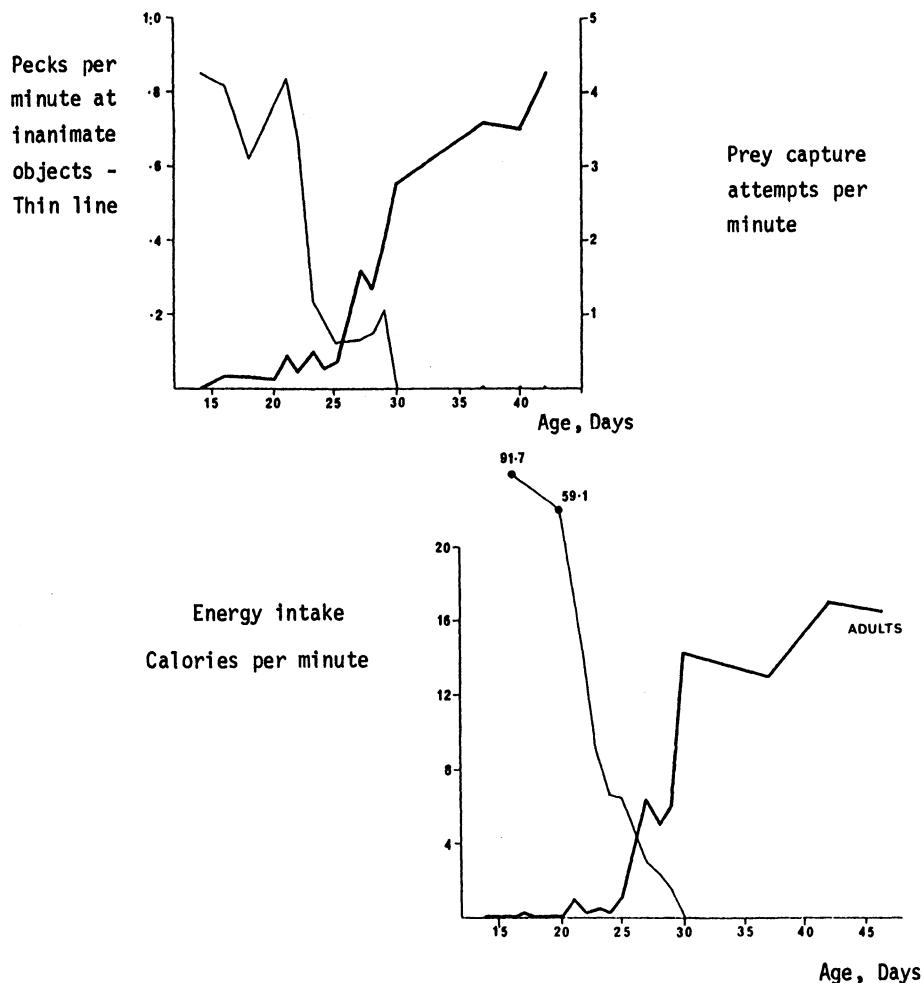


Figure 2 Two examples of how a bird's feeding techniques change with age; these are for Spotted Flycatchers (*Muscicapa striata*), and the data used are from Davies (1976). In the figure on the left, the thin line illustrates the declining rate at which birds peck at inanimate, non-food articles, the thicker line shows the numbers of prey capture attempts made per minute. The figure on the right depicts the amount of food obtained from different sources. Here the thin line is the energy intake, in calories per minute, from food fed to the chick by the parent, the thick line is that obtained by the bird when foraging for itself.

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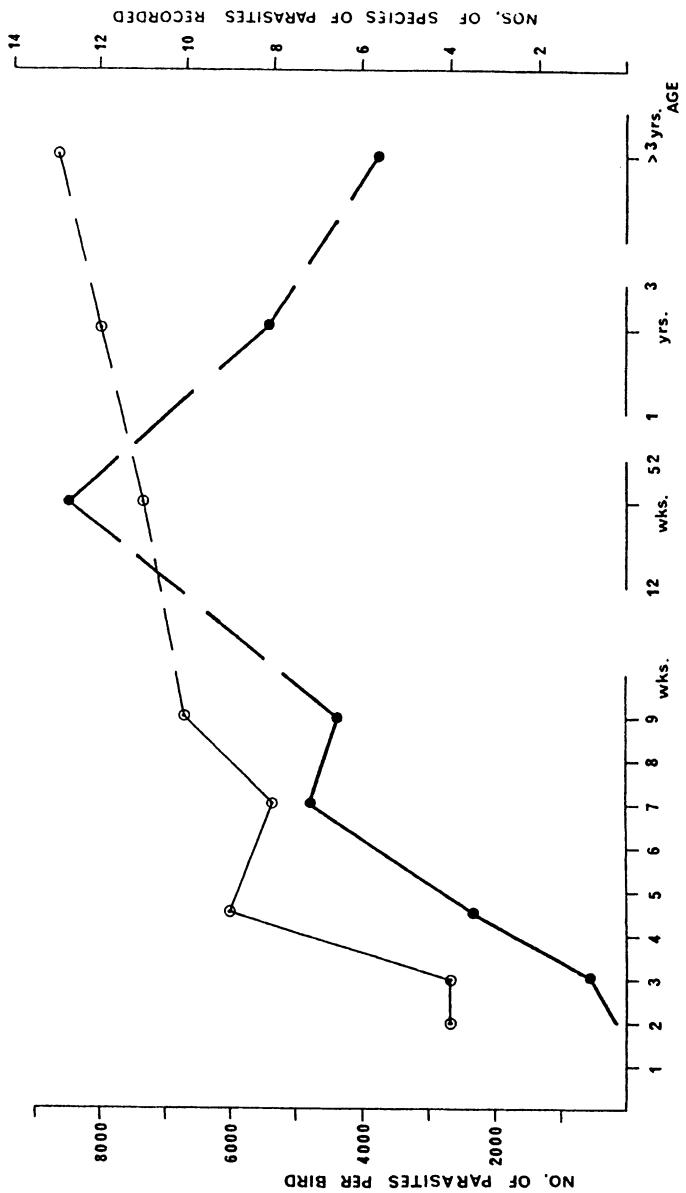


Figure 3 The change in mean burden of parasitic gut helminths with age for a population of Brown Pelicans (*Pelecanus occidentalis*), (Humphrey, Courtney and Forrester, 1978). The thin line is mean numbers of worms per bird, the thick line is number of species of parasites recorded from birds of different ages. The turnover of the former is due to increased mortality of heavily parasitised birds; this lowers the observed mean parasite burden for those birds remaining alive (see Anderson, 1982, and Hassell et al., 1982, for further examples).

Age dependent mortality rates

age in adult birds are of negligible importance for the relatively short-lived species studied. The main biological and population dynamic consequences of this assumption are discussed in Botkin and Miller (1974) and Dobson (1982). Lakhani and Newton (1983) and Lakhani (1985) discuss further statistical aspects of this problem and demonstrate the pitfalls that are inherent in samples based on small sample sizes.

3. STRUCTURE OF THE MODEL AND DESCRIPTION OF THE DATA

It is obvious from the biological considerations discussed above that the first few months of life are the time when a bird's mortality rate is changing most rapidly. After attaining maturity, i.e. the age at which the bird is first capable physiologically of breeding, it seems logical to assume that mortality rates then remain constant at some value whose magnitude is determined by a variety of prevailing biological and ecological conditions. Siler (1979) has suggested an ideal framework upon which to base a mortality function which captures these essential features of age-dependent survival in birds. If we call the instantaneous mortality rate at age t , $\mu(t)$, then equation (1) describes the rate of change of this mortality rate with age.

$$\mu(t) = a \exp(-bt) + c \quad (1)$$

By inspection, we can see that the instantaneous mortality rate at birth ($t=0$) is $(a+c)$, and as the age of the birds, t , tends to infinity, the overall expression becomes equal to c , the instantaneous adult mortality rate. Models of this type are termed "competing risk models". By solving the equation, $\frac{dN(t)}{dt} = -\mu(t) N(t)$, we can readily obtain an expression for the number, $N(t)$, from an initial cohort $N(0)$, that survive to any age t .

$$N(t) = N(0) \exp \left[(a/b) [(\exp(-bt)-1)-ct] \right] \quad (2)$$

Here we are treating $N(t)$ as a deterministic quantity. In terms of random variables, since the numbers surviving are binomially distributed, we can readily obtain the equivalent stochastic expression for the expected mean number of birds surviving, and its variance (Anderson and Whitfield, 1975; Bailey, 1964, p.110).

$$E\{N(t)\} = N(0) \exp \left[- \int_0^t \mu(v) dv \right], \quad (3)$$

equivalent to (2), and

$$\text{Var}\{N(t)\} = N(0) \exp \left[- \int_0^t \mu(v) dv \right] \cdot \left[1 - \exp \left(- \int_0^t \mu(v) dv \right) \right] \quad (4)$$

When given a large cohort of birds allringed at age 0, e.g. as pulli in the nest, it should be possible readily to obtain estimates of $\mu(t)$ at different ages by using

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the formula:

$$\log_e[N(t)] - \log_e[N(s)] = (s-t)\mu\left(\frac{s+t}{2}\right) \quad \text{for } s > t . \quad (5)$$

Here $N(t)$ is the number of birds alive at age t , and $N(s)$ is the number of birds alive at age s . Equation (5) arises by noting that

$$\begin{aligned} \log_e[N(t)/N(s)] &= \log_e\left[\exp\left[-\int_0^t \mu(v) dv\right] / \exp\left[-\int_0^s \mu(v) dv\right]\right] \\ &= \int_t^s \mu(v) dv \quad (s > t) , \end{aligned}$$

and by approximating this expression by the area $(s-t)\mu\left(\frac{s+t}{2}\right)$. The parameters a , b and c can then be estimated by fitting equation (1) to the estimated sets of instantaneous mortality rates using non-linear least squares (Conway, Glass and Wilcox, 1970; Marquardt, 1963). Alternatively, Siler (1979) and Smith and Grenfell (1983) have derived the appropriate maximum likelihood method for estimating the parameters of equation (2) directly.

The wealth of ringing data available is readily subdivisible into different classes; these subsets of data should be used to answer different specific questions about the different factors that affect observed survival rates. For the majority of passerine species the data are for adult birds ringed at an unknown age and later recovered dead after a known period of time. These data should be used to estimate rates of mean adult survival; if sufficiently comprehensive they may also be used to estimate calendar year specific rates of survival and mortality rates at different times of the year (Dobson, 1983d). Only a few species have sufficiently large data sets for birds ringed as pulli; these are the only sets of data that may be used to estimate age-dependent mortality rates. Despite the relative paucity of data, this is the area where the majority of previous estimates of mortality have been made (Botkin and Miller, 1974; North and Cormack, 1981).

Sample sizes of less than around 50 recoveries create systematic biases in estimates of survival (Dobson 1983a), and for this reason all the data used were for species with recoveries well in excess of this figure. The data used were collected by the British Trust for Ornithology; those for Robins, Chaffinches, Pied Wagtails and Great Tits were for birds ringed between the years 1946 and 1965, whilst those for the Jackdaws and Jays were for birds ringed between 1910 and 1965. In all cases, the resultant 16 year gap between ringing and analysis has ensured that no live birds are still extant in the population, i.e. all the data sets are complete. Any mortality parameters estimated will thus be averages for the period of historic time used. Although stochastic effects will create biases in the estimated patterns of survival,

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the paucity of any real quantitative biological information in this area justifies the use of such a relatively crude approach.

4. THE FIT OF THE MODEL TO THE DATA

The fit of the model to the estimated instantaneous mortality rates and the expected and observed survival curves are illustrated in Figures 4 and 5 respectively. Table 1 gives the estimated parameter values and the goodness of fit of the model to each of the six data sets. Plainly, the models are able to give acceptable fits to the observed data; in all cases they are able to explain more than 85% of the observed variation in age-dependent survival. Biologically, the model may be interpreted as suggesting that the first six months of life are the time when instantaneous mortality rate changes most rapidly. The mortality rate stabilises to a constant adult level at about the age of eighteen months for the four smaller species, and at the later age of 2 to 3 years for the two larger crow species.

It is important to note that it is the decline in the instantaneous mortality rate with age of immature birds that is important in determining the shape of the observed survival curve, rather than any variation in survival of the adult birds, and the continuous-time structure of the model allows this effect to be readily quantified.

5. DISCUSSION AND CONCLUSIONS

Keyfitz (1982) has recently pointed out that much of the information present in the columns of a conventional life table is redundant. The goal of human actuaries and animal and plant ecologists is to describe the information present using the minimum set of parameters sufficient to reconstruct the original sets of demographic data. The models discussed above satisfy these criteria by considering age-dependent survival in birds as a continuous process whose instantaneous rate of change can be described as a simple curve. The biologically complex array of factors that give rise to the observed survival curve are then quantified by estimating the three parameters that uniquely determine the shape of this curve. In this final section I would like to discuss briefly some of the assumptions underlying this analysis and also those underlying ringing studies in general.

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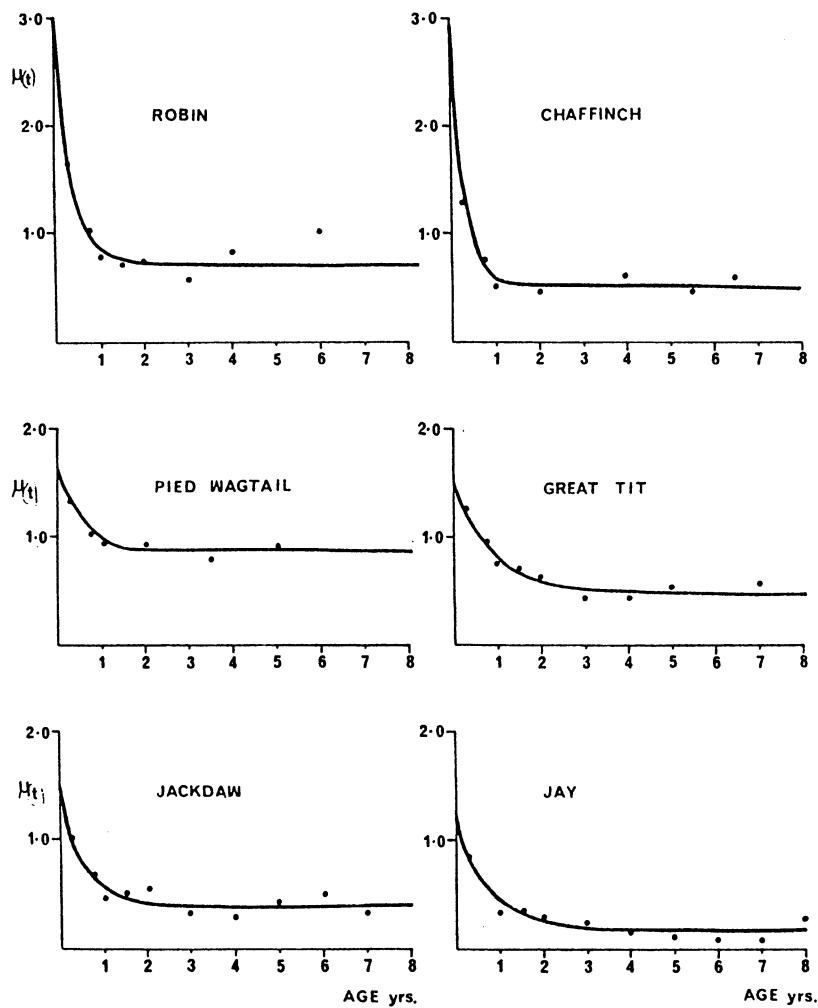


Figure 4 The observed instantaneous mortality rates at different ages for each of the six species (solid circles), and the estimated instantaneous mortality rate function.

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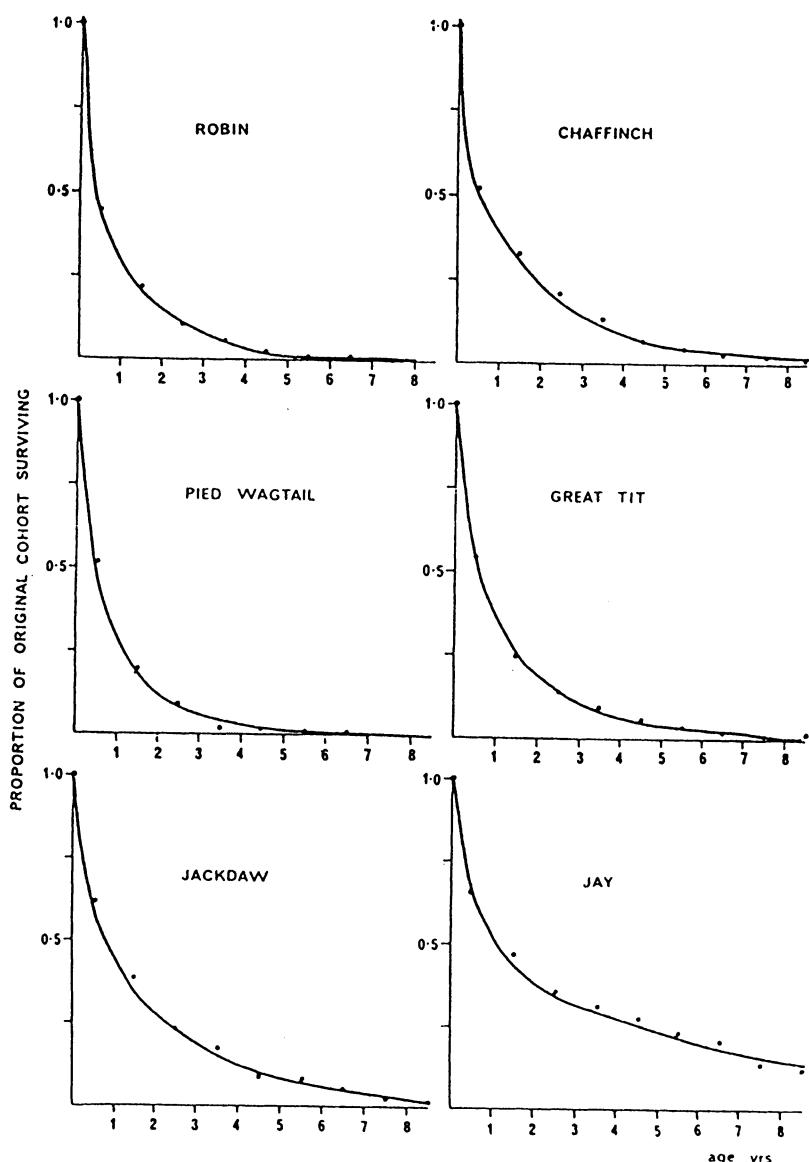


Figure 5 The observed survival data (solid dots), and the estimated survival curves for the six sets of data.

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Table 1
Estimated parameter values for each of the six species

Species	Number of recoveries	a	b	c	r^2	Life expectancy Birth (mths.)	Adult (yrs.)
Robin <i>Erythacus rubecula</i>	302	1.7526	2.1472	0.6200	0.856	5.06	1.61
Chaffinch <i>Fringilla coelebs</i>	79	1.8630	3.3452	0.5098	0.951	5.05	1.96
Pied Wagtail <i>Motacilla alba</i>	112	0.7658	1.3813	0.7832	0.988	7.75	1.28
Great Tit <i>Parus major</i>	335	1.0362	1.0267	0.4261	0.990	8.21	2.35
Jackdaw <i>Corvus monedula</i>	298	1.1109	2.2911	0.3937	0.889	7.98	2.54
Jay <i>Garrulus glandarius</i>	112	0.9227	1.4116	0.1771	0.873	10.91	5.65

This table gives the estimated parameter values for the fit of the model to each of the six data sets and the proportion of the variance (r^2) explained in each case. The final two columns give the life expectancy of the birds at birth, in months, and as adults, in years. Here adult birds are defined as those for whom the value of $a \exp(-bt)$ is negligible.

The prime assumption underlying the analysis of any set of ringing data is that the ringed population is a random subset of the total population of the species under study. Many workers have been harsh upon the validity of this assumption. Theoretically, data sets that are large, annually replicated and collected from animals that spend 100% of their lives living in an undisturbed condition are an ideal that most ecological studies cannot attain. Ironically, few people see ringing data in this light. When compared to other sources of biological data, such as the personal field observations of different behavioural workers or the artificially controlled experiments of the laboratory worker, ringing data would seem to be relatively devoid of potential biases. Those biases that are present should be readily quantifiable as they will be replicated consistently from year to year. This is in marked contrast to the almost undefinable biological biases that occur in the other sources of biological data mentioned above (Caro *et al.*, 1979; Rice and O'Brien, 1980).

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At worst, ringing data can be thought of as an annually repeated experiment. After a time equivalent to several expected life spans for the species under study, sufficient data should have accumulated for models to be constructed which estimate future expected recoveries. As changes in the biology and, particularly, the survival of the species under study are the most important factors in determining variations in the recovery data, then differences between observed and expected recoveries are likely to reflect realistically genuine changes in the species' ecology. Using the past ringing data to monitor the future ringing data thus provides one effective method of monitoring the variations in survival of a variety of species.

The additional assumptions that are required if we are to estimate absolute values of age-dependent survival for a species, concern variation in the recovery rates of ringed birds of different ages. These assumptions remain the Achilles heel of ringing analyses. Attempts to quantify them are given, for example, by Lakhani and Newton (1983). In many cases, these analyses have been applied to small data sets. However, it is only when we require absolute estimates of survival that the quantification of variations in recovery rates is important. Here significant variations may occur between immature birds and adults of the same species. Although these may distort the estimates of survival given in this paper, they will not affect the method's ability to predict future ringing recoveries. The development of predictive mechanistic models that are qualitatively based upon sensible biological assumptions (Pielou, 1981) remains the more pragmatic and immediate demand of the various national ringing schemes.

Even if we could quantify the recovery rates of birds of different ages, it would tell us little about the species' biology that could not better be gained by undertaking a comparative study using data for a number of species. Here the biases due to variations in recovery rate could be minimised by comparing birds of different species but of a similar age. Alternatively, the estimated parameter values could be used to develop simple mathematical models for the species studied. Variations in the survival rates, or our confidence in our ability to estimate them, could then be investigated either analytically or by numerical simulation. This technique is commonly applied to estimates of survival and fecundity obtained from fisheries data (Ludwig and Walters, 1981, 1982; O'Neill *et al.*, 1980). In these studies the standard of data is usually less comprehensive than that obtained from ringing studies; the standard of analysis and interpretation, in contrast, remains conspicuously higher.

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For too long workers in ornithological statistics have focused their attention on potential biases in ringing data. This is a shame, as it has allowed quantitative ornithology to fall behind other areas of population ecology, such as fisheries (Clark, 1976) and epidemiology (Anderson, 1982), both of which have benefited from the interactions between applied ecologists and mathematicians throughout the 1970's and 80's (see May, 1981, for a comprehensive introduction to this area). It would be wise for applied ornithology not only to pay more attention to other areas of ecological development, but also for it to develop a more positive attitude towards the analysis of its most valuable resource.

ESTIMATION AND COMPARISON OF FUNCTIONS OF
DAILY NEST SURVIVAL PROBABILITIES
USING THE MAYFIELD METHOD

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SUMMARY

The Mayfield (1960, 1961, 1975) method of estimating nesting success is used to overcome problems of bias in other estimators. This method is based on estimating daily survival probabilities. Estimates of parameters other than daily survival probabilities are sometimes necessary when considering nesting success. The Mayfield method for estimating daily survivorship can be used in deriving these estimates. A method for estimating parameters which are functions of daily survival probabilities and for deriving the corresponding variances of these estimates is given. Statistical comparisons of these parameters are then possible.

Keywords: REPRODUCTIVE SUCCESS; NEST SURVIVAL; MAYFIELD METHOD; LAYING, INCUBATION, NESTLING PERIODS; FUNCTIONS OF DAILY RATES

1. INTRODUCTION

Recent work by Hensler and Nichols (1981), Johnson (1979), and Bart and Robson (1982) has developed statistical theory supporting the method of estimating nesting success first suggested by Mayfield (1960, 1961, 1975). The method is designed to eliminate a bias associated with other estimates of nesting success. Suppose in field searches for nests one finds and monitors K active nests, recording a random variable Y_k which is 1 if the k^{th} nest is successful and 0 otherwise. Then

$$\bar{Y} = \sum_{k=1}^K Y_k / K,$$

the proportion of observed nests which were successful, might seem an unbiased estimate of the probability that a nest will succeed. However, this estimate is

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biased unless all nests are found on the first day of the nesting period, for otherwise nests which had failed before the sample was initiated are excluded from the population sampled since they will not be found. The probability of finding successful nests is thus higher than that for unsuccessful nests, and the resulting value of \bar{Y} is an overestimate. In Hensler and Nichols (1981) Monte Carlo simulations are presented which demonstrate the magnitude of this bias in many cases. The Mayfield method corrects for this bias by considering not only whether a nest succeeds but also how many days it was observed.

Among the assumptions of the model employed by Hensler and Nichols (*loc. cit.*) are the following: (a) the length of the complete period to success, which we will call the nesting period (for example, the period of incubation of eggs), is the same number of days, say J days, for all nests (this assumption is relaxed in the likelihood function below); (b) there is a constant unknown probability, p ($0 < p < 1$), over this period that a nest observed on day j will survive to day $j+1$; the probability of a nest succeeding from day 1 to full term is then p^J ; (c) there is a fixed unknown probability, θ_j , that an observed nest will have been first found on day j of its nesting period. For the K nests, observed under the above model, we observe independent random vectors $X_k = (Y_k, T_k)$, $k=1, 2, \dots, K$, where (i) Y_k is a random variable taking the value 1 if the k^{th} nest is successful (i.e. survives the complete nesting period) and the value 0 if the nest fails at any time, and (ii) T_k is a random variable denoting the number of days the k^{th} nest is observed until it either succeeds or fails.

For example, an observation of (0,10) would mean a nest was seen on 10 days but on the 11th day visit it had failed; a value of (1,10) would mean a nest was seen on 10 days and on the 11th day was observed to have succeeded. Success for these nesting attempts can be defined in many ways. A usual definition of success for nests during the incubation period is that at least one egg hatches. Failure is always defined as not successful, so that in the above case a failed nest would be one which did not hatch any eggs.

The model requires that daily survival probabilities remain constant during the nesting period being considered. It may be suspected, however, that these daily probabilities will be different during different periods of the nesting cycle. Due to changes in parents' behaviour, for example, one may suspect that the daily survival probability during the egg-laying and incubation period is different from that during the nestling-rearing period. It then is necessary to estimate separate

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daily survival probabilities for each period, and this feature is investigated in §3 of the paper. The results of this paper are useful for combining these separate estimates into a meaningful estimate of overall nesting success and for estimating its variance.

Defining when a nest is in the laying, incubation, or nestling period has some inherent difficulties. For example, a nest may be considered in the laying period if eggs are still being deposited in the nest whether or not incubation of early eggs has begun. Or one may consider a nest to have entered the incubation period once incubation of any egg has begun even though additional eggs are still being laid. It is important that the completion of any period be clearly defined so that a nest can be classified as successful or unsuccessful. In an example cited below concerning Black-crowned Night Herons (*Nycticorax nycticorax*), the laying period extended from the time the first egg was laid until the last egg was laid; the incubation period was from the day after the last egg was laid until the day the first egg hatched; the nestling period extended from the day after the first egg was hatched to 15 days from that date.

Some ambiguity is inherent in these definitions. Suppose a nest is found with 1 egg; two days later a second egg is laid, and two days thereafter the clutch is lost to predation and the nest is abandoned. Was the nest lost during the final stages of egg laying or during the early stages of incubation? If average clutch sizes are 15 eggs, a good assumption would be that predation occurred in the laying period, although it is possible, but unlikely, that the two eggs observed were numbers 14 and 15, the 13 earlier eggs having been lost to predation before the nest was discovered. If clutch sizes are almost always 2, a good assumption would be to place the loss on day 2 of incubation. If clutch sizes are usually between 2 and 4 the choice is not so clear. One would hope that the number of nests falling into these questionable periods would be small and that assumptions about them would have little impact on overall conclusions. Large numbers of such nests might necessitate combining the two periods into one, laying and incubation, which would have a clearly defined beginning and ending. One cannot simply throw out those nests whose loss presents an ambiguity, since only nests which fail present such an ambiguity, and a resulting bias would then be introduced.

2. PARAMETER ESTIMATION FOR THE SIMPLE MODEL

Having observed a random sample of size K (fixed) under the above model (i.e.

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we observe X_1, X_2, \dots, X_K , we wish to estimate p , the daily survival probability. The assumption that all nests have the same length in days (J days) for each complete period can be relaxed. Each nest is now allowed to have an unknown but fixed length, J_k , $k=1, 2, \dots, K$. The log likelihood function is then

$$\begin{aligned} \log L = & \log \prod_{k=1}^K [\theta_{J_k-T_k+1}]^{Y_k} + \left[\sum_{k=1}^K T_k Y_k \right] \log p \\ & + \sum_{k=1}^K (T_k - 1)(1 - Y_k) \log p + (K - \sum_{k=1}^K Y_k) \log(1 - p) \\ & + \log \prod_{k=1}^K \left[\sum_{j=1}^{J_k-T_k+1} \theta_j \right]^{1-Y_k}. \end{aligned}$$

Differentiating, we find the maximum likelihood estimator (mle), \hat{p} , of p to be

$$\hat{p} = 1 - \left[(K - \sum_{k=1}^K Y_k) / \left(\sum_{k=1}^K T_k \right) \right]. \quad (1)$$

and its asymptotic variance,

$$\frac{1}{K I(p)} = \frac{1}{K} \frac{p^2(1-p)^2}{E(T)(1-p)^2 + [E(Y)-1](1-2p)},$$

where $E(T)$ and $E(Y)$ refer to the expected values of the random variables T and Y , respectively (Roussas, 1973, pp. 81-86). This variance can be estimated when $Y \neq 1$, by

$$\hat{\sigma}_p^2 = \hat{p} (1-\hat{p}) \left/ \sum_{k=1}^K T_k \right.. \quad (2)$$

This estimate of variance is not maximum likelihood since the mle's of $E(T)$ and $E(Y)$ will depend on the values of J_k and θ_j . Monte Carlo simulations in Hensler and Nichols (1981) show how close the suggested estimator of variance is to the real value in several cases.

It should be clear from examination of the model and estimators that some choice can be allowed in the unit of time selected, although the "day" unit seems in many respects the most natural. One can use intervals greater than 1 day (for example, visiting nests every 2nd or 3rd day), but a clear determination of success or failure must be possible. If nests are found with eggs on one visit and on the next visit the nest is empty, the second visit must not be so long after the first that one is

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unsure whether the nest was lost and abandoned or whether hatching and fledging occurred.

The complete period to a nest's success is defined in terms of the units chosen; in the above model we defined a nest as successful if it had survived J days. We could have defined a successful nest as one surviving for J^* two-day periods if nests were visited only every other day. The parameter estimated then becomes the two-day survival probability instead of the daily survival probability.

3. MODELLING DIFFERENTIAL SURVIVAL

Consider now the case where all nests have the same number of days in the complete period under consideration (J days). We may wish to estimate the probability that a nest survives the entire period, i.e. p^J . If the nesting cycle is considered to be composed of two or more distinct periods each with distinct p values (say egg incubation and nestling rearing periods), then we may wish to estimate an overall probability that a nest succeeds through all periods. Differences in daily survival probabilities may occur between two populations at each period, and yet differences in overall success may be insignificant. In the case of two periods with daily success probabilities of p_1 and p_2 and of lengths J_1 and J_2 days until completion, the overall parameter of interest is

$$s = p_1^{J_1} p_2^{J_2}.$$

So if for one population we estimate $\hat{s}_1 = (.963)^{18} (.99)^{15} = .436$ and for another we find $\hat{s}_2 = (.98)^{18} (.969)^{15} = .433$, it may well be that \hat{s}_1 and \hat{s}_2 show no statistical difference while the daily rates do (i.e. .963 vs. .98 and .99 vs. .969). We need not only to estimate these parameters, but also to estimate a variance associated with these parameter estimates in order to make comparisons. We can address this problem in general by considering an estimate of $\beta = \beta(p)$ and of its variance where β is any one-to-one transformation of p . It is shown (Roussas, 1973, p.247) that for maximum likelihood estimates (mle), $\hat{\beta} = \beta(\hat{p})$. Further the asymptotic variance is

$$\cdot \frac{1}{KI(\beta)}, \text{ where } I(\beta) = -E \left[\frac{\partial^2 \log f(Y, T | \beta)}{\partial \beta^2} \right],$$

and $f(Y, T | \beta)$ is the joint density of (Y, T) parameterized in terms of β . It can be shown using the theory of the Fisher information (Zacks, 1971, pp.9-15) that

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$$I(\beta) = \left[\frac{dp}{d\beta} \right]^2 I(p)$$

$$\text{Thus } \text{var}(\hat{\beta}) = \frac{1}{KI(\beta)} = \frac{1}{KI(p)} \left[\frac{d\beta}{dp} \right]^2$$

which can be estimated by $\hat{v}_{\hat{\beta}}^2 = \hat{v}_p^2 \hat{\beta}'^2$ where $\hat{\beta}'$ is an estimate for $d\beta/dp$.

Returning to the special case where $\beta(p) = p^J$, we see that $\hat{\beta} = \hat{p}^J$

$$\text{and } \hat{v}_{\hat{\beta}}^2 = \hat{v}_p^2 (J\hat{p}^{J-1})^2 = \frac{\hat{p}(1-\hat{p})}{\sum_{k=1}^K T_k} (J\hat{p}^{J-1})^2 . \quad (3)$$

Suppose we wish to estimate the above overall nesting success parameter $s = p_1^{J_1} p_2^{J_2}$. Day-to-day and nest-to-nest independence is assumed, and using results for the variance of a product of independent random variables (Raj, 1968, p.12) we see that

$$\hat{s} = \hat{p}_1^{J_1} \hat{p}_2^{J_2} = \hat{\beta}_1^{J_1} \hat{\beta}_2^{J_2} , \quad (4)$$

$$\begin{aligned} \hat{v}_{\hat{s}}^2 &= [E(\hat{\beta}_1)]^2 \hat{v}_{\hat{\beta}_2}^2 + [E(\hat{\beta}_2)]^2 \hat{v}_{\hat{\beta}_1}^2 + \hat{v}_{\hat{\beta}_1}^2 \hat{v}_{\hat{\beta}_2}^2 \\ &\approx \hat{p}_1^{2J_1} \hat{v}_{\hat{\beta}_2}^2 + \hat{p}_2^{2J_2} \hat{v}_{\hat{\beta}_1}^2 + \hat{v}_{\hat{\beta}_1}^2 \hat{v}_{\hat{\beta}_2}^2 \end{aligned} \quad (5)$$

is an estimate of its asymptotic variance. We use here the result that a mle is asymptotically unbiased and hence $E(\hat{\beta}_1) \rightarrow \beta_1$ which can be estimated by $\hat{\beta}_1 = \hat{p}_1^{J_1}$.

Having two independent, asymptotically normal estimates of overall nesting success and corresponding variances, given, respectively, by $\hat{s}_1, \hat{s}_2, \hat{v}_{\hat{s}_1}, \hat{v}_{\hat{s}_2}$, (from two areas, for example), one can then compare these two estimates using the statistic

$$\frac{(\hat{s}_1 - \hat{s}_2)}{\sqrt{\hat{v}_{\hat{s}_1}^2 + \hat{v}_{\hat{s}_2}^2}}$$

whose asymptotic distribution is standard normal.

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4. RESULTS

To illustrate the above calculation, data from two studies are used. The first study was of Mourning Dove (*Zenaidura macroura*) nests located on the Patuxent Wildlife Research Center during two years, 1979 and 1980 (Nichols, *et al.*, 1984). For this study nests were visited daily, and the nesting cycle was considered in two periods: (i) a laying and incubation period and (ii) a nestling period. The first period was of fixed length 16 days and ran from the day the first egg was laid until the first egg hatched; the second period was of fixed length 10 days and ran from the day after the first egg hatched until 10 days thereafter. For nests first found during the nestling period approximate aging of nestlings was used in deciding when a nest was 10 days into the nestling period. No nests fledged young before 10 days.

The second study was of Black-crowned Night-Herons on Hope Island, RI, and on Clarks Island, MA, in 1979 (Custer *et al.*, 1983). For this study nests were visited every 3 to 7 days, and the nesting cycle was considered in three periods: (i) laying period, (ii) incubation period, and (iii) nestling period. The definitions of these periods are given above. Since nests were visited only every 3 to 7 days, approximate techniques were used which estimated the day a nesting attempt failed as occurring at the mid-point between the last two visits. Daily survival probabilities estimated using this approximation have been considered in Mayfield (1961) and Miller and Johnson (1978). The number of days in each complete period was allowed to be variable among nests, but these values did not vary often from the expected period lengths of $J_1 = 7$ days for laying, $J_2 = 18$ days for incubation, and $J_3 = 15$ days for the nestling period. Estimates of an overall success probability, \hat{s}_i , and of its variance $\hat{\Sigma}_i$, are calculated from daily parameters for the i^{th} colony as:

$$\hat{s}_i = \hat{p}_{i1}^{J_1} \hat{p}_{i2}^{J_2} \hat{p}_{i3}^{J_3} \quad (6)$$

$$\hat{\Sigma}_i^2 = \hat{p}_{i1}^{2J_1} \hat{p}_{i2}^{2J_2} \hat{p}_{i3}^{2J_3} + \hat{p}_{i1}^{2J_1} \hat{p}_{i3}^{2J_3} \hat{p}_{i2}^{2J_2} \hat{p}_{i3}^{2J_2} \hat{p}_{i1}^{2J_3} \hat{p}_{i1}^{2J_1}$$

$$+ \hat{p}_{i1}^{2J_1} \hat{p}_{i2}^{2J_2} \hat{p}_{i3}^{2J_3} + \hat{p}_{i2}^{2J_2} \hat{p}_{i1}^{2J_1} \hat{p}_{i3}^{2J_3} + \hat{p}_{i3}^{2J_3} \hat{p}_{i1}^{2J_1} \hat{p}_{i2}^{2J_2} + \hat{p}_{i1}^{2J_1} \hat{p}_{i2}^{2J_2} \hat{p}_{i3}^{2J_3}$$

where $\hat{\sigma}_{ij}^2 = \hat{V}_{ij}^2 (J_j \hat{p}_{ij}^{J_j-1})^2$ as in (3). These represent a straight-

forward application of formulae (4) and (5) to three periods.

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In addition, for comparison, a daily success probability for the entire nesting cycle is calculated for the data presented in Tables 1 and 2; these calculations assume no difference in daily success probabilities among the periods of the nesting cycle. From these overall daily success probabilities one can calculate an overall success probability, $\hat{s} = \hat{p}^{\sum j_i}$ for the entire nesting cycle, for comparison with overall success probabilities calculated using formulae (4) and (6) and whose values are shown in Tables 3 and 4.

Shown, also, in Tables 1 and 2 are values of \bar{Y} . Comparisons of \bar{Y} values to values of \hat{p}^j show that in most cases \bar{Y} is considerably higher. When most nests are found on the first day of their nesting period (as in the Mourning Dove nestling period, Table 1) \bar{Y} is not as biased. The Mayfield method corrects for the bias in \bar{Y} when the assumptions of the model are met. For the Mourning Dove nestling period data in Table 1 we note that \bar{Y} is only slightly biased since 17 of the 19 nests were found on the first 2 days of their nesting periods. The Mayfield estimator is, however, also biased since it is even larger than \bar{Y} . This indicates that the data do not fit the model well. An examination of the original nest data reveals that of the 6 nests that failed, 5 failed after being observed for 7 or more days. So the assumption of constant daily survival probabilities for this period may not hold; many more of the nests that failed did so late into the period. Currently, however, no goodness-of-fit statistics have been developed for this model.

In comparing overall success between years or colonies (Tables 3 and 4) we have used overall success probabilities based on formulae (4) and (6). Note that when daily survival rates do not significantly vary between periods, as in the Mourning Dove data (Table 1), the overall success probability based on formula (1) applied to the entire period is practically the same as that based on formula (4). Even when daily rates are shown to be significantly different, as in the Black-crowned Night-Heron data (Table 2), if differences are not large there is close agreement in overall rates based on these two approaches.

The data in Table 4 show that Clarks Island had a significantly ($p < 0.05$) higher success probability during the laying period than did Hope Island. However, Hope Island had insignificantly ($p > 0.05$) but higher success probabilities in the other two periods, so that overall success showed no significant differences between the colonies.

Data from the above studies are used in this methods paper primarily to

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illustrate the calculations. The studies for which these data were collected involved additional data and were designed to address other questions. The mourning dove study was designed to assess the effects of daily *vs.* weekly nest visits on success; in the Black-crowned Night Heron study we investigated differences in organochlorine contaminant levels at different geographical locations and the effects of both contaminants and locations on reproductive success. In particular, the data from Clarks Island and Hope Island were considered to be from similar areas; we wanted to combine these data for comparing against nesting success data from colonies in the southern United States. In order to combine them, we tested for differences between the colonies and found no significant difference in overall success but a difference in laying success. Thus, in searching for regional effects on overall nesting success, these colonies could reasonably be combined in a northern region.

In summary, the Mayfield method can be shown to correct for the bias associated with Y when model assumptions seem to fit the data. If differences in daily survival probabilities are suspected among different periods of the nesting cycle the Mayfield method can be used for each period, and the resulting estimates can be combined to achieve an overall success probability and variance which can be used in statistical comparisons. Differences in success at one period can be offset by those of another period, and the overall success probabilities can show no significant differences. It is important, then, to compare overall success and not just daily success probabilities.

ACKNOWLEDGEMENT

I wish to thank Tom Custer for providing the data on Black-crowned Night Herons which started the work on this problem, and James Nichols for the use of the Mourning Dove data. I thank both for their help in preparing this manuscript.

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Table 1

Nest success for Mourning Doves from the Patuxent Wildlife Research Center, Laurel, MD in 1979. (Data from Nichols et al., 1984)

	Nesting Period		Entire Cycle (laying, incubation, and nestling)
	Laying and Incubation	Nestling	
Expected number of days in period; J	16	10	26
Number of nests; K	27	19	31
Number of successful nests; ΣY_k	15	13	13
Total nest days of observation; ΣT_k	239	167	406
Estimated daily survival probability; \hat{p}	0.9498 A ¹	0.9641 A	0.9557
Estimated standard deviation of \hat{p} ; $\hat{V}_{\hat{p}}$	0.01413	0.01440	0.01022
Estimated success probability for period; \hat{p}^J	0.4386	0.6938	0.3079
Estimated standard deviation of \hat{p}^J ; $\hat{V}_{\hat{p}^J} \hat{p}^{J-1}$	0.1044	0.1036	0.0856
Proportion of observed nests which were successful; \bar{Y}	0.5556	0.6842	0.4194

¹Daily survival probabilities with same letter cannot be separated at $\alpha = .05$ (standard normal test).

Functions of survival probabilities

Table 2

*Nest success for Black-crowned Night Herons from Hope Island,
RI, in 1979. (Data from Custer et al., 1983)*

	Nesting period			Entire Cycle (laying, incubation, and nestling)
	Laying	Incubation	Nestling	
Expected number of days in period; J	7	18	15	40
Number of nests; K	107	154	139	165
Number of successful nests; ΣY_k	97	147	137	146
Total nest days of observation; ΣT_k	433	2781	1948	5162
Estimated daily survival probability; \hat{p}	0.97691 A ¹	0.99748 B	0.99897 B	0.99632
Estimated standard deviation of \hat{p} ; $\hat{V}_{\hat{p}}$	0.0072184	0.0009502	0.0007256	0.0008428
Estimated success probability for period; \hat{p}^J	0.8491	0.9557	0.9847	0.8629
Estimated standard deviation of \hat{p}^J ; $\hat{V}_{\hat{p}^J} \hat{p}^{J-1}$	0.0439	0.0164	0.0107	0.0292
Proportion of observed nests which were successful; \bar{Y}	0.9065	0.9545	0.9856	0.8848

¹Daily survival probabilities with the same letter cannot be separated using the Bonferroni multiple comparison at $\alpha = 0.05$ (Neter and Wasserman, 1974 pp.146-159 and 480-482).

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Table 3

*Nesting success for Mourning Doves from the Patuxent Wildlife Research Center, Laurel, MD for two years, 1979 and 1981.
(Data from Nichols et al., 1984)*

Year	Period (j)		Overall
	Laying and Incubation (J ₁ =16 days)	Nestling (J ₂ =10 days)	
1979 (K=31) ¹	0.9498 ² (0.01413)	0.9641 (0.01440)	0.3043 ⁴ A (0.0862)
	0.4386 ³ A ⁵ (0.1044)	0.6938 A (0.1036)	
1980 (K=28)	0.9434 (0.01833)	0.9517 (0.01780)	0.2400 A (0.0882)
	0.3937 A (0.1224)	0.6095 A (0.1140)	

¹Number of nests observed during the study; not all nests were observed during both periods.

²The estimated daily survival probability \hat{p}_j and, in parentheses below, its estimated standard deviation.

³The estimated survival probability for the period, $\hat{p}_j^{J_j}$, and, in parentheses below, its estimated standard deviation.

⁴The estimated overall success probability, $\hat{s} = \hat{p}_1^{J_1} \hat{p}_2^{J_2}$, and, in parentheses below, its estimated standard deviation.

⁵Success probabilities between years with the same letter could not be separated at $\alpha = 0.05$ (standard normal test).

Functions of survival probabilities

Table 4

Nesting success for Black-crowned Night-Herons from two colonies in 1979. (Data from Custer et al., 1983.)

Colony	Period (j)			Overall
	Laying (J ₁ =7 days)	Incubation (J ₂ =18 days)	Nestling (J ₃ =15 days)	
Clarks Is. MA (K=127) ¹	.99365 ² (.0044753) .9564 ³ A ⁵ (.0302)	.996761 (.00122233) .9433 A (.0208)	.99737 (.00131406) .9613 A (.0190)	.8672 ⁴ A (.0375)
Hope Is., RI (K=165)	.97691 (.0072184) .8491 B (.0439)	.997483 (.00095017) .9557 A (.0164)	.99897 (.00072561) .9847 A (.0107)	.7990 A (.0444)

¹Number of nests observed during the study; not all nests were observed during all periods.

²The estimated daily survival probability \hat{p}_j and, in parentheses below, its estimated standard deviation.

³The estimated survival probability for the period, $\hat{p}_j^{J_j}$, and, in parentheses below, its estimated standard deviation.

⁴The estimated overall success probability, $\hat{s} = \hat{p}_1^{J_1} \hat{p}_2^{J_2} \hat{p}_3^{J_3}$, and, in parentheses below, its estimated standard deviation.

⁵Success probabilities between colonies with the same letter could not be separated at $\alpha = 0.05$ (standard normal test).

PRIOR KNOWLEDGE AND ORNITHOLOGY

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SUMMARY

Most biologists think that the concept of probability is indisputable. Here, subjective inference is introduced as a possible alternative to frequentist statistical inference. The philosophy supporting subjective inference is presented, followed by some examples of the subjective inference of bird ringing data; the data were obtained from a computer simulation of an avian population. The paper concludes with some problems and prospects concerning the introduction of subjective inference in bird ringing analysis.

Keywords: SUBJECTIVE INFERENCE; RINGING DATA; COMPUTER SIMULATION

1. INTRODUCTION

The aim of the statistical inference of bird ringing data is to increase one's knowledge of the dynamics of avian populations. Analysis of these data can give insight into migration habits, mortality factors, mean life span, etc. Extending one's knowledge was once an end to itself, its only purpose being to satisfy the curiosity of the researcher. More and more scientific investigation of population dynamics has a more pragmatic justification: to understand the principles of the relationships within an animal population in order to predict the future (if any) of this population.

A study of the population dynamics of the Grey Heron (*Ardea cinerea L.*) in the coastal area of the Netherlands (Blok, 1973) started in 1963 as the fulfilment of the curiosity of a biologist. Now 20 years later, after ringing nearly 20,000 herons, recovering over 2,500 rings and spending thousands of hours observing mating, brooding and foraging herons, when one is asked to make predictions on the future of the Dutch Grey Herons based on the analysis of ringing data, difficulties might arise. There are two main reasons for this, one practical and one theoretical:

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- (i) Samples obtained from ringing experiments usually are too diverse to be treated as homogeneous; dividing the sample into homogeneous cohorts will almost certainly result in sub-samples that are too small to be of any practical use in a statistical analysis.
- (ii) Ringing data statistics describe the past. Even if one could bypass the practical problem posed above, one can never use the methods proclaimed in texts such as Seber (1973) and Brownie *et al.* (1978) to substantiate a statement of the kind "the probability that the Grey heron colony in Stompetoren in the Netherlands will exist in 1990 is 0.20, but given proper protection the probability will be 0.82". Unfortunately such statements are often asked for, for example in Environmental Impact Assessments that use cost/benefit analyses.

In this paper I wish to bring subjective statistical inference to your attention as an alternative to the more commonly used frequentist statistical inference.

Statistics in general can be defined as: the study of how information should be employed to reflect on, and give guidance for action in a practical situation involving uncertainty (Barnett, 1973). The two different approaches towards statistical inference posed above differ as to what kind of information is legitimate and in which practical situations the inference is applicable.

2. SUBJECTIVE INFERENCE IN GENERAL

Subjective inference gives probability the following meaning:

"Probability measures a particular individual's degree of belief in some eventuality conditional on his relevant experience".
(Barnett, 1973)

Thus here probability expresses one's degree of belief in face of the uncertainty of an event, conditional on the amount of knowledge one has of the occurrence of that event. Sample data may play a major role in this knowledge, but other, particular non-numeric, data can and should be included in the analysis. Hence, not only ringing data provide legitimate information and other relevant information is equally important.

An important criticism of subjective inference follows immediately from the preceding paragraph: if probability is subjective and related to a particular person's knowledge, then what happens to objective science? Another criticism is the (frequentist) dilemma when combining numeric and non-numeric data in a statistical

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analysis. A thorough (and lucid) comparison of statistical inference and the difficulties that can arise can be found in Barnett (1973).

As probability has become a degree of belief, the probability density function can be viewed as the distribution of one's degree of belief over the interval (0,1), hence from here I shall speak of the belief functions instead of probability density functions. There are three kinds of belief functions:

- (i) The prior belief function. This is the function that describes the distribution of the probability before one has knowledge of the data. The knowledge leading to the prior distribution can have been from earlier experiments, knowledge gained through the years or some derivation of a logical fact.
- (ii) The data belief function. The data belief function describes the distribution of one's belief over the possible values of belief (here the (0,1) interval). The data belief function is closely related to the likelihood function. The likelihood function acts as an expression of the information provided by sample data about unknown parameters of the probability model (Barnett, 1973); it provides the necessary data information in Bayes theorem. By multiplying the likelihood function by an appropriate constant a belief function arises that is in the proper proportion to the prior and posterior belief functions.
- (iii) The posterior belief function. Combining the prior and data belief function in Bayes theorem leads to the distributions one would attach to the probability after seeing the data (the mathematical justification of this merger can be examined in text books on this subject, such as Barnett, 1973; Lindley, 1965; Novick and Jackson, 1974).

A final new concept is the credibility interval as an alternative to the confidence interval. The quite complex definition of confidence intervals is replaced with a natural way of expressing one's confidence in a probability statement. A 95%-credibility interval is any interval or collection of intervals in which the curve defining the belief function covers 95% of the total area beneath the curve. Usually one chooses the shortest interval covering the indicated area (see Novick and Jackson, 1974). This High Density Region (HDR) definition always lies within the range 0-1.

3. SUBJECTIVE INFERENCE FROM RINGING DATA

In order to be able to compare the results of a subjective analysis with known

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parameters a ringing experiment was simulated on a computer. The parameters one could define in the hypothetical ringing experiment were the survival probabilities of the young of the year (θ_1), second year birds (θ_2) and male (θ_4) and female (θ_3) adults and the recovery probability of a ring given that the bird had died. The simulation proceeded as follows: of 1,000 ringed young of the year it was calculated how many birds survive to their second year, and of the dead birds a number of rings was reported. The same procedure was followed for the second year and adult birds until the last bird died. The recovery rate was assumed to be normally distributed with mean 0.2. This simulation was part of a larger investigation in which I wanted to be able to distinguish between male and female mortality (field observations hint at a possible difference), but in this paper the distinction is of no importance. In the examples of subjective inference the following simulated data were used (the hypothetical parameters are shown in brackets):

Survival probability	Number of reported rings
Young of the year ($\theta_1 = 0.25$)	140
Second year ($\theta_2 = 0.35$)	29
Adult females ($\theta_3 = 0.50$)	8
Adult males ($\theta_4 = 0.75$)	12

A frequentist likelihood analysis would produce the following results:

Survival estimates	Asymptotic variance estimates
$\hat{\theta}_1 : 0.25$	$\hat{\sigma}_1^2 : 0.001$
$\hat{\theta}_2 : 0.41$	$\hat{\sigma}_2^2 : 0.005$
$\hat{\theta}_3 : 0.60$	$\hat{\sigma}_3^2 : 0.003$
$\hat{\theta}_4 : 0.78$	$\hat{\sigma}_4^2 : 0.012$

The estimates were obtained from extensions of the method of Haldane (see Mead *et al.*,

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1979). A frequentist analysis stops here, given the calculation of some additional confidence intervals. For the subjectivist the example mentioned above would be the same as expressing ignorance. The prior belief function would be uniform, indicating that all probabilities are equi-probable. No difference can be seen between the data belief function and the posterior belief function. The subjectivist will however proclaim that there is more information.

Example 1

A biologist might want to express his vague belief that extremely small or large probabilities are less credible than intermediate values. Figure 1 shows such a prior belief in combination with the data belief function of the female recovery data.

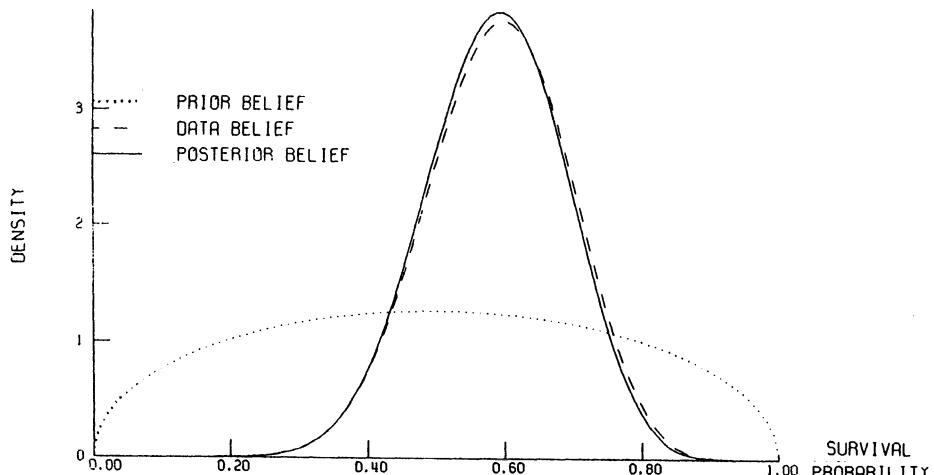


Figure 1 The 'vague' prior belief function has hardly any influence on the distribution of probability arising from the ringing data. If, however, due to outliers, the mode of the data belief function would be near 0 or 1 the effect would be more noticeable.

The prior belief function has hardly any influence on the data belief function, as the mode of the data belief function lies well within the credibility range.

Example 2

A ringing experiment is not performed alone, but in combination with observations of the various aspects of the population dynamics. From these observations one

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might gain insight into the age distribution of the live population (e.g. by colour rings), and thereby be able to calculate the survival estimates (Seber, 1973, p.400). Such observations were also simulated stochastically, resulting in an estimate of the female survival of 0.45. Figure 2 shows the effect of this prior knowledge.

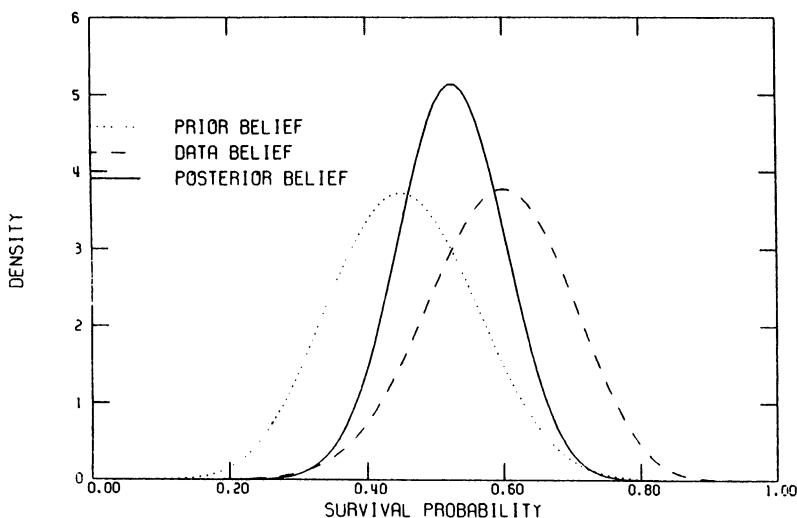


Figure 2 By coincidence the prior distribution is the symmetrical image of the data belief function; subjective inference copes with this by producing a posterior distribution that is the intermediate of both other functions. As more density is concentrated around the mode of the posterior a High Density Region will be narrower.

Example 3

This last example shows that the extra information need not be strictly numerical. Extra information concerning survival probabilities can be obtained from counting the number of eggs in the nests. In Caswell *et al.* (1980) the algebraic relationship between fecundity and survival probability in a population with a stable age distribution is demonstrated. Assuming such an age distribution, and the fact that Herons never raise more than five pulli per season, a prior belief distribution results that contains nearly all its mass in the interval 0.45 to 1.0. Hence knowledge of the fecundity and the relation between fecundity and survival probability results in the analysis illustrated in Figure 3.

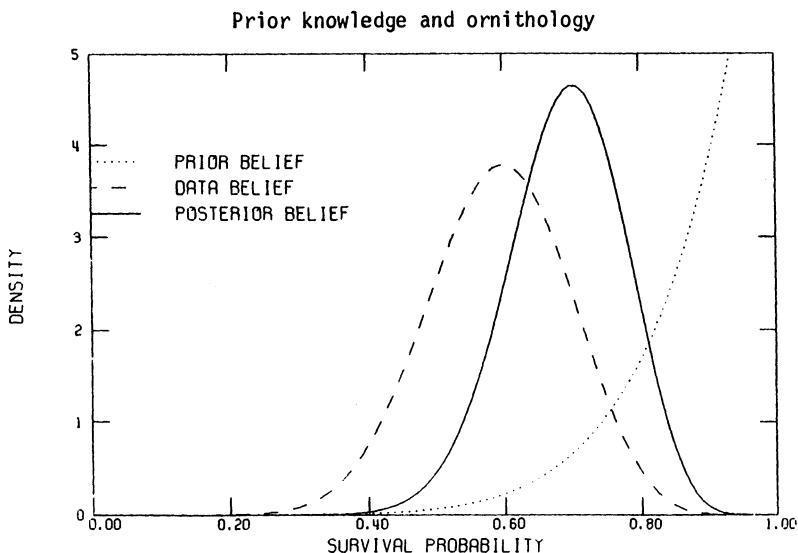


Figure 3 This graph demonstrates the effect of a prior distribution that nearly denies possible values of the survival probability; given this denial is legitimate, the resulting posterior shifts significantly to the right, whilst the High Density Region becomes narrower.

4. CONCLUSION

Reviewing the context of this paper I am fully aware that it cannot serve as a source for alternative inference procedures for ringing data. All that was intended was to point out another view of probability. Before subjective inference can be used in the inference of ringing data, an algebraic basis of subjective ringing inference must be thoroughly presented. I have intentionally omitted any formulae substantiating the graphs presented; they do not fit in with a paper for statisticians and biologists. The algebra of combining prior and data belief functions into a posterior belief function is sufficiently published elsewhere (Barnett, 1973; Novick and Jackson, 1974; de Finetti, 1975; Ramsey, 1931). What remains is the collaboration of statisticians and ornithologists to extract information from various sources (Euring cards, field notes, previous experiments, common knowledge, etc.) and find ways of expressing this as prior knowledge.

In the above example we have concentrated upon a single parameter, θ_3 , as an illustration. In practice one could envisage a multivariate subjective approach.

Although much more can be said on subjective statistical inference I will now

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conclude this paper with a remark concerning a quotation from Hacking (1975, p.40) who traces the frequentist notion of probability back to the 'high sciences of the 17th Century' (mechanics and astronomy):

"subjective probability however is a child of the low sciences such as alchemy or medicine, which had to deal with opinion ..."

In my view biology too is a 'low science', in the sense that a great deal of the information available from experiments and field observations cannot be counted as easily as, say, atomic collisions in a test tube. If this information can be put to use the biological inference of ringing data can make a great step forward; subjective inference can be of great importance in this process.

INHERENT DIFFICULTIES IN ESTIMATING AGE-SPECIFIC BIRD SURVIVAL RATES FROM RING RECOVERIES

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SUMMARY

All methods for estimating age-specific survival rates from ring recoveries depend critically on a number of assumptions. Even if these assumptions hold, the estimating procedures require the further imposition of a constraint. Since survival probabilities of birds are believed to become 'constant' with increasing age, a commonly chosen constraint is that the survival probabilities in successive years for older birds are equal. It is shown here that such a constraint may appear reasonable and acceptable, but its use can produce highly misleading survival estimates. In other words, the constraint makes it possible to obtain a mathematical solution, but does not necessarily give biologically reliable survival estimates, no matter how many birds are ringed. The need to impose the constraint can be avoided altogether if the ring recovery data are supplemented with additional and relevant field information. This should make the problem of survival estimation mathematically feasible and improve the trustworthiness of the estimates.

Keywords: RING RECOVERIES; AGE-SPECIFIC SURVIVAL RATES; BIRD SURVIVAL;
NONIDENTIFIABILITY; CONSTRAINTS.

1. INTRODUCTION

The survival of birds of different age groups is often estimated by analysing ring recovery data arising from birds ringed as nestlings. The existing methods for data analysis depend critically on a number of assumptions. These assumptions have been discussed by various authors, and are well-known to analysts of ring recoveries (Anderson *et al.* 1981; Pollock and Ravelling 1982). However, it is in the nature of the ring recovery data that the survival estimates cannot be obtained uniquely,

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unless an additional constraint (a further assumption) is imposed. It is a common practice to use a constraint such as, that after a specified age the annual survival rate becomes constant - see, for example, Cormack (1970), Seber (1971 and 1972).

Lakhani and Newton (1983) have demonstrated, however, that this apparently innocuous assumption plays such a crucial role in the process of survival estimation, that if the assumption is violated, even in the slightest degree, then the survival estimates are liable to be untrustworthy. This is true even if all the other assumptions hold, and however large the number of birds ringed.

The present paper includes the arguments used by Lakhani and Newton (1983) and, in addition, draws attention to a further difficulty which also renders the use of the existing estimation methods unsatisfactory. This additional difficulty gives further support to Lakhani and Newton's conclusion that, for all practical purposes, age-dependent survival estimates obtained using the ringing recoveries alone, cannot be trusted. These results are of obvious interest not only to ornithologists, but also to scientists using similar methods in other fields, e.g. studies of fish and mammals.

2. DATA

The usual programme of field observations has been well described by Seber (1971) and North and Cormack (1981), but a brief summary using the same notation as in Seber is as follows.

Each year, for s consecutive years, a batch of nestlings is ringed and released. For t years, a record is kept of rings from dead birds reported each year. Denoting the number of nestlings released at the beginning of year i by R_i ($i = 1, 2, \dots, s$), and the number of birds from this cohort dying in year j (whose rings are recovered in the same year) by m_{ij} ($j = i, i + 1, i + 2, \dots, t$) the type of information arising from a four-year study ($s = t = 4$) is shown in Table 1.

3. PREVAILING METHODS

Several methods exist to estimate age-dependent survival from the type of data illustrated in Table 1. The assumptions underlying these methods have been described

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Table 1

*Symbolic representation of ring-recovery data
from a four-year study of birds ringed as nestlings
(after Lakhani and Newton, 1983)*

Year of banding	Number of nestlings ringed	Recoveries (m_{ij}) during year				Total recoveries
i	R_i	j = 1	2	3	4	$r_i = \sum_{j=1}^4 m_{ij}$
1	R_1	m_{11}	m_{12}	m_{13}	m_{14}	r_1
2	R_2		m_{22}	m_{23}	m_{24}	r_2
3	R_3			m_{33}	m_{34}	r_3
4	R_4				m_{44}	r_4

by North and Cormack (1981), and are:

- (a) the annual recovery rate of dead birds, i.e. the annual reporting probability, λ , is the same for all individuals and for all calendar years;
- (b) the annual survival probability, ϕ_i , depends on the age, i , of the bird but not on the calendar year;
- (c) events pertaining to a given bird are independent of those pertaining to any other bird.

It is of course possible for one or more of these assumptions to be unrealistic (see Anderson *et al.*, 1981), but the intention here is to comment on the reliability of some of the generally accepted methods of data analysis when the above assumptions are acceptable.

3.1 The Ratio Method

Cormack (1970) examined the then prevailing practice of using the ratio between the numbers found dead $(n + 1)$ years after release, to the numbers found dead n years after release, as an estimator of the annual survival, ϕ_n . He observed that, if N

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nestlings are released alive, the expected number of recoveries in succeeding years are respectively:

$$N(1 - \phi_1)\lambda, N\phi_1(1 - \phi_2)\lambda, N\phi_1\phi_2(1 - \phi_3)\lambda, N\phi_1\phi_2\phi_3(1 - \phi_4)\lambda, \dots,$$

so that the ratios of successive terms are

$$\phi_1(1 - \phi_2)/(1 - \phi_1), \phi_2(1 - \phi_3)/(1 - \phi_2), \phi_3(1 - \phi_4)/(1 - \phi_3), \dots,$$

and not $\phi_1, \phi_2, \phi_3, \dots$, as was assumed previously by other scientists. Thus, only if successive annual survivals are identical will the ratio provide a valid estimate of survival. Cormack noted further that 'with many species this assumption (of identical survivals) is reasonable when the birds are fully adult', in which case, it is 'possible to adapt this ratio method to obtain valid estimates of all the survivals'. However, he found that the estimates from such a procedure depended critically on the age at which survival is assumed to have become constant, and further, that any reduction in the length of time before constant survival is reached caused a reduction in the estimate of every annual survival, rendering the use of the method most unsatisfactory. Seber (1972) showed why such a reduction will often take place. He also discussed a number of variations of the ratio method, concluded that these were all generally unsatisfactory or invalid for estimating age-specific survival rates, and advocated using the more recent maximum likelihood methods as proposed by Cormack (1970) or Seber (1971).

3.2 Maximum Likelihood Method

The essential rationale of this method is to express the joint probability of observing the experimental data as a function (the likelihood function) of the unknown parameters (e.g. $\lambda, \phi_1, \phi_2, \dots$), and to use whichever set of parameter values ($\hat{\lambda}, \hat{\phi}_1, \hat{\phi}_2, \dots$) which maximises this function, as the estimates of the unknown parameters.

Cormack (1970) analysed the ring recovery data for Dominican Gulls, *Larus dominicanus* Licht., (see Fordham, 1970, Table 6) by setting up a multinomial type probability model and obtaining the maximum likelihood estimates of the recovery rate, λ , and the annual age-dependent survivals, ϕ_i - the joint probability of observing the m_{ij} values and also of not observing the $(R_j - r_j)$ values gave the likelihood function; and, differentiating the likelihood function (or its logarithm) successively with respect to each of the parameters, and equating these derivatives to zero, gave the maximum likelihood equations.

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There is no explicit solution for these equations, i.e. the parameter values cannot be expressed as closed algebraic expressions in terms of R_i and m_{ij} (the data), but instead, the equations must be solved numerically using an appropriate iterative algorithm.

Seber (1971) pointed out that the parameters in the likelihood function 'are not identifiable' (i.e. it is not possible to obtain a unique set of estimates $\hat{\lambda}$, $\hat{\phi}_1$, $\hat{\phi}_2$, etc.), but added that 'only one constraint is necessary for identifiability and, since survival probabilities for birds tend to settle down to a constant value with increasing age, the most natural constraint is $\phi_{t-1} = \phi_t$ '. Thus, the maximum likelihood approach requires not only the numerical solution of non-linear equations, but is also subject to the above (or similar) additional constraint.

3.3 Conditional Maximum Likelihood Method

Seber (1971) proposed a simpler model conditional upon the recoveries, r_i , from each cohort. This approach succeeded in eliminating λ , and led to a mathematically attractive analysis with simple explicit estimates. However, North and Cormack (1981) carried out a detailed study of this method and concluded that, although the method had attractive computational properties, it suffered from serious disadvantages which rendered it practically useless.

In any case, like the maximum likelihood method and indeed the ratio method, Seber's conditional maximum likelihood method is also subject to an additional constraint, such as $\phi_{t-1} = \phi_t$.

4. UNSATISFACTORY ASPECTS OF THE PREVAILING METHODS

Lakhani and Newton (1983) have pointed out that none of the available methods are satisfactory, even if the assumptions (a), (b) and (c) described earlier hold. This is because the unknown parameters cannot be estimated uniquely (unless enough "recovery" years are allowed for all possible recoveries to be reported) i.e. given the "data" values R_i ($i = 1, 2, 3, 4$) and m_{ij} ($j = i, i+1, \dots, 4$) of Table 1, it is simply not possible to obtain a unique set of estimates $\hat{\lambda}$, $\hat{\phi}_1$, $\hat{\phi}_2$, $\hat{\phi}_3$ and $\hat{\phi}_4$ of the corresponding unknown parameters. They point out that the use of the constraint such as $\phi_3 = \phi_4$, makes the parameters arbitrarily identifiable, i.e. it becomes mathematically possible to obtain a unique set of four estimates $\hat{\lambda}$, $\hat{\phi}_1$, $\hat{\phi}_2$ and $\hat{\phi}_3$,

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the need for the estimation of the parameter ϕ_4 having been eliminated through the assumption $\phi_3 = \phi_4$. However, although the imposition of the constraint makes the estimation problem mathematically tractable, this does not mean that the resulting estimates are necessarily reliable biologically. The estimates obtained, subject to the validity of the constraint such as $\phi_{t-1} = \phi_t$, may be so distorted by even small differences between ϕ_{t-1} and ϕ_t , that the ecologist, who assumes an apparently reasonable constraint, may well be grossly misled by the resulting estimates.

4.1 A Demonstrative Example

To demonstrate their point, Lakhani and Newton used artificially generated ring recovery data reproduced here in Table 2. These data are artificial in the sense

Table 2
*Artificial ring-recovery data from
 a four-year study of birds ringed as nestlings
 (after Lakhani and Newton, 1983)*

Year of banding	Number of nestlings ringed	Recoveries (m_{ij}) during year				Total recoveries	Numbers unaccounted for
		j = 1	2	3	4		
i	R_i					r_i	$R_i - r_i$
1	10 000	1200	400	120	84	1804	8196
2	10 000		1200	400	120	1720	8280
3	10 000			1200	400	1600	8400
4	10 000				1200	1200	8800

that for a given set of parameter values, they are the expected number of recoveries from 10,000 nestlings ringed each year. If these data are analysed, without using a constraint, then infinitely many solutions are possible. Some of the possible solutions (i.e. sets of parameter values) are shown in Table 3. Each set will satisfy exactly the equations arising from the "ratio" method or the "likelihood" methods applied to the data, and for each set the expected recoveries are exactly those in Table 2.

Since the intention underlying the study is to estimate survival for each age group, the problem now is to identify, out of an infinite number of sets of

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parameters (of which some sets are shown in Table 3), the particular set which most clearly reflects the one pertaining in nature.

Table 3

A selection of sets of parameter values under which the expected ring recoveries are exactly the same as those in Table 2. λ = recovery rate; ϕ_i = the survival in year i (after Lakhani and Newton, 1983)

Set	Parameters				
	λ	ϕ_1	ϕ_2	ϕ_3	ϕ_4
(a)	0.2	0.4	0.5	0.7	0.7
(b)	0.3	0.6	0.777778	0.914286	0.934375
(c)	0.4	0.7	0.857143	0.95	0.963158
(d)	0.5	0.76	0.894737	0.964706	0.974390
(e)	0.6	0.8	0.916667	0.972727	0.980374
(f)	0.7	0.828571	0.931034	0.977778	0.984091
(g)	0.8	0.85	0.941176	0.981250	0.986624
(h)	0.9	0.866667	0.948718	0.983784	0.988415

If the data of Table 2 are analysed subject to the constraint $\phi_3 = \phi_4$, using the ratio or likelihood methods, the unique solution is given by the set (a) in Table 3. This is because it is for this set alone that ϕ_3 is exactly equal to ϕ_4 . However, a closer inspection of Table 3 immediately draws attention to the unsatisfactory nature of the solution based on the constraint $\phi_3 = \phi_4$, for in Table 3 the ϕ_3 and ϕ_4 values are similar in most sets. This is also the case in other sets of parameter values not included in Table 3. Thus, suppose that the true set of parameters operating in the field is given by, for example, set (e), for which the ϕ_3 and ϕ_4 values are 0.972727 and 0.980374 respectively. These values will of course not be known to the ecologist, but from his knowledge of the bird species he may well consider it reasonable to suppose that $\phi_3 \approx \phi_4$, and so assume the constraint $\phi_3 = \phi_4$. However, the effect of this apparently innocuous assumption is that the estimation procedure converges on to set (a), misleading the ecologist into believing that the set (a) values 0.2, 0.4, 0.5, 0.7, 0.7 are reasonable estimates of λ , ϕ_1 , ϕ_2 , ϕ_3 , and ϕ_4 when, in fact, the true values are much higher at 0.6, 0.8, 0.917, 0.973 and 0.980.

In addition, a full maximum likelihood analysis will include the estimation of

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the variance-covariance matrix, Σ , of the estimates $\hat{\lambda}$, $\hat{\phi}_1$, $\hat{\phi}_2$, and $\hat{\phi}_3$ ($= \hat{\phi}_4$). An estimate of Σ is obtained by substituting the estimates of the parameters in the Hessian, H , of the log-likelihood function and then computing $-H^{-1}$. For the data of Table 2, this is

$$\begin{bmatrix} \hat{\lambda} & \hat{\phi}_1 & \hat{\phi}_2 & \hat{\phi}_3 \\ .000118 & .000343 & .000710 & .000929 \\ .000343 & .001058 & .002131 & .002788 \\ .000710 & .002131 & .004544 & .005808 \\ .000929 & .002788 & .005808 & .007845 \end{bmatrix}$$

from which the estimated asymptotic standard errors of the estimates are 0.011, 0.033, 0.067, and 0.089 respectively, giving the ecologist a totally false sense of the accuracy and reliability of his estimates, unless he is aware of the possibility of large bias in his estimates leading to large mean-squared errors. For example, using the method developed by Roy and Bose (1953), of which a brief account is given in Morrison (1976, p.135), the large-sample 95% simultaneous confidence intervals for the "true" parameter values are given by:

parameter estimate \pm S.E. of parameter estimate \times constant
where the constant = $\left(\frac{\text{the upper } 5\% \text{ critical value of } \chi^2}{v \text{ d.f.}} \right)^{\frac{1}{2}}$

and where v = total number of parameters.

Using this approach, which is known to be highly conservative, the 95% simultaneous confidence intervals are:

$$\begin{aligned} 0.1665 &< \lambda < 0.2335 \\ 0.2998 &< \phi_1 < 0.5002 \\ 0.2924 &< \phi_2 < 0.7076 \\ 0.4272 &< \phi_3 < 0.9728 \\ 0.4272 &< \phi_4 < 0.9728 \end{aligned}$$

all of which fail to include the "true" parameter values given by set (e).

The example given here considers data for only 4 years, but other examples using larger number of years show the same problem. Further, in practice, with more years, the numbers recovered from higher aged birds will tend to be small, causing all survival estimates to be inefficient. For this reason, Seber (1971) recommends using a short sequence of 4 years. Of course, if sufficient years are allowed for all possible recoveries to be reported, then the need to use the constraint can be

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avoided (see point 3 under Concluding Remarks).

Lakhani and Newton make the following points.

- (a) The fact that the data in Table 2 are artificially generated does not affect their argument.
- (b) The data of Table 2 are not an isolated set - it is quite easy to generate many other data sets, for which the analysis based on a constraint will be misleading.
- (c) Any demonstrative data set can be scaled so as to make the standard errors of the estimates as small as we like.
- (d) It is in the nature of the ring recovery data that survival estimates, using ring recoveries alone, cannot be guaranteed to be trustworthy.
- (e) Increasing the sample size does not protect us from the above pitfall.
- (f) Following the estimation of the parameters, if a "goodness-of-fit" test gives a low χ^2 -value, it does not necessarily mean that the estimates are reliable. Thus, in the demonstrative example above, the χ^2 -value corresponding to the parameter estimates given by set (a) is zero, even though the true values of set (e) are much higher. This is comparable to the general problem, often encountered in biological applications, of having different models which describe a data set well.

Lakhani and Newton give a second demonstrative example using real data. They give a detailed discussion of their results, and of the use of further field information to supplement the ring recovery data with a view to obtaining more trustworthy estimates.

4.2 An Additional Difficulty

In analysing Fordham's (1970, Table 6) ring recovery data, Cormack found that for the ratio method the survival estimates depend critically on the specification of the age at which the survival is assumed to have become constant. Thus, using the ratio method, he obtained the following estimates:

- (i) if the adult survival, ϕ_A , is assumed to operate from the third year onwards:-

$$\hat{\phi}_1 = 0.695, \hat{\phi}_2 = 0.781 \text{ and } \hat{\phi}_A = 0.811;$$

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- (ii) if the adult survival is assumed to commence in the second year:-

$$\hat{\phi}_1 = 0.658 \text{ and } \hat{\phi}_A = 0.780;$$

- (iii) if the survival is assumed to be the same in all years:-

$$\hat{\phi}_A = 0.618.$$

Thus, any reduction in the length of time before constant survival is assumed, caused a reduction in the estimate of every annual survival.

Cormack considered that this property of the ratio method 'renders the use of the method most unsatisfactory', and he used the maximum likelihood approach to analyse Fordham's data, assuming constant survival from the third year onwards. Seber (1972) studied this property of the ratio method in detail, and concluded that the ratio method was unsatisfactory for estimating age-specific survival rates; and he advocated using the then recent maximum likelihood methods as proposed by Cormack (1970) or Seber (1971).

It is obviously of interest to check how well the maximum likelihood methods behave if the specification, of the age at which the survival is assumed to have become constant, is allowed to vary. If this is done for Fordham's data, the following results are obtained using the full maximum likelihood approach:

- (i) if the adult survival is assumed to operate from the third year onwards:-

$$(\hat{\lambda} = 0.184), \hat{\phi}_1 = 0.831, \hat{\phi}_2 = 0.899 \text{ and } \hat{\phi}_A = 0.931;$$

(The results given in Cormack's Table A are subject to rounding off errors, and so appear different from the above.)

- (ii) if the adult survival is assumed to commence in the second year:-

$$(\hat{\lambda} = 0.105), \hat{\phi}_1 = 0.703 \text{ and } \hat{\phi}_A = 0.809;$$

- (iii) if the survival is assumed to be the same in all years:-

$$(\hat{\lambda} = 0.085), \hat{\phi}_A = 0.681.$$

It will be seen that, as with the ratio method, any reduction in the length of time before constant survival is assumed causes a reduction in the estimate of every annual survival. Similar results are obtained if, instead of using the full maximum likelihood method, we use Seber's conditional maximum likelihood method. Thus, the likelihood procedures appear to be capable of exhibiting the very property which is supposed to render the ratio method "unsatisfactory".

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5. CONCLUDING REMARKS

1. Though a constraint such as $\phi_{t-1} = \phi_t$ gets round the problem of nonidentifiability, the decision to use the constraint can be tantamount to discarding all other apparently equally good sets of possible survival estimates (as in Table 3) except the one set for which the exact equality of ϕ_{t-1} and ϕ_t holds. However, the set, for which the exact equality holds, may not necessarily be the one closest to the set prevailing in reality. The use of the constraint is, therefore, liable to yield misleading estimates.
2. It is a common practice to assume that the survival probabilities for birds settle down to a constant value with increasing age. The ratio method has been criticised and rejected on the grounds that the estimates obtained using the ratio method depend critically on the age at which survival is assumed to have become constant. It is demonstrated here that the likelihood methods are not necessarily free from this limitation.
3. Lakhani and Newton have pointed out that, if enough years are allowed for all possible recoveries to be reported, then the problem of nonidentifiability and the need to use the constraint can be avoided. However, if the time period of the study is extended, then the assumptions, of λ and ϕ_i remaining constant, are unlikely to hold true.
4. As discussed by Lakhani and Newton, the usual ring recovery data could be over a short duration, but supplemented by additional parallel research to obtain independent information about at least one of the required parameters. For example, it may be feasible to estimate ϕ_1 by attaching radio transmitters to a sample of same-age birds and monitoring their fate over a period of one year. Any parameter estimated from the additional independent information will, of course, be subject to error. The problem of using the ring recovery data to obtain efficient conditional estimates of the remaining parameters (conditional upon the estimate of the independently estimated parameter which is itself subject to estimation error) is not straightforward. A paper describing a numerical solution to this problem is under preparation.

ACKNOWLEDGEMENT

I thank the British Ecological Society for permission to quote from *The Journal of Animal Ecology*. I am grateful to Mr P.Rothery for many useful discussions, and to Dr B.J.T. Morgan and Dr P.M. North for their detailed and constructive comments on an earlier draft.

THE EFFECT OF AGE ON SURVIVAL IN THE CANADA GOOSE,
(*BRANTA CANADENSIS*) IN NOTTINGHAMSHIRE

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SUMMARY

The number of Canada Geese in Nottinghamshire rose dramatically between 1965 and 1980. Birds in the north of the county have been trapped and ringed during the annual moult since 1968. These mark-recapture data have allowed estimates to be made for the annual survival of birds that hatched in all years from 1970 to 1980. There is evidence that the probability of survival is lowest for birds in their first year, rising through the second and third year. Older (adult) birds have the highest survival rates. Superimposed upon this is a progressive decline in survivorship of all age classes through the 1970's. This is probably due to a combination of factors, of which increased shooting pressure is one.

Keywords: SURVIVAL ESTIMATES, MARK-RECAPTURE, CANADA GOOSE.

1. INTRODUCTION

A recent paper by Lakhani and Newton (1983) (see also Lakhani, 1985, in this volume) has drawn attention to the facts that firstly the majority of estimates of age-specific survival of birds are based upon the recovery of dead birds, and secondly that these estimates frequently make assumptions that may be biologically unsound. More accurate estimates of survival rates can be obtained from the recapture alive of previously marked birds, but for many species the recapture rates are so low that the errors in the estimates become unreasonably large.

In only a few situations have species been studied that provide a sufficiently high recapture rate to generate confidence in the estimates, and it is only in these instances that it is possible to compare the estimated survival rates for animals of different ages. Examples where the data set is sufficiently complete to allow estimation both from live recaptures and dead recoveries are even fewer. We report here

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upon a study of Canada Geese (*Branta canadensis*) in north Nottinghamshire that has continued for fifteen years. There is now an extensive array of recapture data that have been analysed to provide sets of survival estimates for each year of life of a series of cohorts. These reveal that survival is not constant over all age classes, nor is age the only parameter that can affect annual survival probabilities.

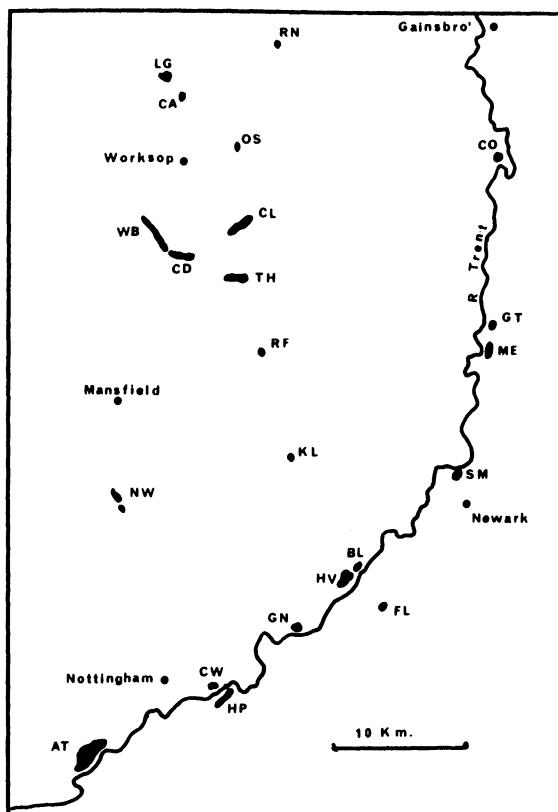
2. FIELD METHODS

As with all palaearctic geese, Canadas moult their primary and secondary wing feathers more or less simultaneously towards the end of the breeding period. Although there is some individual variation in the timing of this moult, and some difference between breeding and non-breeding birds, for a short period virtually all the adult Canada Geese on a single lake will be flightless. This period tends to coincide with a time when birds that hatched earlier in the season are still incapable of flight, so it is then possible to trap all of the geese on a single lake by a procedure akin to herding sheep.

The birds are accumulated in one part of the lake, and then gently driven towards a suitable beaching site where a catching funnel and pen have been constructed. By strategically siting people around the periphery of the lake, it is possible to deter the geese from coming ashore elsewhere than in front of the pen, and theoretically all of the geese on a lake can be captured simultaneously. In practice, difficulties can arise. Stray dogs, adjacent livestock, fishermen, youths and over-exuberant handlers have all wrought havoc in the past, and even a few small islands can rapidly fragment one large flock into a plethora of small ones. However, an experienced team of handlers can usually trap over 90% of the available birds, and frequently in excess of 98% are captured.

In 1968, John McNeeking began the programme of captures in Nottinghamshire (Notts) that has expanded down the years so that in 1981 no fewer than sixteen lakes were trapped during a two week period in early July. The first-ever capture was at Thoresby Lake in 1968, and was to some extent a bird-removal exercise, for twenty-nine of the ninety trapped geese were transported for release at Attenborough (see Figure 1 for location of sites). The following year, birds were trapped at Clumber Park, and since 1970 both Clumber and Thoresby have been trapped every year. Table 1 shows how additional lakes were added to the list each year, as the geese spread and increased in numbers.

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AT: Attenborough	BL: Bleasby	CA: Carlton
CD: Carburton	CL: Clumber	CO: Cottam
CW: Colwick	FL: Flintham	GN: Gunthorpe
GT: Girton	HP: Holme Pierrepont	HV: Hoveringham
KL: Kirklington	LG: Langold	ME: Meering
NW: Newstead	OS: Osberton	RF: Rufford
RN: Ranskill	SM: South Muskham	TH: Thoresby
WB: Welbeck		

Figure 1 The study area in Nottinghamshire

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Table 1

Total number of Canada Geese captured at eleven of the principal lakes in north Nottinghamshire between 1968 and 1982

	TH*	CL	CD	WB	RF	CA	KL	RN	OS	GT	LG
1968	64	1	0	0	0	0	0	0	0	0	0
1969	0	78	1	0	0	0	0	0	0	0	0
1970	59	209	0	0	0	0	0	0	0	0	0
1971	89	110	0	23	18	0	0	0	0	0	0
1972	141	132	25	1	0	0	0	0	0	0	0
1973	197	196	33	20	0	0	0	0	0	0	0
1974	125	261	0	4	0	0	0	0	0	0	0
1975	90	226	0	56	27	0	0	0	0	0	0
1976	151	337	7	22	36	127	0	0	0	0	0
1977	112	316	0	38	58	106	9	14	36	0	0
1978	109	494	0	0	43	106	9	0	0	25	0
1979	114	500	0	0	44	83	0	0	0	0	0
1980	99	447	0	0	49	79	17	14	99	1	0
1981	93	390	0	55	54	69	19	14	147	33	12
1982	38	212	0	0	44	100	17	0	159	64	0

* See key to Figure 1 for location of the lakes

Once the geese had been trapped, the procedure was fairly similar at all lakes in all years. Unringed birds were aged either as full grown or birds of the year ("juveniles"). They were ringed and released. The ring numbers of all previously-marked birds were recorded, whether or not the ring had initially been applied in Nottinghamshire. Old, worn or damaged rings were replaced. Young birds were processed before adults, to minimise the risk of physical damage in the pen, and all were released as quickly as possible. In 1980 and 1981, a number of birds were given lettered plastic rings in addition to standard metal ones, to facilitate their identification during the winter months.

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3. ANALYTICAL METHODS

Between 1968 and 1982, a total of 4,523 geese were handled by the Nottinghamshire ringing team, of which 2,359 were young birds in their first few weeks of life. The repeated trapping and re-trapping of these birds in subsequent years has generated a substantial volume of information in the form of mark-recapture data. These are now too complex for manual analysis, and have been stored in the Nottingham University ICL2900 computer as a two-dimensional array. Each bird is recorded as a separate row, consisting of a series of columns holding ring number, age at ringing and handling history, plus re-ringing details, fate and date and place of death where appropriate. It is thus possible relatively speedily to extract the history of any bird or group of birds for analysis.

A series of techniques have been developed over the years for the analysis of mark-recapture data from species as diverse as ducks, black-kneed capsids, butterflies and fish. These have recently been reviewed in an eminently readable form by Begon (1979) and Blower *et al.* (1981), who agree that care should be taken to select the most appropriate method for the data and problem. Our problem is to assess annual survival probabilities from fairly complete data, and the best method seems to be that developed independently, and in slightly different forms, by Jolly (1963, 1965) and Seber (1965). Jolly's method is more directly applicable, and since the analysis becomes cumbersome when the number of capture dates increases, we are fortunate that Dr. Michael Hounsome has written and made available an ALGOL programme for the relevant computations.

We will show elsewhere that, although Canada Geese range widely during the winter months, they seem to return to the natal area either to nest or pass the summer as non-breeding adults. We have clear evidence that mixing does not occur between the Trent Valley geese in the south and east of the county, and the Dukeries geese in the north during the breeding season. For the purposes of analysis, it has been necessary to separate the two areas, and, although this reduces the sample sizes, to examine the data separately. We have extracted all records relating to birds ringed as youngsters at one or other of the following lakes: Carburton, Carlton, Clumber, Rufford, Thoresby, Welbeck and, more recently, Girton, Kirklington, Langold, Osburton and Ranskill. We have separated birds hatched in different years, and produced a table for each cohort listing the capture or otherwise of every bird in the cohort in each year. These tables form the basis of the remainder of the analysis, and although they are too bulky to publish here, we can make them available to interested readers on request.

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We present the data here (Appendix 1) in the form of a series of "Jolly trellises" (Jolly, 1965). Each table or trellis relates to birds ringed in a particular year. The first column gives the number of these recaptured in each subsequent year, and the figures in the body of the table show the number of birds captured in any year that were last handled in each previous year. Thus, in the table for 1970, fifty-nine young geese were initially marked, and nineteen and twenty-seven were recaptured in 1971 and 1972 respectively. Of the twenty-seven from 1972, ten had been last handled in 1971 and seventeen in 1970 - presumably being elsewhere in the intervening year. Similarly, in 1973, twenty-seven of the 1970 cohort were captured; twenty-one of these had been handled in 1972, two in 1971 but not in 1972, and four had not been recaptured since they were first marked in 1970.

4. RESULTS AND DISCUSSION

From the data in each trellis, it is possible to derive a series of annual survival estimates from the first year of life through to the penultimate year of the study (in our case 1980-81). Standard errors can also be computed which give some idea of the accuracy of the estimates, although these tend to correlate both with the survival estimate itself and (particularly with our data) the number of geese re-trapped in the relevant year. These survival estimates have been computed using Dr. Hounsome's programme and are listed in Table 2.

A problem that is immediately raised in the analysis of recapture data relates to ring loss. A certain proportion of rings work loose and become detached from the birds each year. These will not be recorded again, and will be effectively 'dead', so that the survival estimates will be somewhat reduced. This has been shown to occur in south Yorkshire, where Thomas (1977) found that about 2.3% of rings were lost in this way. We only have a small amount of data relating to this, but at present it seems that ring loss is no higher than Thomas' figure. In any case, we have no reason to believe that it will occur differentially, so that its effect will be to enhance the survivorship estimates more or less consistently by that amount.

There are three parameters that might influence the survival of Canada Geese. Firstly, the age of the bird might be important, for it is well-known from other species that many young birds succumb during the first few weeks of life. This has been shown to be the case even in social animals like geese (e.g. Henny, 1967), when experience is being gained in the recognition and avoidance of danger. Secondly,

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Table 2

Survivorship estimates based upon the data in the Appendix. The first column shows the year of study, the second shows the year of birth, and the third gives the year of the bird's life. The fourth and fifth columns show the estimated probability of survival through the year in question and its standard error

Yr	Coh	Age	Surv	Se	Yr	Coh	Age	Surv	Se
70	70	1	0.903	0.115	76	73	4	0.731	0.100
71	70	2	0.735	0.113	77	73	5	0.823	0.116
72	70	3	0.827	0.075	78	73	6	0.864	0.166
73	70	4	0.931	0.051	79	73	7	0.748	0.178
74	70	5	1.086	0.081	80	73	8	1.065	0.364
75	70	6	0.657	0.106	74	74	1	0.743	0.058
76	70	7	0.863	0.118	75	74	2	0.785	0.071
77	70	8	0.701	0.220	76	74	3	0.632	0.084
78	70	9	0.538	0.234	77	74	4	0.843	0.106
79	70	10	0.429	0.213	78	74	5	0.730	0.114
80	70	11	0.667	0.272	79	74	6	0.811	0.104
71	71	1	0.666	0.058	80	74	7	0.918	0.079
72	71	2	0.856	0.077	75	75	1	0.705	0.048
73	71	3	0.814	0.085	76	75	2	0.684	0.062
74	71	4	0.805	0.081	77	75	3	0.781	0.070
75	71	5	0.982	0.062	78	75	4	0.887	0.096
76	71	6	0.662	0.100	79	75	5	0.649	0.101
77	71	7	0.778	0.114	80	75	6	1.250	0.319
78	71	8	0.761	0.184	76	76	1	0.601	0.040
79	71	9	0.763	0.296	77	76	2	0.785	0.051
80	71	10	0.556	0.310	78	76	3	0.778	0.068
72	72	1	0.741	0.054	79	76	4	0.629	0.072
73	72	2	0.882	0.083	80	76	5	1.003	0.083
74	72	3	0.745	0.103	77	77	1	0.683	0.040
75	72	4	0.763	0.101	78	77	2	0.707	0.059
76	72	5	0.632	0.099	79	77	3	0.710	0.071
77	72	6	1.004	0.089	80	77	4	0.907	0.090
78	72	7	0.795	0.134	78	78	1	0.596	0.045
79	72	8	0.763	0.143	79	78	2	0.643	0.065
80	72	9	0.863	0.128	80	78	3	0.681	0.080
73	73	1	0.492	0.050	79	79	1	0.479	0.040
74	73	2	0.830	0.076	80	79	2	0.815	0.070
75	73	3	0.739	0.087	80	80	1	0.525	0.043

the year itself may be significant, for climatic differences between years may directly or indirectly affect a goose's survival. Severe winter weather, excessive drought during the summer, and variations in shooting or predator pressure might all play a part in this. Thirdly, the actual cohorts themselves may differ in their life-expectancy. Birds hatched in some years may differ in their general fitness and this might be manifest throughout an individual's life. This is perhaps less likely to be of biological significance in a long-lived species like a goose when compared with the other two factors. Nevertheless, the possibility exists, and can be sought for in our data.

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Table 3 shows the results of a preliminary analysis of the data in Table 2. The sampling errors of some of the survival rates are rather large, so we have attempted to compensate for this by ascribing 'confidence weights' to the latter equal to the reciprocal of their variances. We have used the GENSTAT Mark 4.03 package to regress

Table 3

The results of performing Regression Analysis on the data in Table 2. The survival rates have been regressed against age, year and cohort, as explained in the text, weighting each value by the reciprocal of its variance

	SS	DF	MS	F	P
Age	113.1	10	11.31	9.8	0.01
Year	57.2	10	5.72	5.0	0.01
Cohort	17.6	9	1.96	1.7	NS
Resid.	41.5	36	1.15		
Total	229.4	65			

these survival rates against age, year and cohort, treating year as a variable, and age and cohort as factors. It is apparent from Table 3 that age and year make significant contributions to the variation in survival rate, but that cohort is relatively unimportant. Age alone accounts for 40% of the variance, and the addition of year increases this to over 62%.

Examining these two parameters in more detail is informative. Table 4 shows the results of the regression analysis for survival upon age alone. It seems from the values of the coefficients that there are three stages in a goose's life that can be distinguished from these figures. The probability of survival from ringing to one year of age is only 62%, but this rises to approximately 75% through the next two years. It then increases again to about 90% at age five, perhaps declining slightly thereafter. This is an interesting result for it is in keeping with the known biology of the species. It has already been suggested that the first year of life will be the most hazardous, as the inexperienced young geese learn to feed and fend for themselves. It was shown by Thomas (1977) that Yorkshire birds have a 'marginally' higher mortality in their first year, and the difference is substantial in native North American birds (Henny, 1967, and Williams, 1967). Cramp and Simmonds (1977) report that Canada Geese usually breed for the first time at three years of

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age, so the second and third years of life will be spent as immature individuals before the attainment of sexual maturity. The ecology and behaviour of these immatures will be different from the mature birds whether or not the latter are actually breeding. Consequently, the ecological and environmental forces acting upon the two groups of birds will differ. While there is no *a priori* reason for supposing that the probability of survival will be higher in one group or the other, it is perhaps not too surprising that they should be different.

Table 4

The estimated survival rate of Canada Geese of different ages - derived from the results in Table 2 by Regression Analysis

Year of Life	Survival Estimate	SE
1	0.615	0.021
2	0.763	0.059
3	0.748	0.065
4	0.827	0.067
5	0.893	0.074
6	0.815	0.092
7	0.850	0.097
8	0.772	0.164
9	0.785	0.175
10	0.470	0.277
11	0.667	0.417

Note that the errors associated with these estimates increase as the year of life progresses, and the number of survivors declines.

We have examined the effects of year upon survival rate by a further regression analysis. Regrouping the geese by age into first year, second and third year, and adults gives three age classes. Table 5 shows the results of regressing the survival rate against these age classes, again using the reciprocal of the variance as a 'con-

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fidence weight'. We then extended the analysis to include years within age class, regarding 1970 as the base year, or time zero. The Analysis of Variance table in Table 5 shows that there are significant contributions to the variation in survival rate from both of these components. The regression coefficients are shown in the lower part of Table 5. The increase in survival with age is clearly seen in the first three coefficients. The lower three coefficients are all negative, indicating that there is a decline in survival among the birds of all age classes between 1970 and 1980. The coefficient pertaining to the first year birds differs significantly from zero, possibly because the sample sizes are greater for these birds, and so the

Table 5

Results of regression analysis of survival rate against year in birds of three different age classes, as described in the text

A. Analysis of Variance Table					
Component	SS	DF	MS	F	p
Age Class	104.1	2	52.05	31.4	0.01
Year in Age Class	23.8	3	7.93	4.8	0.01
Residual	101.5	60	1.66		
Total	229.4	65			

B. Regression Coefficients		
	Estimate	SE
Constant	0.738	0.045
Age Class 2*	0.843	0.072
Age Class 3*	0.939	0.082
Years in Age 1*	-0.020	0.007
Years in Age 2*	-0.014	0.008
Years in Age 3*	-0.014	0.010

*Age Class 1 = 1st year of life

Age Class 2 = 2nd and 3rd years of life

Age Class 3 = over 3 years of age

Note that the regression coefficients are appreciably less for age classes 2 and 3, suggesting that the decrease in survival in later years is greater for young birds.

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variances are less. Alternatively, the enhanced decline among younger birds could be biologically real, if competition is greater in the early months of life. Be that as it may, there is clear evidence of a decline in survival among all three age classes through the period of the study.

There is a further result that may or may not be real. It seems that older geese, those above seven years of age, show some slight sign of a decrease in survivorship compared with younger adults. This result may well be real, in which case it is probably the first record of a declination in survivorship among older geese. However, since survival is decreasing in later years, and since the data concerning older geese all come from the final years of the study, it is not possible to be definite about this result. A couple more years of field work will probably clarify the situation.

It seems then that the annual probability of survival changes with age in our geese, and also has declined through the study period. There seem to be very few instances where it has proved possible to examine the effect of age and time on survival in wild geese. Owen (1982) found evidence of an increase in mortality with age in Barnacle Geese after the first eighteen months of life. The number of some age classes was small, but the results suggested there to be a slightly higher mortality in the first year of life. He also suggested mortality to be higher among young birds following a good breeding season, suggesting that the young birds were then more mobile and hence suffered an enhanced vulnerability to shooting.

It is tempting to postulate similar causal relationships between the survival of Notts Canada Geese and the dramatic increase in population size that has been described by McMeeking and Parkin (*in press*). As the number of geese has risen in a relatively limited habitat, so the density has increased in parallel. Consequences of this might be a rise in the amount of predation, an increase in mobility and hence emigration, or greater competition for food or space.

Considering these in turn, a major component of predation among our birds is 'quasi-natural' in the form of shooting or other human pressure. Farmers and land-owners are not particularly appreciative of large numbers of geese on their land (White-Robinson, *in prep.*) and predation ('control') has increased over the years. Table 6 shows that the proportion of our geese that had been shot increased significantly during the period of the study. This is undoubtedly a consequence of deliberate shooting having increased following more and more complaints about agricultural

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damage. In some situations, this was an attempt to reduce the goose numbers directly, in others the intention was merely to move the bulk of the flocks away from sensitive areas (White-Robinson, in prep.). In either case, the effect is the same: more geese have been killed by man in recent years.

Table 6

Proportion of shot birds among those geese ringed in North Notts that were subsequently found dead by members of the public. The total number of birds involved is given in parentheses.

Year	Adults	Juveniles
1968	0.0 (4)	-
1969	46.2 (13)	-
1970	43.8 (16)	18.2 (11)
1971	80.0 (5)	20.0 (10)
1972	0.0 (1)	50.0 (14)
1973	86.7 (15)	73.3 (15)
1974	66.7 (6)	42.9 (21)
1975	100.0 (4)	54.6 (11)
1976	69.2 (26)	80.0 (15)
1977	71.4 (14)	75.0 (20)
1978	83.3 (18)	73.3 (15)
1979	85.7 (7)	54.6 (11)

Both sets of data increase significantly with year (Spearman's Rank Correlation Coefficient: for adults, $\rho=0.64$ [$p < 0.05$] ; for juveniles, $\rho=0.70$ [$p < 0.05$])

This might seem to lend support to the contention that mortality rates have increased in recent years. However, it is well-known that mark-recapture methods do not measure true mortality, but confound this with permanent emigration from the study area. Thus, we must consider the second possibility, that mobility has increased as a result of rising population size, and permanent emigration is confounding the mortality estimates. We can check for this from records of geese captured alive outside the study area. There are three other locations where Canada Geese are trapped during the moult, and over the years twenty-six juvenile and twenty-seven full-grown geese that were ringed in Notts have been trapped at one or other of these sites. One of them is a moulting area in Scotland, and the other two are breeding areas in the West Midlands and in South Yorkshire. Table 7 shows that there is no evidence that juveniles are more likely to stray outside the Notts study area in June or July than older birds. It is also clear from this table that there is no sign of an increase in the capture of Notts birds outside the study area in later years. The

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numbers are small, but the results are virtually identical, so it seems that differential emigration does not occur either between ages or years in our birds.

Table 7

The proportion of Canada Geese ringed in North Notts that were subsequently recaptured. The birds have been separated by age, into those ringed early and later in the study that were captured in North Notts or elsewhere in Britain.

Year	Adults			Juveniles		
	Local	Distant	Total	Local	Distant	Total
1968-73	95.6%	4.4%	271	95.9%	4.1%	222
1974-79	96.0%	4.0%	377	96.7%	3.3%	515

There is no evidence of difference in the proportion of recaptures between adults and juveniles, nor between early and later years of the study.

The third alternative is that reduced food availability could act, together with increased predation, to reduce survival in later years. It seems that our Canada Geese have good food reserves (White-Robinson, in prep.) and starvation is not frequent. Thus, we have no evidence that mortality was appreciably higher during the recent severe winter of 1981/82.

In conclusion, it seems that the population of Canada Geese in north Nottinghamshire has increased dramatically in recent years. The results from the recapture of ringed birds indicate that the annual survival probability of first-year birds is significantly lower than second and third year birds, which in turn is lower than birds of three years and older. The survival rates of all age classes have declined in recent years, more steeply among the youngest age class, and much of this might be ascribed to an increase in shooting pressure. We are currently analysing the results from south and east Nottinghamshire which show a broadly similar pattern, and the recovery details of dead birds to confirm the significance of human predation.

ACKNOWLEDGEMENTS

We are extremely grateful to all those members of the unofficial Nottinghamshire goose-trapping team for giving up their time to brave geese, swans, midges, canoes, storm and tempest over the years. In particular, Norman Lewis who always seems to go

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in the pento pick up the geese and pass them out, and John McMeeking who co-ordinates the team and (usually) arranges for traps, rings, handlers and geese to arrive at the lake simultaneously. Finally, our thanks go to Dr. Myrlyn Owen for taking time out of his busy schedule to read a draft of this paper.

APPENDIX 1

The recapture data for Canada Geese first ringed as goslings in each year from 1970 to 1980. NR indicates the total number of birds handled in each year, and the columns show the number of these that were last handled in each previous year. For further details, see the text.

Recapture Data From 1970 Cohort

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Recapture Data from 1971 Cohort

Recapture Data from 1972 Cohort

 Canada geese survival rates

Recapture Data from 1975 Cohort

Year	NR	75	76	77	78	79	80	81
1975	116							
1976	71		71					
1977	44		6	38				
1978	36		1	6	29			
1979	26		0	1	2	23		
1980	18		0	0	1	4	13	
1981	17		0	0	1	1	3	12
1982	8		0	1	0	0	0	3
								4

Recapture Data from 1976 Cohort

Year	NR	76	77	78	79	80	81
1976	163						
1977	90		90				
1978	63		5	58			
1979	47		0	7	40		
1980	31		1	2	5	23	
1981	30		0	0	0	6	24
1982	19		0	0	0	0	4
							15

Recapture Data from 1977 Cohort

Year	NR	77	78	79	80	81
1977	158					
1978	97		97			
1979	54		3	51		
1980	37		1	8	28	
1981	40		2	3	7	28
1982	21		1	0	1	2
						17

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Recapture Data from 1978 Cohort

Year	NR	78	79	80	81
1978	159				
1979	78	78			
1980	47	4	43		
1981	37	6	3	28	
1982	18	0	0	2	16

Recapture Data from 1979 Cohort

Year	NR	79	80	81
1979	178			
1980	73	73		
1981	55	9	46	
1982	33	0	7	26

Recapture Data from 1980 Cohort

Year	NR	80	81
1980	218		
1981	91	91	
1982	53	11	42

ESTIMATION OF AGE-SPECIFIC SURVIVAL OF HEN
HARRIERS (*CIRCUS C. CYANEUS*) IN ORKNEY

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SUMMARY

This paper obtains survival estimates of Hen Harriers (*Circus c. cyaneus*) in Orkney using resightings of colour-marked individuals. Estimated survival varied with age and sex: a higher proportion of females than males survived to 2 years old and subsequently as adults. Computer simulation was used to allow for small sample sizes and the assumption of equal resighting rate was examined.

Keywords: HEN HARRIER; AGE-DEPENDENT SURVIVAL; RESIGHT DATA; COMPUTER SIMULATION

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1. INTRODUCTION

Hen Harriers (*Circus c. cyaneus*) on the Orkney island of West Mainland, off the north coast of Scotland, are polygynous (Picozzi, 1983). From 1976-81, 53-100% of adult males associated with more than one female. The average sex ratio in the breeding population varied between 1.8 and 2.7 with harems as large as 6. Differential mortality of males and females is a possible explanation of this state of affairs and part of the above study involved the estimation of survival from observations on colour-marked individuals. This paper (a) discusses the collection of these data; (b) develops an appropriate method for estimating survival rates of birds of different ages; (c) applies the method to both males and females, and compares the sexes; (d) tests and discusses the assumptions implicit in the method. A fuller account of sex ratio and territoriality of Hen Harriers in Orkney can be found in Picozzi (1983).

2. RESIGHT DATA

Colour-marked birds of known age were introduced into the West Mainland population each year from 1975-80 inclusive. Six cohorts, with a total of 177 females

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and 186 males were marked as nestlings together with a further 63 females and 15 males aged 1 year or older. Males were aged using plumage, females from eye-colour, or in both cases using the ring number from an earlier study of Balfour and Cadbury (1975). The oldest recorded male was 10 years old, the oldest female 12 years old. Resights of individuals in the 1976-81 breeding seasons were obtained using systematic searches of the suitable nesting habitat, covering about 86 km², from mid March to mid July. Females were conspicuous in aerial displays, but not all marked birds seen could be identified so that resighting was largely dependent on being able to see clearly the coloured tags. Males were more difficult to find, so the searching scheme was supplemented with periods of continuous observation on territories of individual hens. As with females, males were sometimes seen but not identified. Observations were also made at a winter roost, but because of failing light, individuals could not be identified reliably.

3. METHOD

Primarily we wish to estimate survival rates of birds of different ages separately for males and females. This involves some consideration of annual variations in survival rates and of the resighting probability in relation to age and calendar year. A suitable approach is given by Pollock (1981a) who has developed the models of Jolly (1965) and Seber (1965) to allow for age-dependent survival and resighting rates. Details of the method can be found in Pollock's paper; only a brief account is given here.

In each year we assume that there are ($\ell+1$) distinguishable age classes of birds 0, 1, ..., ℓ which move forward one class each year. We further assume that each age class has a different resighting rate in the i th year, and a different survival rate from the i th to the $(i+1)$ th year, $i = 1, \dots, K$. Colour-marked birds of a given age in a particular year are assumed to have the same survival and resighting rates, and to survive and be resighted independently of each other.

In the present context, survival refers to those birds which have neither died nor emigrated in the year.

The following notation will be used:

M_{ih} the number of birds of age h in the population at the end of the i th breeding season marked in previous years, $h = 1, \dots, (\ell+1)$ and $i=1, \dots, K$. Note that $M_{i(\ell+1)}$ refers to birds of at least age $(\ell+1)$.

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- m_{ih} the number of previously marked birds of age h which are sighted during the i th breeding season.
 R_{ih} the number of marked birds of age h known to be in the population at the end of the i th breeding season. Individual colour-marked birds were seen throughout the breeding season so that R_{ih} is m_{ih} plus the number of additional marked birds introduced in year i .
 r_{ih} those birds of the R_{ih} which are sighted at least once after the i th year.
 Z_{ih} those birds of the $(M_{ih} - m_{ih})$ which are sighted at least once after the i th year.
 T_{ih} those birds of the M_{ih} which are sighted in or after the i th year.
 Note that $T_{ih} = r_{(i-1)(h-1)} + Z_{(i-1)(h-1)}$.

Maximum likelihood estimators, \hat{M}_{ih} , of the number of previously marked individuals in the population at the end of the i th breeding season are then given by:

$$\hat{M}_{ih} = m_{ih} + \frac{R_{ih} \cdot Z_{ih}}{r_{ih}}, \quad h = 1, \dots, (\ell-1) \quad (1)$$

$$\hat{M}_{il} + \hat{M}_{i(\ell+1)} = m_{il} + \frac{R_{il} \cdot Z_{il}}{r_{il}} \quad (2)$$

where

$$\hat{M}_{il} = \frac{T_{il}}{[T_{il} + T_{i(\ell+1)}]} \cdot [\hat{M}_{il} + \hat{M}_{i(\ell+1)}] \quad (3)$$

(1) and (2) give a series of Petersen estimates (Seber, 1982) for the M_{ih} . They can be obtained by considering those marked birds in the population at the end of the breeding season of the i th year and by equating the proportion of those seen which are seen subsequently, r_{ih}/R_{ih} , to the proportion of those not seen but seen subsequently, $Z_{ih}/(M_{ih} - m_{ih})$. Equation (3) is obtained by considering those marked birds of age 1 and older in the population in the i th year which are seen subsequently and equating the proportion of birds aged 1 to the proportion of marked birds in the population.

Estimates of survival, $\hat{\phi}_{ih}$, of age class h in year i , are

$$\hat{\phi}_{ih} = \frac{\hat{M}_{(i+1)(h+1)}}{[\hat{M}_{ih} - m_{ih} + R_{ih}]}, \quad h = 0, \dots, (\ell-1).$$

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$$\hat{\phi}_{il} = \frac{\hat{M}_{(i+1)(l+1)}}{[\hat{M}_{il} + M_{i(l+1)} - m_{il} + R_{il}]} ,$$

for $i=1, \dots, (K-1)$.

The probability, P_{ih} , that a marked bird of age class h is sighted in year i , given that it is alive in that year, is then estimated by

$$\hat{p}_{ih} = \frac{m_{ih}}{\hat{M}_{ih}} , \quad h = 1, \dots, (l-1) .$$

$$\hat{p}_{il} = \frac{m_{il}}{[\hat{M}_{il} + \hat{M}_{i(l+1)}]} .$$

The above estimates of M_{ih} derived by Pollock are biased. For small samples this bias can be large, but it can be reduced and the complications arising from zero values of r_{ih} can be avoided by adopting the modification suggested by Bailey (1951) and using

$$\hat{M}_{ih} = m_{ih} + \frac{(R_{ih} + 1)}{(r_{ih} + 1)} Z_{ih} \quad (4)$$

In the analysis of the Hen Harrier data, values of \hat{M}_{ih} obtained from (4) were combined to examine survival patterns in relation to both age and calendar year. Overall estimates of survival and resighting rates for birds age h are given by

$$\hat{\phi}_h = \sum_{i=1}^{(k-2)} \hat{M}_{(i+1)(h+1)} / \left[\sum_{i=1}^{(k-2)} (\hat{M}_{ih} - m_{ih} + R_{ih}) \right] \quad (5)$$

$$\hat{p}_h = \frac{\sum_{i=1}^{(k-1)} m_{ih}}{\sum_{i=1}^{(k-1)} \hat{M}_{ih}} \quad (6)$$

Pollock obtains approximate standard errors for the estimates, $\hat{\phi}_{ih}$, but the sampling theory relies on relatively large numbers of birds being resighted. For the Hen Harrier data the asymptotic results are inapplicable because of the small number of birds involved. Instead, computer simulation was used to obtain the sampling properties of the estimators. Examples of the approach in the analysis of data from capture-recapture studies can be found in Carothers (1979) and Buckland (1980) who discusses the advantages and disadvantages of simulation and large-sample analytic

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methods. Briefly, for given survival and resighting rates, sets of data are simulated and the corresponding estimates of survival are derived. From a large number of such simulations the sampling distribution of an estimator can be obtained and its properties evaluated. In practice, the survival and resighting rates are not known and estimates based on the sample are used in the simulation. The resulting sampling distribution is then used to approximate that corresponding to the unknown parameter values. The approach is a particular application of a more general statistical technique called the "bootstrap" (Efron, 1979). In the simulation, pseudo random numbers uniformly distributed in (0,1) were obtained using the NAG routine G05CAF. The computing in this exercise, and the rest of the work reported here, was carried out on the Cambridge University IBM 3081 machine. To simulate 500 realisations of a particular model took at most 15 seconds and the main effort was in the development of the computer program. This amounted to about 3-man weeks, a relatively small proportion of the 30 or so months spent in the field collecting the data.

4. APPLICATION

4.1 Females

Of the 249 colour-marked females, three birds were found dead in the autumn without being sighted earlier in the breeding season. Because the number involved was so small, no attempt was made to estimate recovery rates of dead birds. Instead, all the information on the resightings of these birds before they died was used but from their year of death onwards they were regarded as never being seen again. The observations treated in this way can then be incorporated into the analysis without introducing any bias in estimating survival rates. The method was applied using eight distinguishable age classes 0, ..., 6 and 7 years or older. This guarantees estimates of M_{ih} for each age class in every year using the values of m_{ih} , R_{ih} , r_{ih} and Z_{ih} given in Table 1. Overall estimates of survival and resighting probability for each age class obtained using expressions (5) and (6) are given in Table 2. Standard errors were obtained from 500 computer simulations and they reflect sampling errors when survival and resighting rates are the same in each year with values given in Table 2. The exercise also showed that there was no appreciable bias of estimation (less than 1% in all cases) and that estimates ± 2 standard errors gave approximate 95% confidence intervals for the estimated parameters.

Nestlings survived less well than yearlings (difference = 55%, SE = 11%) but there was little variation in survival rates of adult birds aged 2-6 years about the

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Table 1

Basic data used to estimate survival in male and female Hen Harriers (*Circus c. cyaneus*). See text for definition of m , R , r , Z .

age \ year	1975	1976	1977	1978	1979	1980	1981
Females							
0	$m = 0$ $R = 24$ $r = 7$ $Z = 0$	0 35 7 0	0 31 10 0	0 34 13 0	0 7 2 0	0 46 3 0	0 0 - -
1	0 2 2 0	1 3 3 6	1 4 4 6	4 5 3 6	9 9 7 4	2 2 1 0	3 3 - -
2	0 1 1 0	2 6 6 0	6 7 5 3	10 11 10 0	6 7 7 3	9 11 8 2	1 1 - -
3	0 6 6 0	1 6 5 0	6 10 8 0	7 8 7 1	10 10 10 0	10 10 8 0	10 10 - -
4	0 2 2 0	6 8 8 0	4 5 5 1	8 9 8 0	7 7 5 1	9 9 7 1	8 8 - -
5	0 2 2 0	2 4 4 0	7 8 6 1	6 7 7 0	8 8 7 0	6 6 5 0	8 8 - -
6	0 4 4 0	1 2 2 1	3 4 2 1	7 7 7 0	7 7 6 0	7 10 6 0	5 5 - -
6+	0 3 2 0	6 7 7 0	10 11 9 0	12 13 9 0	14 15 10 2	18 19 15 0	21 21 - -
males	1975	1976	1977	1978	1979	1980	1981
0	0 23 3 0	0 39 9 0	0 32 4 0	0 33 5 0	0 11 1 0	0 48 2 0	0 0 - -

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Table 1
(continued)

males (cont'd)	1975	1976	1977	1978	1979	1980	1981
1	0	1	1	1	3	1	2
	0	1	2	1	3	2	2
	0	1	1	1	0	1	-
	0	2	8	3	2	0	-
1+	0	3	8	17	18	13	10
	3	6	13	18	18	14	9
	3	5	6	15	10	8	-
	0	0	0	1	2	1	-

average value 90% (SE = 3%). Birds older than 6 years appeared to survive less well than younger adults but the sampling variation is relatively large (difference = 14%, SE = 7%). An estimated 29% (SE = 4%) of female nestlings survived to adults.

Marked yearlings in the populations were less likely to be sighted than 2 year olds (difference = 36%, SE = 10%), which in turn had a lower resighting rate than older birds (difference = 18%, SE = 7%).

Table 2

Estimated age-specific survival rate and resighting rate for male and female Hen Harriers (*Circus c. cyaneus*)

Age Females	Survival rate (%)	SE (%)	Survival rate (%)	SE (%)
0	33	5	-	-
1	87	8	40	8
2	90	6	77	7
3	91	5	97	3
4	91	5	91	5
5	91	6	96	4
6	88	7	90	6
6+	76	6	95	4
Males				
0	26	7	-	-
1	53	18	16	9
1+	72	7	90	5

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The parameter estimates given in Table 2 are not independent of each other and the above comparisons allow for the correlations between them. However, high correlations could affect the interpretation of the confidence interval statements and some consideration of the sizes involved is worthwhile. Correlation coefficients between all pairs of parameter estimates were estimated from the 500 computer simulations but found to be relatively small: the highest, between nestling and one year old survival estimates, was -0.4 and all the others were less than 0.2 in absolute value.

4.2 Males

A similar analysis to the above was carried out for the 78 colour-marked males. The observations on the four birds found dead in autumn were treated as before but, because far fewer birds were resighted, only three age classes 0,1 and 2 years or older were used. The corresponding values of m_{ih} , R_{ih} , r_{ih} and Z_{ih} are given in Table 1. Estimates of survival and resighting rates were obtained and their sampling properties examined as for females using computer simulation. It emerged that even when survival and resighting rates were constant in time, the procedure for estimating nestling and yearling survival was appreciably biased. Nestling survival was underestimated by an estimated 3% whereas yearling survival was overestimated by an estimated 7%. No bias was detected for the estimated adult survival rate. The reason for the bias was the small number of marked 1 year old males known to be in the population at the end of their first year leading to underestimates of the number of marked 1 year olds in the population. The estimation procedure was therefore modified to reduce the bias. Using computer simulation, survival and resighting rates were found for which the original method of estimation produced, on average, values equal to the initial estimates. The resulting new estimates are given in Table 2. As in the case of females, male nestlings survived less well than adults (difference = 46%, SE = 7%) but any differences between either nestlings and yearlings or between yearlings and adults were obscured by the large sampling variation. Despite the difficulties in estimating nestling and yearling survival separately, it was found that when survival and resighting rates were constant in time, survival from nestling to adult stages (i.e. 0 to 2 years old) could be estimated with negligible bias and more precisely than the separate components. An estimated 14% (SE = 5%) of male nestlings survived to adults. The pattern of resighting was similar to that for females with marked yearlings being less likely to be sighted than marked adults.

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Correlations between the parameter estimates were estimated as for females: the highest values, between estimated nestling survival and estimates of survival and resighting rates of 1 year old birds, were -0.6 and -0.4 respectively, with all others less than 0.2 in absolute value.

4.3 Comparison of Sexes

Nestling survival was 7% (SE = 9%) higher in females but the sampling error was large. However, approximately twice as many female nestlings survived to adults (difference = 15%, SE = 5%), and subsequent adult survival was higher in females (difference = 18%, SE = 7%).

4.4 Annual Variations

The preceding analysis rests on the tacit assumption that survival and resighting rate are constant from year to year. This assumption can be tested as follows. Let S_1, \dots, S_m be a set of survival or resighting rate estimates for m years of the study. Under the assumed model, each S_i has the same mean value and an estimate of its sampling variance, say $1/W_i$, can be obtained from the computer simulations. A possible test statistic is then

$$S = \sum_{i=1}^m W_i (S_i - \bar{S}_w)^2$$

where \bar{S}_w is a weighted average of the S_i with weights W_i . Asymptotically, the S_i are statistically independent and S follows a chi-square distribution with $(m-1)$ degrees of freedom. Examination of the distribution of S over the 500 realisations of the model shows that the variance exceeds that of its chi-square counterpart. Significance levels for the test have therefore been estimated using the tail-probabilities of the simulated distribution. Table 3 shows the results for both males and females. Based on the findings of Section 4, some pooling of female age categories was adopted to increase the power of the test. Tests for survival rates grouped birds of 1 year or older while those on resighting rates combined birds older than 2 years. The only suggestion of annual variation is in the resighting rate of 1 year old females ($p = 0.04$). However, this finding is sensitive to the inclusion of the data for 1979 when a mere seven marked nestlings were introduced: without these birds, $p > 0.10$. The data are therefore consistent with survival and resighting rate being constant in time. However, since this might be reflecting the low power of the test,

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the main findings that males survived less well than females over their first two years and subsequently as adults are now examined allowing for annual variations in survival and resighting probabilities.

Table 3

Tests of annual variations in survival and resighting rates.

Age	Survival rate		Resighting rate			
	Females	Test Statistic (S)	Significance level*	Males	Test Statistic (S)	Significance level*
0		3.6	0.40		-	-
1		9.6	0.10		11.1	0.04
2					5.5	0.22
2+					3.4	0.45
0		3.0	0.43		-	-
1		4.8	0.11		4.3	0.40
1+		5.5	0.25		1.4	0.75

*Significance levels obtained from 500 computer simulations of the null hypothesis.
See Section 4.4.

From the estimated values of M_{ih} an adult survival rate of birds aged 2-6 years was calculated for both sexes in each year. To avoid the difficulties of estimating nestling and yearling survival in males separately for each year, survival over the first two years was obtained using only the data from the cohorts of nestlings. The above method was used to estimate the number of marked yearlings present in the population 2 years after release. Using this approach there was no need to estimate the number of marked yearlings present in the population. Table 4 gives the resulting estimates of survival for the two stages. Average survival over the whole period was measured both by the arithmetic mean and, as suggested by Cormack (1964), the geometric mean of the separate yearly values. Some justification for using the latter is that the logarithmic transformation of the survival estimates helps to stabilize the within year sampling variability. Sampling errors of the estimates were obtained again using computer simulation except that in this exercise survival and resighting probabilities were allowed to vary between years by using the observed values for nestlings, yearlings and adults. For the set of values used in the simulation the

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estimates of annual survival, their geometric and arithmetic means were found to have negligible bias (less than 1%). The overall differences between males and females are very similar to those found previously. As measured by the geometric mean, estimated survival was higher in females both to 2 years (difference = 14%, SE = 5%) and subsequently (difference = 17%, SE = 6%).

Table 4

*Estimated survival to breeding (0 to 2 years) and subsequent adult survival in 1975-79 for male and female Hen Harriers
(*Circus c. cyaneus*)*

	Survival rate to breeding (0 to 2 years) (%)					Adult survival rate (%)			
	Year	Females	SE	Males	SE	Females	SE	Males	SE
1975	29	11		13	7	100	2	100	3
1976	20	7		26	7	99	5	83	16
1977	27	8		12	6	77	7	56	14
1978	34	9		7	4	94	4	89	11
1979	-	-		-	-	91	5	59	12
Geometric mean	27	4		13	3	92	2	75	6
Arithmetic mean	27	4		14	3	92	2	77	5

5. TEST FOR EQUAL RESIGHTING RATES

5.1 Method

An assumption in the analysis is that colour-marked birds of a given age in a particular year have the same resighting rates and that resightings are independent from year to year. Heterogeneity in the probability of being resighted leads to negative bias in the survival estimates $\hat{\phi}_i$ (Carothers, 1979; Buckland, 1982a). For a given cohort of birds the effect is most pronounced in the first year and the last few years of the study. Thus, Buckland suggests plotting

$$\log \prod_{i=2}^{(k-1)} \hat{\phi}_i$$

against k and looking for points which start to deviate below a straight line. There

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is little scope for using this method with the Hen Harrier data because the sequence of years is too short to establish a linear baseline. Instead, the approach of Carothers was modified to allow for both annual variations and age effects in resighting rate. For each bird, the sequence of years starting with the year after marking and ending with the year preceding the last resighting is obtained. Over this period the bird is known to be alive, but not necessarily seen, in a particular year. If R_j is the number of times the jth bird is resighted in its sequence, the test statistic is

$$T = \sum_{j=1}^N (R_j - \mu_j)^2 / \sigma_j^2$$

where N is the number of birds whose sequence is one year or longer, and μ_j and σ_j^2 are the mean and variance respectively of R_j on the null hypothesis of equal resighting probabilities.

If P_{ih} denotes the probability that an individual of age h is seen in year i, then

$$\mu_j = \sum_{i=f_j}^{g_j} p_i(h+i-f_j)$$

$$\sigma_j^2 = \sum_{i=f_j}^{g_j} p_i(h+i-f_j) [1 - p_i(h+i-f_j)] .$$

f_j is the year following the year of marking, h the age in that year and g_j is the year preceding the last resighting. The statistical significance of T was assessed from the randomisation distribution of resightings of birds of a given age in a particular year over those birds of that age known to be alive using independent allocations for different years. For the P_{ih} , the corresponding sample proportions were used in the test. The null sampling distribution of T is approximately chi-square with N degrees of freedom but when the μ_j are small and some of the P_{ih} are near 1, as is the case here, the approximation requires checking. Significance levels were based on 1000 samples from the randomisation distribution using the algorithm of Ernvall and Nevalainen (1982).

5.2 Application

For females aged 3 years and older, Table 2 shows that there is no systematic relationship of resighting rate with age. Thus, in the application of the test the

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three age categories yearlings, second year and 3 years and older were used. Seventy seven birds gave $T = 94.8$ (randomisation $p = 0.09$).

For males, only twenty three birds yielded an admissible sequence of years and it was necessary to combine those of 1 year and older. This gave $T = 27.2$ (randomisation $p = 0.33$).

In both cases the significance levels of the randomisation test are close to those using a chi-square approximation which are 0.08 and 0.25 respectively.

A further assumption in the analysis is that birds are resighted independently of each other. Females belonging to the same harem or males associating with particular females could violate this assumption. A specific test of the effect is not possible because switches of mates occur from year to year so that unless a bird is resighted its harem cannot be determined. However, it might be expected that lack of independence would affect the precision of estimation but not bias the survival estimates. In particular, any positive correlation between the estimates for males and females would make their comparisons in Section 4.3 conservative.

6. CONCLUSIONS

As in many mark-recapture studies, it was not possible to distinguish between mortality and permanent emigration. Thus, the low survival of birds to 1 year old could be due to birds leaving the area to breed elsewhere. Nestlings which leave and never return have no effect on adult survival estimates except to restrict the class of birds to which they refer. Mead (1973) reports four breeding season recoveries of Orkney birds at sites over 100 km. away but little else is known about permanent emigration rates or of possible differences between the sexes. In Picozzi's study, of the birds tagged as nestlings, 3% of the males and 5% of the females have been seen or found dead outside of the islands. However, these figures are affected by the reporting rates and it is not clear how they reflect permanent emigration. Males and females do differ in their short-term movements. From observations at a winter roost in Orkney, Picozzi and Cuthbert (1982) showed that a higher proportion of males than females left the islands in winter, but they found no evidence of a difference in permanent emigration.

Further downward bias in the survival estimates would arise from unequal resighting rates. The evidence for this is not very strong but again the effect

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would be expected to be greatest in the estimation of survival of nestlings since only the number of marked 1 year old birds is being estimated. On this point, there could be some consolation in the findings of Carothers' study on Fulmars (*Fulmarus g. glacialis*) where, in spite of an extreme significance level in his test for equal catchability, the bias in the estimated mean survival was less than 1% of the true value.

Despite the difficulties of interpreting the observed pattern of age-dependent survival, the analysis of the Orkney Hen Harrier data shows that the proportion of the birds which survive to 2 years and return to the area to breed is about twice as high in females as in males, and that in the adults which bred in Orkney survival of females was about one and a quarter times that of males.

ACKNOWLEDGEMENTS

I am grateful to Ken Lakhani, Byron Morgan, Malcolm Mountford and Philip North for constructive criticism of the paper, and to Nick Picozzi for advice on ornithological aspects and for the use of his data.

APPROXIMATE UNBIASED ESTIMATION IN THE MULTI-SAMPLE SINGLE RECAPTURE CENSUS

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SUMMARY

A common model used in bird ringing studies is the so-called multi-sample single recapture census in which adult ringed birds are released into the population at the beginning of each year and the numbers of rings recovered from dead birds recorded. The problem of unbiased estimation is considered in two cases:

- (i) Continuous sampling in which rings are recovered continuously throughout the year.
- (ii) Instantaneous sampling in which rings are recovered from hunted birds only during a short intensive hunting season just prior to the next ring release.

Keywords: BIRD-RINGING, UNBIASED ESTIMATION, SURVIVAL RATES, RING RECOVERY RATES.

1. INTRODUCTION

The multiple recapture model, developed independently by Jolly (1965) and Seber (1965), has been used for studying a wide range of animal populations. However, a special case of this model, in which animals are removed on capture and tagged animals are released into the population from outside, has been particularly useful for bird and fish populations. As there are several samples, but animals are recaptured only once, the model has been called the multi-sample single recapture census (Seber, 1962, 1982). Jolly (1965) demonstrated that it is a special case of the multiple recapture model (the J-S model of Seber and Manly, 1985) but with 100% losses on capture, and releases independent of the capture samples. In this paper we shall construct estimates and variance estimates which are approximately unbiased for the multi-sample single recapture census.

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2. GENERAL MODEL

Suppose that we have an open population of animals, that is a population with birth, death and migration. We assume that all emigration is permanent, so that death and emigration can be lumped together as a single process "death". Let R_i marked animals be released at the beginning of year (period) i ($i = 1, 2, \dots, s$). Suppose that recaptures are made during each period, and the animals removed from the population, for t periods ($t > s$). We now make the following assumptions:

- (i) Every marked animal has probability α_j of surviving, remaining in the area, and not being caught, in period j ($j = 1, 2, \dots, t$).
- (ii) Every marked animal has probability β_i of being caught (and its tag recovered) during period i .

If all animals act independently of one another, and m_{ij} is the number from release i caught in period j , then the joint distribution of the m_{ij} is proportional to (Seber, 1982, Section 13.1.4):

$$\prod_{i=1}^s \beta_i^{m_{ii}} (\alpha_i \beta_{i+1})^{m_{i,i+1}} \dots (\alpha_i \alpha_{i+1} \dots \alpha_{t-1} \beta_t)^{m_{it}} (1-\theta_i)^{R_i - r_i} \\ = \left\{ \prod_{i=1}^{s-1} \alpha_i^{T_i - m_i} \beta_i^{m_i} (1-\theta_i)^{R_i - r_i} \right\} \gamma_{s+1}^{m_{s+1}} \gamma_{s+2}^{m_{s+2}} \dots \gamma_t^{m_t}, \quad (1)$$

where $\gamma_j = \alpha_s \alpha_{s+1} \dots \alpha_{j-1} \beta_j$ ($j = s+1, s+2, \dots, t$), and

$$\begin{aligned} \theta_i &= \beta_i + \alpha_i \beta_{i+1} + \dots + \alpha_i \alpha_{i+1} \dots \alpha_{t-1} \beta_t \\ &= \beta_i + \alpha_i \theta_{i+1}. \end{aligned}$$

Here θ_i is the probability of capture at some time during the experiment from the i th release, r_i is the number recovered during the experiment from R_i , m_i is the number of recaptures in the i th period, and T_i is the number of animals recaptured after the i th release from the first i releases. Let $a_i = T_i - m_i$ ($= T_{i+1} - r_{i+1}$ and often referred to as z_{i+1}), the number recaptured after the $(i+1)$ th release from releases $1, 2, \dots, i$. We note that r_i has a binomial distribution, that is $r_i \sim \text{Bin}(R_i, \theta_i)$; and from Robson and Youngs (1971), $a_i | T_i, r_i \sim \text{Bin}(T_i, 1 - \beta_i \theta_i^{-1})$, which does not contain r_i . Furthermore, r_{i+1} is independent of (r_i, T_i) , coming from a different release. Hence, conditional on T_i , we see that a_i , r_i and r_{i+1} are mutually independent.

Brownie *et al.* (1978, p.211) (see also Seber, 1982, p.513) showed that a slight

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modification of the maximum likelihood estimate of α_i , namely

$$\alpha_i^* = \frac{a_i}{T_i} \cdot \frac{r_i}{R_i} \cdot \frac{R_{i+1} + 1}{r_{i+1} + 1} \quad (= XYZ, \text{ say}),$$

is approximately unbiased as

$$E[\alpha_i^*] = \alpha_i \left\{ 1 - (1-\theta_{i+1})^{R_{i+1} + 1} \right\}$$

Since, conditionally on T_i , X , Y and Z are mutually independent, we can use Lemmas 1 and 2 in the appendix to find an approximately unbiased estimate of $\text{var}[\alpha_i^*]$, namely

$$\begin{aligned} v(\alpha_i^*) &= (\alpha_i^*)^2 - \frac{a_i(a_i-1)}{T_i(T_i-1)} \cdot \frac{r_i(r_i-1)}{R_i(R_i-1)} \cdot \frac{(R_{i+1}+1)(R_{i+2}+2)}{(r_{i+1}+1)(r_{i+1}+2)} \\ &= \alpha_i^* \left\{ \alpha_i^* - \frac{(a_i-1)(r_i-1)(R_{i+1}+2)}{(T_i-1)(R_i-1)(r_{i+1}+2)} \right\} \end{aligned}$$

Approximate unbiasedness follows as

$$\begin{aligned} E \left[\frac{\bar{a}_i(a_i-1)}{T_i(T_i-1)} \cdot \frac{r_i(r_i-1)}{R_i(R_i-1)} \cdot \frac{(R_{i+1}+1)(R_{i+2}+2)}{(r_{i+1}+1)(r_{i+1}+2)} \mid T_i \right] \\ \approx (1-\beta_i\theta_i)^{-1} \cdot \theta_i^{-2} \cdot \theta_{i+1}^{-2} = \alpha_i^2. \end{aligned}$$

The maximum likelihood estimate of β_i ,

$$\hat{\beta}_i = \frac{m_i}{T_i} \cdot \frac{r_i}{R_i}.$$

is unbiased and, using a similar argument to that above,

$$v(\hat{\beta}_i) = \hat{\beta}_i \left\{ \hat{\beta}_i - \frac{(m_i-1)(r_i-1)}{(T_i-1)(R_i-1)} \right\}$$

is an unbiased estimate of $\text{var}[\hat{\beta}_i]$.

The above model (1) has two important applications. Firstly, the model represents an exploitation model in fisheries in which the sampling (exploitation) is continuous throughout the sampling period. Here α_i is the probability that a tagged fish survives in period i and is sometimes called the total survival rate as it refers to survival from both natural and exploitation mortality (see Youngs and Robson, 1975).

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The parameter β_j is sometimes referred to as the observed exploitation rate.

Secondly, the model represents a time specific bird-ringing model developed independently by Robson and Youngs (1971) and Seber (1970a), and discussed by Brownie *et al.* (1978, Chapter 2, Model 1). In the notation of the latter authors, $\alpha_i = s_i$ (the probability of survival from natural and hunting mortality in year i), and $\beta_j = f_j$ (the so-called ring recovery rate).

For model (1) the (biased) maximum likelihood estimate of α_i is $\hat{\alpha}_i = a_i r_i R_{i+1} / T_i R_i r_{i+1}$ with large sample variance given by Seber (1982, equation (5.37) with $\alpha_i = \phi_i$). Replacing parameters by their unbiased estimates in the large sample variance leads to an estimate \hat{v}_i , which is the one commonly used in practice. It is of interest, therefore, to compare the mean and standard deviation of \hat{v}_i with those of $v_i^* = v(\alpha_i^*)$ using simulation. Table 1, kindly computed for me by Mr. Roy Felton for the case $s = t = 3$, $\alpha_i = \alpha$, $\beta_i = \beta$ and $R_i = R$ ($i = 1, 2, 3$) and using 1000 simulations for each of the four cases, shows that v^* is superior, particularly with smaller samples: it has not only less bias, but also a smaller standard deviation.

Table 1

A comparison of the true mean and standard deviation of the large sample variance estimate \hat{v}_i with the approximately unbiased variance estimate $\hat{v}_i^* (\times 10^3)$, using simulation.

$\text{var}[\alpha_i^*]$	$E[v_i^*]$	$E[\hat{v}_i]$	$(\text{var}[v_i^*])^{1/2}$	$(\text{var}[\hat{v}_i])^{1/2}$
$R = 500 \quad \alpha = 0.7 \quad \beta = 0.1$				
α_1^* 12.5	12.3	12.5	3.8	3.9
α_2^* 18.0	18.5	19.1	8.0	8.4
$R = 500 \quad \alpha = 0.9 \quad \beta = 0.1$				
α_1^* 14.9	15.0	15.3	4.3	4.4
α_2^* 26.2	26.6	27.5	11.8	12.3
$R = 100 \quad \alpha = 0.7 \quad \beta = 0.1$				
α_1^* 63.4	64.4	70.5	49.2	57.2
α_2^* 99.4	106.0	139.9	216.6	528.2
$R = 100 \quad \alpha = 0.9 \quad \beta = 0.1$				
α_1^* 78.8	79.0	85.9	54.5	62.4
α_2^* 149.1	155.1	206.1	300.4	691.6

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 3. INSTANTANEOUS SAMPLING

Model (1) can also be used for the case when sampling is essentially instantaneous, for example when the sample is taken at the end of each period just prior to the release. Let ϕ_i be the probability of survival between the i th and $(i+1)$ th releases, and let p_i ($= 1 - q_i$) be the probability of capture in the i th sample: it is assumed that these probabilities are the same for all marked animals. Then $\alpha_i = \phi_i q_i$ and $\beta_i = \phi_i p_i$, and an approximately unbiased estimate of ϕ_i is

$$\begin{aligned}\phi_i^* &= \alpha_i^* + \hat{\beta}_i \\ &= \frac{a_i}{T_i} \cdot \frac{r_i}{R_i} \cdot \frac{R_{i+1} + 1}{r_{i+1} + 1} + \frac{T_i - a_i}{T_i} \cdot \frac{r_i}{R_i} \\ &= XYZ + (1 - X)Y, \text{ say} \\ &= Y\{X(Z - 1) + 1\}.\end{aligned}$$

This estimate is in fact the one proposed by Seber (1982, p.204) for the multiple recapture model, but derived using a Taylor expansion method.

To find an approximately unbiased estimate of $\text{var}[\phi_i^*]$ we condition on T_i and apply Lemma 3 twice. Firstly, using Lemma 2, an approximately unbiased estimate of $\text{var}[X(Z - 1)|T_i]$ is

$$\begin{aligned}v_{13} &= \frac{a_i^2 (R_{i+1} + 1)(R_{i+1} - r_{i+1})}{T_i^2 (r_{i+1} + 1)^2 (r_{i+2} + 1)} + \frac{(R_{i+1} - r_{i+1})^2 a_i (T_i - a_i)}{(r_{i+1} + 1)^2 \cdot T_i^2 (T_i - 1)} \\ &\quad - \frac{(R_{i+1} + 1)(R_{i+1} - r_{i+1}) a_i (T_i - a_i)}{(r_{i+1} + 1)^2 (r_{i+2} + 1) T_i^2 (T_i - 1)}.\end{aligned}$$

Secondly, an approximately unbiased estimate of $\text{var}[\phi_i^*|T_i]$ is

$$v(\phi_i^*) = Y^2 v_{13} + \{X(Z - 1)\}^2 v_2 - v_2 v_{13}$$

where

$$v_2 = \frac{r_i(R_i - r_i)}{R_i^2(R_i - 1)}$$

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We now have

$$\begin{aligned} E[v(\phi_i^*)] &= \underset{T_i}{E}[E[v(\phi_i^*)|T_i]] \\ &\approx \underset{T_i}{E}\{\text{var}[\phi_i^*|T_i]\} \\ &\approx \underset{T_i}{E}\{\text{var}[\phi_i^*|T_i]\} + \underset{T_i}{\text{var}}\{E[\phi_i^*|T_i]\} \\ &= \text{var}[\phi_i^*] \quad , \end{aligned}$$

and $v(\phi_i^*)$ is approximately unbiased.

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APPENDIX

Lemma 1 Let X, Y and Z be mutually independent random variables with means μ_X etc., and suppose there are mutually independent unbiased estimates A_X, A_Y and A_Z of μ_X^2, μ_Y^2 and μ_Z^2 respectively. Then

$$v^* = (XYZ)^2 - A_X A_Y A_Z$$

is an unbiased estimate of $\text{var}[XYZ]$.

Lemma 2 Given $V \sim \text{Bin}(n, p)$, then:

$$(i) E\left[\frac{V(V-1)}{n(n-1)}\right] = p^2 = \left(E\left[\frac{V}{n}\right]\right)^2;$$

$$(ii) E\left[\frac{V(n-V)}{n^2(n-1)}\right] = \text{var}\left[\frac{V}{n}\right] \quad ; \quad \text{and}$$

$$(iii) E\left[\frac{(n+1)(n+2)\dots(n+k)}{(V+1)(V+2)\dots(V+k)}\right] = \frac{1}{p^k} \left\{ 1 - \sum_{u=0}^{k-1} \binom{n+k}{u} p^u q^{n+k-u} \right\}$$

In particular

$$E\left[\frac{n+1}{V+1}\right] = \frac{1}{p} (1 - q^{n+1}) \approx \frac{1}{p},$$

$$\begin{aligned} E\left[\frac{(n+1)(n+2)}{(V+1)(V+2)}\right] &= \frac{1}{p^2} \{ 1 - q^{n+2} - (n+2) pq^{n+1} \} \\ &\approx \frac{1}{p^2} \\ &= \{E\left[\frac{n+1}{V+1}\right]\}^2, \end{aligned}$$

and

$$\begin{aligned} \text{var}\left[\frac{n+1}{V+1}\right] &\approx E\left[\left(\frac{n+1}{V+1}\right)^2\right] - E\left[\frac{(n+1)(n+2)}{(V+1)(V+2)}\right] \\ &= E\left[\frac{(n+1)(n-V)}{(V+1)^2(V+2)}\right] \end{aligned}$$

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Lemma 3 Let B and C be independent random variables with independent unbiased estimates, v_B and v_C respectively of their variances. Then

$$v_{BC} = B^2 v_C + C^2 v_B - v_B v_C$$

is an unbiased estimate of $\text{var}[BC]$.

APPROXIMATELY UNBIASED VARIANCE ESTIMATION FOR THE
JOLLY-SEBER MARK-RECAPTURE MODEL : POPULATION SIZE

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SUMMARY

Large sample variances for the Jolly-Seber estimates from a mark-recapture experiment are usually estimated by replacing unknown parameters by their estimates in the variance formulae obtained by the so-called delta method. These variance estimates are subject to large biases for small and moderate sized samples. To overcome this problem a new variance formula that is almost unbiased has been developed for population size estimates.

The new formula does not, unfortunately, overcome the problem of the correlation between estimate and estimated variance which leads to underestimates appearing to be more accurate than they are. Indeed removing the bias in the variance estimate tends to make this problem worse.

Key words: MARK-RECAPTURE METHODS; JOLLY-SEBER MODEL; POPULATION SIZE

1. INTRODUCTION

A general model for analysing capture-recapture data from a population open to mortality, immigration etc., which we shall call the J-S model, was developed independently by Jolly (1965) and Seber (1965), and reviewed by Seber (1982, Chapters 5 and 13) and Cormack (1979). This model has wide applications and can be applied, for example, to live recapture data from unexploited bird populations (Brownie *et al.*, 1978, p.170; Pollock, 1981b). The asymptotic variances of the estimates of the population size and survival probability given by Jolly have been studied by a number

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of authors using simulation (*cf.* Manly, 1970, 1971; Gilbert, 1973; Carothers, 1973; Bishop and Sheppard, 1973). Apart from robustness considerations, Manly (1971) noted that large sample confidence intervals based on estimated variances are not very reliable, mainly because the variances are proportional to the squares of the parameters estimated: if the parameter is underestimated the variance is also underestimated thus giving a false picture of precision. Later, Manly (1977b) proposed alternative variance estimates based on the generalised jackknife approach of Gray and Schucany (1972). However this approach has the disadvantage of requiring empirical correction factors for the jackknife variances.

In the present paper we discuss an alternative approach for obtaining estimates of the true (small sample) variances. These estimates were derived using an extension of a technique given by Seber (1970b) for the two sample Petersen method. (Lincoln index) and applied to the tag loss situation by Seber and Felton (1981). Details of the technique are outlined below.

The so-called Petersen capture-recapture experiment consists of taking a sample of n_1 individuals (called sample 1) from a closed population of size N , marking them, and then releasing the marked sample into the population. After allowing time for the marked and unmarked to mix, a second sample (sample 2) of size n_2 is taken and the number (m_2) of marked recaptured in the sample noted. Making the usual assumptions about random sampling, no loss of tags etc. (*cf.* Seber, 1982, Chapter 3) and assuming fixed sample sizes, m_2 has the hypergeometric distribution

$$f(m_2 | n_1, n_2) = \binom{n_1}{m_2} \binom{N-n_1}{n_2-m_2} \binom{N}{n_2} \quad (1)$$

where $\max\{0, n_1+n_2 - N\} \leq m_2 \leq \min\{n_1, n_2\}$.

A modification of the maximum likelihood estimate of N is

$$N^* = (n_1+1)(n_2+1)/(m_2+1) - 1, \quad (2)$$

proposed by Robson and Regier (1964), which is minimum variance unbiased when $n_1+n_2 \geq N$ and approximately unbiased otherwise. In this latter case

$$E(N^* | n_1, n_2) \approx N(1 - e^{-\mu}),$$

where $\mu = E(m_2 | n_1, n_2) = n_1 n_2 / N$. Using a normal approximation, Robson and Regier note that if $m_2 \geq 7$ we are 95 per cent confident that $\mu > 4$ and the proportional bias is negligible (less than 2 per cent). Seber (1970b) and Wittes (1972) showed

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independently that an estimate of $\text{var}(N^*|n_1, n_2)$, the variance of N^* , with similar properties is given by

$$v^* = (N^*+1)^2 - A^* + (N^*+1) \quad (3)$$

$$= (n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)/(m_1+1)^2(m_1+2) \quad (4)$$

where A^* is $(N^*+1)^2$ expressed as factorials instead of powers, that is

$$A^* = (n_1+1)(n_1+2)(n_2+1)(n_2+2)/(m_2+1)(m_2+2).$$

Approximate unbiasedness follows from

$$\begin{aligned} E(A^*|n_1, n_2) &\approx (N+1)(N+2) \{ 1 - (\mu+1)e^{-\mu} \} \\ &\approx (N+1)(N+2) \end{aligned} \quad (5)$$

for moderate μ . Since $(\mu+1)\exp(-\mu)$ decreases as μ increases, and a 10 per cent bias in a variance formula can be tolerated, the above approximation will be satisfactory if $\mu > 4$. Thus for $m_2 \geq 7$,

$$\begin{aligned} E(v^*|n_1, n_2) &\approx \text{var}(N^*|n_1, n_2) + (N+1)^2 - (N+1)(N+2) + N+1 \\ &= \text{var}(N^*|n_1, n_2). \end{aligned} \quad (6)$$

2. THE J-S MODEL

A natural extension of the Petersen experiment is to consider s samples from an open population with a mark or tag release made immediately after each sample (*cf.* Seber 1982, Chapter 5). We shall assume that each mark release is a subset of those captured in the sample, though, as pointed out by Jolly (1965), the estimates given below have wider applicability. If individually numbered tags are used, then members of the population need to be tagged only once, the first time they are caught. For $i = 1, 2, \dots, s$, let

M_i = total number of marked (tagged) individuals in the population just before the i th sample,

N_i = total number in the population just before the i th sample,

n_i = number caught in sample i ,

m_i = number of marked caught in sample i ,

R_i = number of marked released from sample i ,

r_i = number of R_i subsequently captured,

z_i = number of different individuals caught before sample i which are not caught in sample i but are caught subsequently,

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$$T_i = r_i + z_i,$$

B_i = number of new individuals joining the population in the interval from the i th release to the $(i+1)$ th sample which are still alive and in the population at the time of the i th release,

$N_i(h)$ = number in the population at the time of the i th sample which are members of B_h ($1 \leq h \leq i-1$).

Data from such a multiple recapture experiment can be modelled using either a multinomial or hypergeometric-type model (cf. Cormack, 1979, for a helpful discussion). The multinomial model leads to the following estimates and asymptotic expressions for their variances (Jolly, 1965):

$$\hat{M}_i - m_i = R_i z_i / r_i, \quad (i = 2, 3, \dots, s-1)$$

$$\hat{N}_i = \hat{M}_i n_i / m_i, \quad (i = 2, 3, \dots, s-1)$$

$$\text{var}(\hat{N}_i) \underset{N_i}{\approx} E \{ \text{var} (\hat{N}_i | N_i) \} + \text{var}(N_i)$$

and

$$\begin{aligned} \text{var}(N_i) &\approx E [N_i] - \sum_{h=0}^{i-1} E \{ N_i^2 (h) \} / B_h \\ &= \sum_{h=0}^{i-1} E [N_i(h) \{ B_h - N_i(h) \} / B_h]. \end{aligned} \quad (7)$$

If expected values of random variables are replaced by random variables, then

$$\text{var}(\hat{N}_i | N_i) \approx N_i(N_i - n_i)(M_i - m_i + R_i) (1/r_i - 1/R_i) / M_i. \quad (8)$$

An alternative hypergeometric-type model can be developed if N_i , M_i , R_i and n_i are regarded as fixed constants (cf. Robson, 1969; Pollock, 1974, 1975). In this case the likelihood function for the model contains the term

$$\frac{\binom{R_i}{r_i} \binom{M_i - m_i}{z_i}}{\binom{M_i - m_i + R_i}{T_i}} \cdot \frac{\binom{M_i}{m_i} \binom{N_i - M_i}{n_i - m_i}}{\binom{N_i}{n_i}}. \quad (9)$$

By considering $E(r_i | T_i, m_i)$ and $E(m_i | n_i)$ we are led once again to the estimates \hat{M}_i and \hat{N}_i which, suitably rounded to integers, are the maximum likelihood estimates for the above model. Pollock (1975) has shown that the asymptotic variances are essentially the same as for the multinomial model except that the term $\text{var}(N_i)$ is now

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zero. However this term will often be negligible for the multinomial model and, as indicated by (7), will be less affected by bias than (8).

3. UNBIASED ESTIMATION

Clearly we can identify the first term of (9) with (1) by setting $R_i = n_1$, $r_i = m_2$, $T_i = n_2$ and $M_i - m_i + R_i = N$. Thus, by analogy with (2), we have the estimate

$$M_i^* - m_i + R_i = (R_i + 1)(T_i + 1)/(r_i + 1) - 1$$

or, $M_i^* - m_i = (R_i + 1)z_i/(r_i + 1)$, an estimate proposed by Seber (1982, p.204). Applying the same approach to the second term of (9) leads to

$$N_i^* = (M_i^* + 1)(n_i + 1)/(m_i + 1) - 1. \quad (10)$$

Then setting $\mathbf{y} = (R_i, m_i, T_i, M_i, N_i, n_i)'$, for $r_i \geq 7$ we can be confident that

$$E(N_i^* | \mathbf{y}) \approx (M_i + 1)(n_i + 1)/(m_i + 1) - 1.$$

Similarly, for $m_i \geq 7$, we have

$$E(N_i^* | M_i, N_i, n_i) \approx N_i,$$

which leads finally to $E(N_i^* | N_i) \approx N_i$.

To find an approximately unbiased variance estimate we consider the expression

$$N_i^* + 1 = \left\{ \frac{(R_i + 1)(T_i + 1)}{(r_i + 1)} + m_i - R_i \right\} \left[\frac{n_i + 1}{m_i + 1} \right]$$

and apply the technique of (3), namely defining

$$v_i^* = (N_i^* + 1)^2 - B_i^* + (N_i^* + 1), \quad (11)$$

where

$$B_i^* = \left\{ \frac{(R_i + 1)(R_i + 2)(T_i + 1)(T_i + 2)}{(r_i + 1)(r_i + 2)} + 2(m_i - R_i) \frac{(R_i + 1)(T_i + 1)}{(r_i + 1)} \right. \\ \left. + (m_i - R_i)(m_i - R_i + 1) \right\} \frac{(n_i + 1)(n_i + 2)}{(m_i + 1)(m_i + 2)}.$$

Using an approximation like (5) twice we then find that

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$$E(B_i^* | \underline{y}) \approx (M_i+1)(M_i+2)(n_i+1)(n_i+2)/\{(m_i+1)(m_i+2)\}$$

and

$$E(B_i^* | N_i) \approx (N_i+1)(N_i+2) .$$

Thus arguing as in (6) we have

$$E(v_i^* | N_i) \approx \text{var}(N_i^* | N_i)$$

for the hypergeometric model, and

$$E(v_i^*) \approx E_{N_i} \{\text{var}(N_i^* | N_i)\}$$

for the multinomial model. In the latter case we either ignore the term $\text{var}(N_i)$ or estimate it using (7).

4. SIMULATION

We have carried out some simulation-experiments to see how the new variance formula compares with the formula given by Jolly. It is convenient to think of these as simulating natural populations over periods of three "days". The general approach to the simulations was the same as that used earlier by Manly (1970, 1971, 1977b).

The numbers of animals "born" were fixed in the simulations so that three levels of population size (50, 200 and 1000) could be maintained. Two survival probabilities (0.6 and 0.9 per "day") were used and also two levels for the probability of capture in a sample (low and high, with the actual probabilities depending upon the population size). These possibilities for population size, survival and probability of capture give $3 \times 2 \times 2 = 12$ different situations. Each of these situations was independently simulated five times for three "days", to give 60 different populations. Each population was then sampled independently 40 times, where each sampling involved samples being taken on "days" 1, 2 and 3.

If samples are taken from a population on days 1, 2 and 3 then it is possible to estimate N_2 , the population size on day 2. Thus 40 independent estimates of N_2 were available for each of the 60 simulated populations, together with the estimated variance from Jolly's formula and the formula of the present paper.

The simulation results are summarised in Table 1. The results have been averaged for populations with the same size, survival and capture probabilities because the differences between these populations were generally small.

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Table 1
Summary of the simulation results

Approx N	ϕ	p	Bias N_2^*	Observed $\text{Var}(N_2^*/N_2)$	Mean of variance estimates		Mean of Z values		Variance of Z values		Observed Mean r_2	Mean m_2
					A	B	A	B	A	B		
50	0.6	0.6	-1	173	236	176	-0.4	-0.5	1.1	1.4	11	11
	0.8	0	48	56	48	56	-0.2	-0.2	1.0	1.1	18	19
0.9	0.6	1	85	114	94	94	-0.3	-0.3	1.8	2.1	16	17
	0.8	0	11	11	10	10	-0.4	-0.4	1.5	1.6	30	30
200	0.6	0.25	2	11575	23238	14036	-0.6	-0.6	1.6	2.1	7	8
	0.6	2	833	858	800	800	-0.2	-0.2	1.2	1.3	42	42
0.9	0.25	6	8308	10690	7817	7817	-0.5	-0.6	1.8	2.2	11	11
	0.6	-2	273	288	276	276	-0.3	-0.3	1.2	1.2	65	65
1000	0.6	0.15	-25	169096	272196	214697	-0.6	-0.7	2.5	3.0	14	14
	0.3	8	37409	39965	37866	37866	-0.2	-0.2	1.1	1.2	54	54
0.9	0.15	-26	101465	129109	111029	111029	-0.4	-0.5	1.0	1.2	20	20
	0.3	-4	15678	18670	18043	18043	-0.2	-0.2	1.0	1.0	82	82

The columns headed A were calculated using Jolly's variance formula while the columns headed B were calculated using the new variance formula proposed in the present paper. In some cases both variance formulae gave variance estimates of zero. This happened 15 times with N=50, $\phi=0.6$ and p=0.6, 22 times with N=50, $\phi=0.6$ and p=0.8, four times with N=200, $\phi=0.6$ and p=0.25. These cases were simply excluded from the calculations involved in columns eight to eleven of this table.

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5. DISCUSSION

The population size estimator that was used in all the simulations was N_2^* of equation (10). The bias $N_2^* - N_2$ is shown in the fourth column of Table 1. There is no obvious pattern and none of them are significantly different from zero. It appears therefore that N_2^* generally has small bias.

The fifth column of Table 1 shows the observed variance of N_2^* , given N_2 . (In the case of population size it seems to be generally true that the non-sampling variance given by equation (7) is not considered important and we have therefore ignored this.) The sixth column of the table shows the mean value of the estimate of $\text{var}(N_2^*|N_2)$ from Jolly's formula (8). In most cases this formula has overestimated the variance to some extent. Overall the estimated variances are about 28% larger than they should be. The seventh column of the table shows the mean value of the estimate of $\text{var}(N_2^*|N_2)$ from equation (11). In almost every case the mean estimate from this equation is closer to the true variance than the mean based upon Jolly's equation. Equation (11) still seems to give variance estimates that are slightly large since 8 out of the 12 means are higher than the observed variance. However, overall the estimated variances are only about 6% higher than they should be and this is rather better than the 28% over-estimation from Jolly's formula.

Columns eight and nine in the table give the mean values of Z statistics of the form

$$Z = (N_2^* - N_2)/\{\text{var}(N_2^*|N_2)\}^{1/2} \quad (12)$$

with $\text{var}(N_2^*|N_2)$ being estimated by (A) Jolly's formula (8), and (B) formula (11). If confidence intervals of the form

$$N^* \pm 1.96\{\text{Var}(N_2^*/N_2)\}^{1/2}$$

based upon the normal distribution are to be valid then it is necessary for the Z values to follow standard normal distributions approximately.

The Z distributions obtained from the two variance equations are very similar. In both cases the conspicuous negative means are caused by the correlation between a population size estimate and its estimated variance. A very low size estimate tends to have a very low variance estimate with the result that the Z value becomes very negative. Strangely enough, the positive bias in Jolly's variance estimate works in the opposite direction to this effect with the result that using a less biased variance estimate actually makes the effect worse. The correlation between estimates and their variances also shows up by the Z values tending to have variances rather

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larger than 1.0 as is shown in columns ten and eleven in Table 1.

The last two columns of Table 1 shows the mean values for r_2 and m_2 . It may be recalled that for unbiased estimation it was suggested earlier that r_i and m_i should be rather larger than 7. It is clear that for Z values, given by equation (12), to have a mean of approximately zero and standard deviation of one, then r and m values will have to be very large indeed. For example, with a population size of 1000, r and m will have to be much larger than 20. However it does appear that if r and m are larger than 7 then N_i^* and v_i^* are approximately unbiased.

6. GENERAL COMMENTS

The above methodology is admittedly of limited application to bird populations. It leans heavily on the assumption that tagged and untagged birds have the same probability of being caught in a given sample. This rules out the situation where birds become trap-addicted and the case there "capturing" is done by the sighting of marked birds only. As the theory stands, the model also assumes that the survival rates are not age-dependent so that it applies to adult birds only. However, from Pollock (1981a) we see that the J-S model generalises naturally to the case of age-dependent survival and that, in the estimation of population size, the age classes are effectively treated as separate populations, except for the last. This means that above estimates can be used for each age class but the oldest.

The use of approximately unbiased estimates instead of the maximum likelihood estimates seems most appropriate for small populations and low numbers of recaptures. However if the normal approximation is used for finding confidence intervals, for example, $N_i^* \pm 1.96\sqrt{v_i^*}$ for a 95% confidence interval, then the unbiased estimates do not fare so well. In either case the normal approximation does not work very well and the construction of suitable confidence intervals needs further investigation.

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