



<https://theses.gla.ac.uk/8343/>

This is a digitised version of the original print thesis.

Copyright and moral rights for this work are retained by the author

A copy can be downloaded for personal non-commercial research or study, without prior permission or charge

This work cannot be reproduced or quoted extensively from without first obtaining permission in writing from the author

The content must not be changed in any way or sold commercially in any format or medium without the formal permission of the author

When referring to this work, full bibliographic details including the author, title, awarding institution and date of the thesis must be given

Enlighten:Theses
<http://theses.gla.ac.uk/>
theses@ gla.ac.uk

ProQuest Number: 10390499

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



ProQuest 10390499

Published by ProQuest LLC (2017). Copyright of the Dissertation is held by the Author.

All rights reserved.

This work is protected against unauthorized copying under Title 17, United States Code
Microform Edition © ProQuest LLC.

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 – 1346

Evolutionary Influences on Avian Clutch Size

David Lindsay Thomson

Submitted for the Degree of Ph.D, Glasgow University, Division of
Environmental and Evolutionary Biology, March 1995.

Thesis
10153
Copy 2

GLASGOW
UNIVERSITY
LIBRARY

Except for the contributions of others mentioned in the acknowledgements section, I confirm that the work presented in this thesis is my own. The thesis has been prepared largely as a series of manuscripts, some of which have been accepted for publication, and others which I hope to publish. Authorship of these has been shared with my supervisors Dr. Robert W. Furness and Dr. Pat Monaghan. The late Henry Douglas-Home initiated the study of swifts, and so authorship is shared also with him in those manuscripts reporting results principally from this source.

Summary

I conducted a series of studies which looked at influences on avian clutch size. Firstly I examined the traditional view that the demands of rearing chicks create a bottleneck at which clutch size is shaped by natural selection. I considered whether instead other stages such as incubation might also be important. I proposed that reproductive demands at each stage of the breeding season may be interdependent, and by developing a mathematical model, I formalised the argument and showed that data on the relationship between the number of offspring and the expenditure of resources at many stages of the season could reveal the importance of natural selection on clutch size at each stage. I then reviewed the literature on the importance of incubation for clutch size determination. Results indicated that metabolic demands of incubation were appreciable and that the incubation of enlarged clutches imposed penalties on the adults. In a field study of kittiwakes I found that breeding success was depressed during incubation and chick rearing by enlargement of clutches and broods respectively. I measured metabolic rates of kittiwakes during incubation and found them to be comparable with those during chick-rearing.

Secondly, I examined whether individual adults within populations differed in their reproductive capacities (i.e. whether there was a range of 'adult quality') and whether this could then affect clutch size. In a study of kittiwakes I found clusters of birds with similar breeding performance, but found that these clusters did not persist between years. In a study of swifts, I found that some individuals were consistently good breeders but that this had negligible effects on the distribution of lifetime reproductive success between individuals.

I then examined whether the low clutch sizes and high survival of swifts might reflect a bet-hedging strategy in a fluctuating environment, but found little evidence of this. I looked at whether differences in the amount of space available at the nest site could account for differences in clutch sizes of

kittiwakes, but could find no such evidence. Lastly I developed a theoretical model to look at how clutch size might be affected by changes in reproductive effort with age. I examined whether the predictions of optimality models were borne out by the more appropriate population genetics approach and found that in birds the optimality models are robust.

Contents

Title Page.....	1
Summary.....	3
Contents.....	5
Acknowledgements.....	7
<u>Introduction.</u>	
Chapter 1.	
Life History Theory and Avian Clutch Size Determination.....	11
<u>Methods.</u>	
Chapter 2.	
Section 1. Methods for Comparing Alternative Clutch Size Strategies.....	24
Section 2. The Proximate Measurement of Fitness.....	27
Section 3. Statistical analysis and the GENSTAT package.....	36
Section 4. Calculating Nesting Success: Some Refinements on the Mayfield Method.....	42
Section 5. The Technique of Ordinal Logistic Regression for Analysing Ecological Data.....	72
Section 6. Direct and Indirect Approaches.....	95
Section 7. The Kittiwake as a Study Species.....	100
Section 8. The Swift as a Study Species.....	105
Section 8b. Breeding success and survival in the common swift <u>Apus apus</u> : a long term study on the effects of weather.....	110
<u>Results.</u>	
Chapter 3. Are there Bottlenecks on Avian Reproduction? Clutch Size and the Temporal Distribution of Reproductive Demands.....	134
Chapter 4. Avian Clutch Size and the Demands of Incubation.....	152

Chapter 5. Clutch Size Determination in Kittiwakes <i>Rissa tridactyla</i> : an Experimental Study of Incubation and Chick Rearing Stages.....	181
Chapter 6. Field Metabolic Rates of Kittiwakes During Incubation and Chick Rearing: a Study with Doubly Labelled Water.....	202
Chapter 7. Breeding Performance, Colony Structure, and Nest Site Quality: a Study of Kittiwakes <i>Rissa tridactyla</i>	208
Chapter 8. Does adult quality account for the uneven division of lifetime reproductive success among individual Swifts <i>Apus apus</i> ?.....	252
Chapter 9. Does the life history strategy of the Swift <i>Apus apus</i> provide insurance in a fluctuating environment?.....	268
Chapter 10. Do Spatial Constraints Influence Clutch Size in a Cliff Nesting Seabird?.....	285
Chapter 11. Age-specific Life History Tactics in Organisms with Determinate Growth: Optimal Models for Non-optimal Behaviour?.....	300

Discussion and Conclusions.

Chapter 12. General Discussion.....	329
-------------------------------------	-----

APPENDIX

Two papers from unrelated work published during the period of my PhD, are included as an appendix to the thesis. These are:

Thomson, D.L. 1994. Growth and development in Dotterel chicks *Charadrius morinellus*. *Bird Study* 41: 61-67.

Thomson, D.L. and Douglas-Home, H. 1993. Long term changes in weather and in the breeding schedule of Common Swifts *Apus apus*. In 'Recent advances in the study of the Apodidae', Malacarne, G., Collins, C.T. and Cucco, M. (eds) Turin, *Avocetta* 17: 199-202.

This thesis is dedicated to my wife, my mother, and my sister, all of whom came to terms with serious illness while I was doing my PhD, and to David Searle who's recent sudden and tragic death has shocked all members of the department.

Acknowledgements

The work presented in this thesis would not have been possible without the help of many people to whom I am extremely grateful. Bob Furness and Pat Monaghan supervised me throughout my PhD and have provided much help and guidance. Pat managed to fulfill her role as well as meeting the demands of two fine offspring - her breeding season overlapped my period of research. Both Pat and Bob encouraged/discouraged, supported/contradicted, protected/exposed, attacked/defended, accommodated/ignored, backed/abandoned, stimulated/depressed, incited/placated, enthused/demoralised as appropriate/inappropriate. I am grateful to them for everything.

The Carnegie Trust for the Universities of Scotland provided me with financial backing in the form of a Postgraduate Scholarship. Throughout my research they have been very good to me, and have always been keen to help whenever asked. The facilities of the Zoology Department (as it was then) and the Division of Environmental and Evolutionary Biology (as bits of it and other bits of other things are now) were made available to me by Prof. G. Coombs and Prof. F. Huntingford respectively, and I am grateful to all members of staff, including Mr. P. Meadows and Dr. A. Taylor, who have helped postgraduates like myself in various ways. Kenny, Davie, Janette, Cathy, Willie, Alan, Nosrat, Toby, Peter, Golda, Murthy, Liz, Patricia and Shirley have all helped me with diverse things, often at short notice. Willie's endless supply of jokes always guaranteed a memorable day-trip to the stores.

My colleagues in Bob's and Pat's groups particularly have made my time here very enjoyable. Richard, Norman, Belen, David, Fiona, Mustafa, Keith, Justin, Luis, Jose-Pedro, Sharon, Rosli, Paulo, Geoff, Brendan, Paul, Graham, Vicky, Wyllie, Roy, Mark, Tom, John and Bernie have created a lively atmosphere and shared some fine evenings in Tennants, The Arragon, and the Brewery Tap. The christmas and post-viva face-stuffing sessions definitely stick out in my memory for their pleasurability, tempered only by excessive distension.

Others at Glasgow University have made my time enjoyable and productive. I am particularly grateful to staff at the Computing Service for their assistance and for numerous special favours. James, John, Mark, Paul, Elizabeth, Woody, Gary, Jim, Liz, Lesley, George, Alan, Walter, and Reid have all been especially helpful. Staff at S.U.R.R.C., particularly Terry, Jim, Steve, Fred, David, Susan, and Andrew, all helped me with the analysis of doubly labelled water samples. David Bryant gave me broader advice on the doubly labelled water technique itself.

Fieldwork was made possible by the help of several people. Mike Harris, Sarah Wanless, Scottish Natural Heritage, John, Andy, and Chris all made my time on the Isle of May useful and enjoyable. Rob Barrett and Geir Gabrielsen enabled me to work on Hornoya, and together with Torkild, Magne, Espen, Per, Geir, Oysten and Frode, introduced me to Norwegian culture in all its splendour.

The data on swifts used in chapters 2, 8 and 9 were collected largely by others. The late Henry Douglas-Home initiated the study in 1954, and continued it together with Bill Murray, Andrew MacMillan, Stan da Prato, Alan Kerr, Chris Badenoch, the late Rob Robertson, and Lady Caroline Douglas Home. Staff at the meteorological office provided weather records. Robin McCleery and Christine Donnelly offered help with the analytical techniques used in the analyses of these data.

As well as to my supervisors, I am grateful to others for their comments on manuscripts. James Currall read several and offered constructive criticism as well as checking the statistical analyses. Neil Metcalfe, Stuart Daldry, Nick Barton, Raymond O'Connor, Douglas Johnson, John Coulson, Chris Perrins and Thais Martins all read manuscripts and provided helpful comments. I would like to thank Richard Sibly and David Houston for a lengthy and rigorous viva and for their constructive comments on all chapters of my thesis.

Bernie Zonfrillo, Phil Whitfield, Bill Harper and the Scottish Ornithologists Club helped me to track down elusive information on exotic species for the purpose the review in chapter 4. Jeff Hancock and Bob George identified ectoparasites for me.

My wife, Anna, helped and supported me in many ways and endured the side effects of my PhD. I am grateful to my own family, and also to Anna's, for their support throughout my research.

INTRODUCTION

Chapter 1

Life History Theory and Avian Clutch Size Determination

Lack(1947) proposed that avian clutch size was a heritable trait exposed to natural selection, and that the most common clutch size would be adapted to the number of chicks the parents could rear under the prevailing circumstances. An individual laying too many eggs would be unable to nourish all its chicks. It would not maximise its reproductive success and so its genes would be unlikely to spread in the population. The genes of an individual which layed too few eggs would suffer a similar fate.

Many have since pursued an evolutionary understanding of avian clutch size (for overviews see e.g. Godfray et al. 1991, Van der Werf 1992), and the success of this field has made it a prominent empirical example in the study of life-history theory (Stearns 1992, Roff 1992). Although Lack's ideas lie behind many of the approaches currently employed, the discovery that most birds can rear additional offspring has highlighted imperfections in his original hypothesis (Van der Werf 1992), and the many modifications have added new components and redirected the focus of attention.

Lack (1947) assumed that the average clutch size was largely determined by the number of growing chicks the adults could feed, but there is evidence of more than this simple bottleneck. Bolton et al. (1992) found that the provision of particular nutrients during egg-laying led to an increase in the clutch size of lesser black-backed gulls *Larus fuscus* and Monaghan et al. (in press) found that fledging success was reduced when birds were induced to lay additional eggs. Moreno et al. (1991) found that hatching success was depressed if larger clutches were incubated. Weathers and Sullivan (1989) found that the number of dependent fledglings may place particularly high demands on the parents. Studies which focus simply on the number of chicks and the fledging success overestimate the optimal clutch size by omitting the other stages.

Attention has shifted from the average clutch size of the population, to the clutch size of individual birds, and recent studies have looked at whether adults differ in their reproductive capacities (i.e. in their 'quality'), and at whether this influences clutch size. Differences in reproductive capacity could arise either through intrinsic differences in the birds themselves (e.g. disease resistance or foraging efficiency) or through

differences in the resources held by the birds (e.g. nest site quality or territory quality). These two components may often be confounded if good birds command good resources. I will use the term 'adult quality' to describe all components of an individual's reproductive capacity.

Hogstedt (1980) demonstrated that individual magpies *Pica pica* occupying high quality territories laid larger clutches than those occupying poor quality ones. Even though clutch size showed considerable variance within Hogstedt's study population, the optimal clutch size for a bird which chose to lay 'n' eggs was on average 'n' eggs. As well as identifying a spectrum of adult quality within his population, and presenting evidence of individual optimisation, Pettifor *et al.* (1988) also proposed that the spectrum of quality could explain why the average clutch size of all the birds was less than the clutch size which seemed to maximise productivity. If the quality of individuals does differ within populations and if this variance is important for clutch size, then the modal clutch size in which Lack was so interested ceases to be important. The trait of most interest in the context of evolution may not be any fixed clutch size, but rather the ability of individuals to make a clutch size decision in response to circumstances.

As well as individual optimisation, there are many other reasons why the most common clutch size may be less than that which seems to maximise productivity. Charnov and Krebs (1974) used a theoretical model to demonstrate that if adult survival declines with increasing clutch size, then the clutch size which maximises lifetime reproductive success is smaller than the one which maximises annual reproductive success. If the costs of reproduction increase with clutch size (Bell and Koufopanou 1986, Nur 1988, Stearns 1989), then it may pay birds to temper their reproductive effort and to forego current reproductive success for the sake of residual reproductive value. Increasing clutch size may not only depress chick body condition and post-fledging survival (Perrins 1965, Nur 1984b, Richner *et al.* 1989, Smith *et al.* 1989, Magrath 1991), it can reduce the probability of re-nesting (Smith and Roff 1980, Tinbergen 1987), depress adult survival (Askenmo 1979, Nur 1984a, Ekman and

Askenmo 1986, Reid 1987), and lower adult breeding performance in following years (Roskaft 1985, Gustafsson and Sutherland 1988)(see also Nur 1988, Stearns 1989, 1992, Linden and Moller 1989, Roff 1992 for general discussion). Any process of natural selection which optimises fitness will operate on all of these components together, rather than on say clutch size in isolation, and balances may be struck between the current benefits and the future losses associated with reproductive effort (Williams 1966). The optimal reproductive effort will be higher where residual reproductive value is low, e.g when there is high random mortality or where an individual is growing older and approaching senescence (Clutton-Brock 1991).

There may however exist circumstances where the maximisation of average reproductive success is not equivalent to the maximisation of fitness (Murray 1988, 1992, Newton 1989, Stearns 1992), and in fluctuating environments especially this also may account for clutch sizes which are commonly below that which maximises breeding success (Boyce and Perrins 1987, but see also Liou et al. 1993). When there are environmental fluctuations in breeding success/ juvenile survival, in optimal clutch size, or in population size, then appreciable selection on the variance in reproductive success appears (Boyce 1988). The resulting 'bet-hedging' strategies forego the maximisation of average breeding success for safer strategies with lower risks of complete failure and extinction. A bird may lay a small clutch which maximises 'geometric' rather than the conventional 'arithmetic' mean fitness. It may perform less well than large clutches in good years, but overall it will be less prone to catastrophic failure.

Whatever the appropriate currency of fitness, there may be constraints on evolution. Under certain circumstances, mutation may be as important as selection (Rose 1991). In fluctuating environments, selection may track, but rarely attain moving optima (Van Noordwijk et al. 1981). Disruptive processes such as gene flow may prevent birds from reaching the optimal state for the prevailing conditions (Dhondt *et al.* 1990). If birds disperse between habitats, strategies which are locally adapted to one area may be poorly adapted to another. The existence of these constraints does not nullify the evolutionary approach to questions of avian life history, indeed these

examples are drawn from studies which themselves tackled questions within the context of evolution.

Here I aim to tackle questions related to the evolution of avian clutch size, using a variety of empirical, theoretical, experimental, observational, ecological and physiological techniques. Individual investigations are outlined in chapters 3-11, and each contains a detailed introduction outlining the background and specific aims.

Methodological issues common to several of these studies are outlined in Chapter 2. Chapter 2 is split into 8 sections, including 3 manuscripts which report novel results. The first section discusses the alternative methodologies available for comparing alternative clutch size strategies. The second section considers methods by which short term studies can assess the fitness implications of different strategies. In the third section, I clarify details of the statistical analyses undertaken and outline the use of the GENSTAT software package. Section 4 outlines a new technique for measuring nesting success using daily survival rates, and demonstrates appreciable errors in the conventional Mayfield method (Mayfield 1961, 1975, Johnson 1979). Section 5 is a manuscript which illustrates the application of ordinal logistic regression (McCullagh 1980) for analysing ecological data, and Section 6 discusses the relative advantages and disadvantages of employing empirical and theoretical approaches. Sections 7 and 8 discuss the use of the Kittiwake *Rissa tridactyla* and the Swift *Apus apus* respectively as study species and Section 8b is a manuscript giving background ecology of the Swift study population, outlining the long term effects of weather on breeding success and survival.

In Chapter 3, I use a theoretical model to ask whether reproductive bottlenecks are stable in evolutionary time. Although it is widely assumed that natural selection operates on clutch size during the chick rearing period when the demands of reproduction may be greatest, I study whether this bottleneck can persist if birds are able to adjust their behaviour so as to spread demands more evenly through the breeding season.

In Chapter 4, I review literature on the demands of incubation and clutch size evolution, comparing results between species and between physiological and ecological approaches. I ask whether incubation demands can safely be ignored in studies of clutch size determination, and if not, I seek to identify when they are most important.

In Chapter 5, I report a study of clutch size regulation in Kittiwakes in which clutch and brood size were manipulated at various times during the season. I aimed to determine whether the demands of reproduction always increased with the number of eggs and the number of chicks, or whether the number of offspring had particularly severe consequences at any one particular stage in the season.

In Chapter 6, I compare the metabolic rates of adult Kittiwakes during incubation and during chick rearing. I aim to determine whether the chick-rearing phase demands higher energy expenditure than the incubation phase (see e.g. Tatner and Bryant 1993).

In Chapter 7, I look at whether there are groups of high and low quality adults within a Kittiwake colony (c.f. Coulson 1968, Coulson and Thomas 1985), and assess whether this may be related to the quality of the nest site.

In Chapter 8, I aim to assess whether there is a spectrum of adult quality in a colony of Swifts, and use simulations to study whether this could account for the uneven division of lifetime reproductive success in these birds (see Newton 1989).

In Chapter 9, I study whether the high adult survival rates and low clutch sizes of Swifts in fluctuating environments might constitute a bet-hedging adaptation which serves to reduce variance in lifetime reproductive success.

In Chapter 10, I look at whether the clutch size of a cliff-nesting seabird such as the Kittiwake might be influenced by the amount of space available at the nest site. Nutritional and energetic factors, together with predation and parasitism, are widely assumed to determine clutch size (see Godfray et al. 1991) but some studies of both hole-nesting and open-nesting birds have found evidence that clutch size may sometimes be constrained by the amount of space available (Van Balen 1984, Slagsvold 1989a, Slagsvold 1989b).

In Chapter 11, I identify inappropriate assumptions in the optimization models used to study the trade-offs between reproductive effort and residual reproductive value, and I ask whether the prediction that reproductive effort should increase with age is robust despite these (Gadgil and Bossert 1970, Pianka and Parker 1975, Charlesworth and Leon 1976). I employ population genetics as an alternative to optimisation, and look at whether a strategy of increasing reproductive effort can invade the population.

Chapter 12 discusses the results together, and draws general conclusions.

Askenmo, C. 1979. Reproductive effort and return rate of the male Pied Flycatcher.

Amer. Nat. 114:748-753.

Bell, G. and Koufopanou, V. 1986. The cost of reproduction. Oxford Surveys in

Evolutionary Biology. Vol 3. Eds. Dawkins, R. and Ridley, M. pp 83-131.

Oxford University Press, Oxford.

Bolton, M., Houston, D.C., and Monaghan, P. 1992. Nutritional constraints on egg

formation in the lesser black backed gull: an experimental study.

J. Anim. Ecol. 61: 521-532.

Boyce, M.S. and Perrins, C.M. 1987. Optimizing Great Tit clutch size in a

fluctuating environment. Ecology 68:142-153.

Boyce, M.S. 1988. Bet Hedging in Avian Life Histories.

Proc XIX Int. Orn. Congr.: 2131-2139.

Charlesworth, B. and Leon, J.A. 1976. The relation of reproductive effort to age.

Am. Nat. 110: 449-459.

Charnov, E.L. and Krebs, J.R. 1974. On clutch size and fitness. *Ibis* 116: 217-219.

Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Monographs in Behaviour and Ecology. Princeton University Press, Princeton, N.J.

Coulson, J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature* 217:478-479.

Coulson, J.C. and Thomas, C.S. 1985. Differences in the breeding performance of individual kittiwake gulls *Rissa tridactyla* L. in 'Behavioural Ecology: Ecological Consequences of Adaptive Behaviour.', Sibly, R.M. and Smith, R.H. (eds.). pp489-503. Blackwell Scientific, Oxford.

Dhondt, A.A., Adriaensen, F., Matthysen, E., and Kempenaers, B. 1990. Non-adaptive clutch sizes in tits. *Nature* 348:723-725.

Ekman, J. and Askenmo, C. 1986. Reproductive cost, age-specific survival and a comparison of the reproductive strategy in two European tits (Genus *Parus*). *Evolution* 40: 159-168.

Gadgil, M. and Bossert, W.H. 1970. Life historical consequences of natural selection. *Am. Nat.* 104:1-24.

Godfray, H.C.J., Partridge, L., and Harvey, P.H. 1991. Clutch size. *Ann. Rev. Ecol. Syst.* 22:409-429.

Gustafsson, L. and Sutherland, W.J. 1988. The cost of reproduction in the Collared Flycatcher *Ficedula albicollis*. *Nature* 335:813-815.

- Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territorial quality. *Science* 210:1148-1150.
- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89:302-352.
- Linden, M. and Moller, A.P. 1989. Cost of reproduction and covariation of life history traits in birds. *Trends in Ecology and Evolution* 4:367-371.
- Liou, L.W., Price, T., Boyce, M.S. and Perrins, C.M. 1993. Fluctuating environments and clutch size evolution in Great Tits. *Am. Nat.* 141:507-516.
- Magrath, R.D. 1991. Nestling weight and juvenile survival in the Blackbird, Turdus merula. *J. Anim. Ecol.* 60:335-351.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255-261.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456-466.
- McCullagh, P. 1980. Regression Models for Ordinal Data. *J. Roy. Statist. Soc. B* 42:109-142.
- Monaghan, P., Bolton, M. and Houston, D.C. (in press). Egg production constraints and the evolution of avian clutch size. *Proc. Roy. Soc. Lond. B.*

- Moreno, J., Gustafsson, L., Carlson, A. and Part, T. 1991. The cost of incubation in relation to clutch-size in the Collared Flycatcher Ficedula albicollis. Ibis 133: 186-193.
- Murray, B.G. Jr. 1988. On measuring individual fitness: A reply to Nur. Oikos 51:249-250.
- Murray, B.G. Jr. 1992. The evolutionary significance of lifetime reproductive success. Auk 109:167-172.
- Newton, I. 1989. Lifetime reproduction in birds. Academic Press, London.
- Nur, N. 1984a. The consequences of brood size for breeding blue tits. I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53:479-596.
- Nur, N. 1984b. The consequences of brood size for breeding blue tits. II. Nestling weight, offspring survival and optimal brood size. J. Anim. Ecol. 53: 497-517.
- Nur, N. 1988. The cost of reproduction in birds: An examination of the evidence. Ardea 76: 155-168.
- Perrins, C.M. 1965. Population fluctuations and clutch size in the great tit, Parus major L. J. Anim. Ecol. 34: 601-647.
- Pettifor, R.A., Perrins, C.M., and McCleery, R.H. 1988. Individual optimization of clutch size in Great Tits. Nature 336: 160-162.

- Pianka, E.R. and Parker, W.S. 1975. Age-specific reproductive tactics. *Am. Nat.* 109: 453-464.
- Reid, W.V. 1987. The cost of reproduction in the glaucous winged gull. *Oecologia* 74: 458-467.
- Richner, H., Schneider, P. and Stirnimann, H. 1989. Life-history consequences of growth rate depression: an experimental study on carrion crows (Corvus corone corone L.). *Functional Ecology* 3: 617-624.
- Roff, D.A. 1992. *The Evolution of Life Histories. Theory and Analysis.* Chapman and Hall, New York.
- Rose, M. 1991. *Evolutionary biology of aging.* Oxford University Press, Oxford.
- Roskaft, E. 1985. The effect of enlarged brood-size on the future reproductive potential of the Rook. *J. Anim. Ecol.* 54: 255-260.
- Slagsvold, T. 1989a. On the evolution of clutch size and nest size in passerine birds. *Oecologia* 79: 300-305.
- Slagsvold, T. 1989b. Experiments on clutch size and nest size in passerine birds. *Oecologia* 80: 297-302.
- Smith, J.N.M. and Roff, D.A. 1980. Temporal spacing of broods, brood size, and parental care in song sparrows (Melospiza melodia). *Can. J. Zool.* 58:1007-1015.

- Smith, H.G., Kallander, H. and Nilsson, J.-A. 1989. The trade-off between offspring number and quality in the Great Tit *Parus major*. *J. Anim. Ecol.* 58: 383-401.
- Stearns, S.C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259-268.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Tatner, P. and Bryant, D.M. 1993. Interspecific variation in daily energy expenditure during avian incubation. *J. Zool.* 231:215-232.
- Tinbergen, J. 1987. Costs of reproduction in the great tit; interseasonal costs associated with brood size. *Ardea* 75: 111-122.
- Van Balen, J.H. 1984. The relationship between nest-box size, occupation and breeding parameters of the great tit *Parus major* and some other hole-nesting birds. *Ardea* 72:163-175.
- Van der Werf, E. 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. *Ecology* 73:1699-1705.
- Van Noordwijk, A.J., van Balen, J.H. and Scharloo, W. 1981. Genetic and environmental variation in clutch size of the great tit. *Neth. J. Zool.* 31:342-372.
- Weathers, W.W. and Sullivan, K.A. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monographs*. 59:223-246.
- Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Amer. Nat.* 100:687-690.

Chapter 2 Methods

Section 1. Methods for comparing alternative clutch size strategies.

An understanding of the constraints on avian clutch size may entail estimating how fitness can be changed by altering the number of eggs laid. Two main approaches have been used to tackle this: the first has been to compare the performance of birds which naturally lay different clutch sizes, and the second has been to adjust the number of offspring experimentally. By observing natural variance, it is possible to study birds under natural and relatively undisturbed conditions, free from any artefacts of experimentation, but confounded by differences in the quality of birds laying different clutch sizes. By experimentally adjusting the number of offspring, it is possible to control for these confounding variables. Both approaches are imperfect, but the use of natural variance in particular has been widely rejected in recent years, especially as a tool for studying the costs of reproduction in the evolution of clutch size (Partridge 1989, Roff 1992). I aim here to compare the two approaches, to consider the criticisms which have been raised of each, and to consider further criticisms raised by geneticists (Reznick 1985, 1992, Reznick et al. 1986).

High quality birds, or birds with abundant resources can lay and rear larger clutches more efficiently (Hogstedt 1980, Pettifor et al. 1988), and so natural variance has lost favour as a means of studying the role of reproductive costs in clutch size evolution. Because different clutch sizes may partly reflect difference in quality and resources, they often can not be used to understand the fitness implications of selecting alternative clutch size strategies. Coulson and Thomas (1985) have found that high quality birds lay larger clutches with higher hatching success, higher fledging success, and higher growth rates. These high quality birds also have higher adult survival. It would seem counter-intuitive that performance could increase as demands increase. Roff (1992) reviewed 8 studies which had studied the relationship between natural clutch size and adult survival; only 2 found that adult survival was negatively correlated with clutch size, while 6 found either no relationship or a positive correlation. With recent attention on individual optimisation of clutch size (Pettifor et al. 1988), and with

numerous indications that adult quality and clutch size are confounded, the use of natural variance clearly has problems.

There have also been some criticisms of experiments which manipulate the number of offspring. Adults may recognise and reject offspring which are not their own. Adults may prepare themselves physiologically and behaviourally for a certain number of offspring and may therefore be unable to cope with additional chicks. Manipulations may adjust only some of the demands, and in particular the manipulations of brood size which have been particularly popular (Dijkstra et al. 1989, Van der Werf 1992) may ignore the effects of egg formation and incubation (Partridge 1989, Monaghan et al. in press).

Another type of criticism has been raised against these phenotypic approaches to clutch size (Reznick 1985, 1992). Natural selection acts not on phenotypic but on genotypic variance. It is possible to mimic a mutation by manipulating the number of offspring the parents tend, but this affects the phenotype, not the genotype. Trade-offs and selection could be understood at the genetic level either by applying artificial selection, or by looking for genetic correlations. In wild birds however, this would entail formidable practical problems. Until these are overcome, the choice is whether to disregard the results of preceding experiments, or to accommodate them but acknowledge their imperfections. Perfection may not have been attained, but progress has still be made.

Coulson, J.C. and Thomas, C. 1985. Differences in the breeding performance of individual kittiwake gulls *Rissa tridactyla* (L.). in Sibly, R.M. and Smith, R.H. (eds). *Ecological Consequences of Adaptive Behaviour*. pp489-503. Blackwell Scientific, Oxford.

Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. and Zijlstra, M. 1990.

Brood size manipulations in the kestrel (*Falco tinnunculus*): effects

- on offspring and adult survival. *J. Anim. Ecol.* 59:269-285.
- Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territorial quality. *Science* 210:1148-1150.
- Monaghan, P., Bolton, M. and Houston, D.C. (in press). Egg production constraints and the evolution of avian clutch size. *Proc. Roy. Soc. Lond. B.*
- Partridge, L. 1989. Lifetime Reproductive Success and Life-history Evolution. in Newton, I. (ed). *Lifetime Reproduction in Birds*. Academic Press, London.
- Pettifor, R. A., Perrins, C.M. and McCleery, R.H. 1988. Individual optimization of clutch size in Great Tits. *Nature* 336:160-162.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44: 257-267.
- Reznick, D., Perry, E., and Travis, J. 1986. Measuring the cost of reproduction: a comment on papers by Bell. *Evolution* 40:1338-1344.
- Reznick, D. 1992. Measuring the costs of reproduction. *Trends in Ecology and Evolution* 7:42-45.
- Roff, D.A. 1992. *The evolution of life histories: theory and analysis*. New York, London.
- Van der Werf, E. 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. *Ecology* 73:1699-1705.

Section 2. The proximate measurement of fitness.

True fitness - the rate of increase of a gene within a population - is rarely measurable. In long term studies of birds, it may sometimes be possible to measure lifetime reproductive success, but even this still does not equate with fitness (Newton 1989). Most commonly, particularly in short-term studies of long-lived birds, it is necessary to use some shortcut measure presumed to correlate with fitness, and to measure current breeding performance or levels of physiological stress. Although these certainly do not equate with fitness, they may still offer answers to the questions in hand (Bryant 1988, Bryant and Tatner 1988). Here I aim to outline these techniques, and in particular to explain the techniques of doubly labelled water (measuring energy expenditure from the turn-over of isotopically labelled hydrogen and oxygen)(Tatner and Bryant 1989, Nagy 1989), and ptilochronology (measuring physiological stress from rates of feather regrowth)(Grubb 1989, 1991). Section 3 outlines a new technique for measuring current breeding success in terms of daily survival rates.

Current breeding performance, whether quantified in terms of the number of offspring reaching a particular stage or in terms of daily survival rates (Mayfield 1961, 1975, Johnson 1979, see also section 3), is a widely used measure but ignores both the survival of the offspring after the observation period, and any trade-off between current and future reproductive success. Both of these have important implications for lifetime reproductive success (Clutton-Brock 1988), and so the suitability of current breeding performance depends on the question being asked.

Offspring survival and trade-offs can themselves be measured proximately. Chick body condition provides some indication of quality and of post-fledging survival (Perrins 1965, Richner et al. 1989, Smith et al. 1989, Magrath 1991). Changes in adult body condition, parental energy expenditure (Bryant 1988, Bryant and Tatner 1988), and rates of feather regrowth (Grubb 1989, 1991, Grubb and Cimprich 1990, Waite 1990) have all been used to assess levels of parental stress. Taken in isolation, these measures can be misleading, but when combined together they may be informative (Bryant 1988).

Loss of body condition can either be induced by the environment outwith the control of the bird, or it can be a regulated response to changing lifestyle which is under the bird's control (Freed 1981, Drent and Daan 1980, Lima 1986, Croll et al. 1991). Flight economy, manoeuvrability and predator avoidance are enhanced by minimising body weight (Pennycuik 1989). If access to food is unpredictable, then insurance against starvation can be provided by depositing fat. After hatching, parental weight loss is commonly observed (Freed 1981, Croll et al. 1991), but it may reflect either increased stress or a change to a lifestyle where flight is used more abundantly. A poor picture of physiological stress may be produced if only body condition alone is studied.

Measuring energy expenditure might shed additional light on the patterns of demands experienced by reproducing birds. Again however, the results are open to multiple interpretations and energy expenditure may be a poor measure of demands if used on its own (Bryant 1988). Just as a person who spends a lot of money need not be financially stressed, a bird which spends a lot of energy may do so because food is abundant or because it is a competent forager. Stress may also arise when individuals are unable to raise their energy expenditure easily. Increased energy expenditure has rarely been found in response to enlarged broods (Williams 1987, Bryant 1988), but this does not necessarily show that the adoption of additional chicks is easy.

Under restricted conditions, the measurement of energy expenditure may be achieved by respirometry (Brown 1984, Gabrielsen et al. 1991), but for free-living birds the doubly-labelled water technique (Lifson and McClintock 1966, Nagy 1980, Tatner and Bryant 1989), time-energy budgets (Mugaas and King 1981, Masman et al. 1988, Gabrielsen and Mehlum 1988) or the analysis of food consumption (Wijnandts 1984) are the only available methods. For birds such as seabirds and aerial feeders which forage over wide areas, the only feasible method is often the doubly-labelled water technique (Bryant and Westerterp 1980, Gabrielsen et al. 1987, but see also Gabrielsen and Mehlum 1988). The method is difficult and expensive, and can generally be performed on only small samples of birds. These birds must be caught,

injected, released and recaptured for blood-sampling after a further 24 or 48 hours (Bryant and Tatner 1989). The blood samples then require processing in the laboratory. The technique has been found to interfere with the natural behaviour of some birds (Uttley et al. 1994).

The doubly labelled water technique makes the standard assumption that the energy expenditure of birds can be measured from the rate of production of carbon dioxide (Nagy 1980, Williams and Nagy 1984, Speakman and Racey 1988). Technically, the energy released per unit of CO₂ varies depending on the substrate being metabolised, but even when it is not possible to measure O₂ consumption and calculate the respiratory quotient ('RQ'), the problem can be overcome by assuming a constant RQ (Schmidt-Nielsen 1983, Butler and Bridges 1989).

There are two main routes by which oxygen atoms are lost from the avian body - as exhaled CO₂ and as water. Hydrogen is essentially lost only as water. Any individual oxygen atom is not bound rigidly into either carbon dioxide or water molecules but moves between them in the body pool. H₂O exists in equilibrium with H⁺ and OH⁻. Carbon dioxide then also exists as HCO₃⁻. When this recombines with H⁺, the resulting water and carbon dioxide molecules may have the oxygen atoms which originated from either.

By adding labelled atoms of hydrogen (²H) to a bird's body, establishing their initial abundance and their abundance after a set time, it is possible to calculate the rate of water loss. By adding labelled oxygen (¹⁸O) to the body and correcting for water loss, it is possible to calculate the rate of CO₂ production and the average energy expenditure over the period between samples. The abundance of labelled hydrogen and oxygen can be determined using isotope ratio mass spectrometry, after isolating water from blood using cryogenesis. It is also possible to use radioactive tritium (³H) instead of stable deuterium (²H), in which case abundance can be determined by scintillation counting. Nagy (1980) reports an accuracy of $\pm 10\%$ for measurements of energy expenditure using doubly labelled water. The finer details of the protocol used in

measuring energy expenditure with doubly labelled water are given in (Bryant and Tatner 1989, Nagy 1989).

In using the doubly labelled water technique to measure energy expenditure of kittiwakes, I followed this standard protocol. Selected adults were caught at the nest using a noose mounted on a long pole. Two and a half millilitres of doubly labelled water were injected into the peritoneal cavity. Birds were ringed and individually dye-marked with picric acid. The birds were then kept in a wooden box (roughly 80cm x 60cm x 50cm) for one hour to allow the injected isotopes to mix fully with the body water pool. Eight 100 microlitre glass capillary tubes of blood were then sampled from the femoral vein, and sealed with a flame torch. After 24, 48, or 72 hours, I attempted to recapture these birds and repeat the blood sampling procedure, though not all birds could be caught within the required period.

Blood samples were then processed and isotope levels measured in the laboratory following the standard methods of Tatner and Bryant (1989). I checked the accuracy of the measurements using prepared standards of deuterium and ¹⁸Oxygen. Close agreement between standards and measured values was obtained with the oxygen standards (5493 and 5552 ppm for the 5500 ppm standard, 4523 and 4544 ppm for the 4500 ppm standard, and 7209 and 7525 ppm for the 7500 standard) and so no correction to the measured values was applied. Measurements of deuterium abundance were corrected to allow for deviations of measured values from standards (841.9 and 849.2 ppm for the 1000 ppm standard).

As well as trying to estimate physiological stress from body condition and energy expenditure, it is possible to look at the resources a bird is prepared to channel into non-essential functions such as feather growth (Grubb 1989, 1991, Waite 1990). Although there are fewer alternative interpretations of these 'ptilochronological' results, there has been debate over whether the method itself is sound (Murphy and King 1991). Birds are caught at the start of the observation period, and a tail feather is plucked. In my study, Kittiwakes were then recaptured and the rates of feather regrowth

plucked. In my study, Kittiwakes were then recaptured and the rates of feather regrowth determined directly, but more conventionally, the birds are recaptured after regrowth is complete and rates are estimated from 'growth bars' on the feathers - as the feather grows, there are diurnal cycles of feather production which produce visible but faint bars. Nutritionally stressed birds may have fewer resources to channel into feather production and so have lower feather growth rates and narrower bars.

Murphy and King (1991) argue that ptilochronology involves untested assumptions. They point out that feather growth rates may be affected in complex ways which depend on the type and severity of the nutritional stress, and that changes in feather regrowth need not indicate changes in fitness. In the present study, feather regrowth rates were measured directly and so the further five criticisms raised regarding the interpretation of feather bars are not relevant here (Murphy and King 1991).

Brown, C.R. 1984. Resting metabolic rate and energetic cost of incubation in Macaroni Penguins *Eudyptes chrysopholus* and Rockhopper Penguins *E. chrysocome*. *Comp. Biochem. Physiol. A.* 77:345-350.

Bryant, D.M. 1988. Energy expenditure and body mass changes as measures of reproductive costs in birds. *Functional Ecology* 2:23-34.

Bryant, D.M. and Westerterp, K.R. 1980. The energy budget of the house martin *Delichon urbica*. *Ardea* 68:91-102.

Bryant, D.M. and Tatner, P. 1988. The costs of brood provisioning: effects of brood-size and food supply. *Proceeding of the 19th International Congress.* pp 364-379.

Physiology. Cambridge University Press, Cambridge.

Clutton-Brock, T.H. 1988. Reproductive Success. University of Chicago Press, Chicago.

Croll, D.A., Gaston, A.J., Noble, D.G. 1991. Adaptive loss of mass in Thick-billed Murres. *Condor* 93: 496-502.

Drent, R.H. and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225-252.

Freed, L.A. 1981. Loss of mass in breeding wrens: stress or adaptation? *Ecology* 62:1179-1186.

Gabrielsen, G.W., Mehlum, F., and Nagy, K. 1987. Daily energy expenditure and energy utilization of free-ranging Black-legged Kittiwakes. *Condor* 89:126-132.

Gabrielsen, G.W. and Mehlum, F. 1988. Kittiwake Activity Monitored by Telemetry. *Biotelemetry*.

Gabrielsen, G.W., Mehlum, F., Karlsen, H.E., Andresen, O., and Parker, H. 1991. Energy cost during incubation and thermoregulation in the female Common Eider *Somateria mollissima*. *Norsk Polarinstitutt Skrifter* 195:51-62.

Grubb, T.C. Jr. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. *The Auk* 106:314-320.

Grubb, T.C. Jr. 1991. A deficient diet narrows growth bars on induced

- feathers. *The Auk* 108:725-727.
- Grubb, T.C.Jr. and Cimprich, D.A. 1990. Supplementary food improves the nutritional condition of wintering woodland birds: evidence from ptilochronology. *Ornis. Scand.* 21:277-281.
- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *The Auk* 96:651-661.
- Lifson, N. and McClintock, R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *J.Theor.Biol.* 12:46-74.
- Lima, S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377-385.
- Magrath, R.D. 1991. Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. *J.Anim.Ecol.* 60:335-351.
- Masman, D., Daan, S., and Dijkstra, C. 1988. Time allocation in the kestrel (*Falco tinnunculus*), and the principle of energy minimization. *J.Anim.Ecol.* 57:411-432.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255-261
- Mayfield, H.F., 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456-466.

- Mugaas, J.N. and King, J.R. 1981. Annual variation of Daily Energy Expenditure in the Black-billed Magpie: A Study of Thermal and Behavioural Energetics. Studies in Avian Biology No.5. Cooper Ornithological Society.
- Murphy, M.E. and King, J.R. 1991. Ptilochronology: a critical evaluation of assumptions and utility. *The Auk* 108: 695-704.
- Nagy, K.A. 1980. CO₂ production in animals: analysis of potential error in the doubly labelled water method. *Am. J. Physiol.* 238: 466-473.
- Nagy, K.A. 1989. Doubly labelled water studies of vertebrate physiological ecology. pgs 270-287. in Rudel, P.W., Ehleringer, J.R., Nagy, K.A. (eds). *Stable Isotopes in Ecological Research*. Springer-Verlag, New York.
- Newton, I. (ed). 1989. *Lifetime reproduction in birds*. Academic Press, London.
- Pennycuik, C.J. 1989. *Bird flight performance. A practical calculation manual*. Oxford University Press, Oxford.
- Perrins, C.M. 1965. Population fluctuations and clutch size in the great tit, *Parus major* L. *J. Anim. Ecol.* 34:601-647.
- Richner, H., Schneider, P. and Stirnimann, H. 1989. Life-history consequences of growth rate depression: an experimental study on carrion crows (*Corvus corone corone* L.). *Functional Ecology* 3:617-624.
- Schmidt-Nielsen, K. 1983. *Animal Physiology: adaptation and environment*. Third Edition. Cambridge University Press, Cambridge.

- Smith, H.G., Kallander, H., and Nilsson, J.-A. 1989. The trade-off between offspring number and quality in the Great Tit *Parus major*. *J. Anim. Ecol.* 58:383-401.
- Speakman, J.R. and Racey, P.A. 1988. The doubly labelled water technique for measurement of energy expenditure in free-living animals. *Sci. Prog. Oxford* 72: 227-237.
- Tatner, P. and Bryant, D.M. 1989. The doubly labelled water technique for measuring energy expenditure. In Bridges, C.R. and Butler, P.J. (eds). *Techniques in Comparative Respiratory Physiology*. pp77-112. Cambridge University Press, Cambridge.
- Uttley, J., Tatner, P., and Monaghan, P. 1994. Measuring the daily energy expenditure of free-living Arctic Terns (*Sterna paradisaea*). *Auk* 111: 453-459.
- Van der Werf, E. 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. *Ecology* 73:1699-1705.
- Waite, T.A. 1990. Effects of caching supplemental food on induced feather regeneration in wintering gray jays *Perisoreus canadensis*: a ptilochronology study. *Ornis. Scand.* 21:122-128.
- Wijnandts, H. 1984. Ecological energetics of the long-eared owl (*Asio otus*). *Ardea* 72: 1-92.
- Williams, J.B. 1987. Field metabolism and food consumption of Savannah Sparrows during the breeding season. *Auk* 104:277-289.

Williams, J.B. and Nagy, K.A. 1984. Validation of the doubly labelled water technique for measuring energy metabolism in Savannah Sparrows. *Physiol. Zool.* 57:325-328.

Section 3. Statistical analyses and the GENSTAT package

Most of the analyses undertaken for this thesis were performed using the GENSTAT software (see manuals/textbooks: Genstat5 1987, Lane et al. 1987, Digby et al. 1989). Analyses were generally performed within the framework of generalised linear modelling (see McCullagh and Nelder 1983 for the definitive reference). Because many of these techniques are not widely used by field ecologists, I aim here to outline the advantages of the approach, to clarify terminology, and to explain how the analyses were undertaken.

The generalised linear modelling approach is an expansion of techniques such as multiple linear regression or logistic regression in which one dependent variable can be affected by a number of independent variables. Under the umbrella of generalised linear modelling, the rigid details of individually named techniques such as multiple linear regression are treated as the specific details of a wider family of assumptions. For example, firstly, in multiple linear regression it is assumed that variance around the model is independent of the values of the dependent variable, and secondly that the values for the dependent variable are distributed normally around the model. Separate transformations or link functions (for example fitting a multiple linear regression model to the log of the dependent variable) can be applied to the dependent variable if this brings residual distributions into line with assumptions. Thirdly, the independent variables in multiple linear regression would not conventionally be categorical. By contrast, generalised linear modelling can accommodate dependent variables with a

wider variety of residual distributions, link functions and variance functions which respectively transform the dependent variable and take into account variances which change according to the magnitude of the dependent variable can be specified intrinsically. Categorical independent variables can be incorporated into generalised linear models. Provided the residual distribution and the nature of the independent variables (continuous or categorical) are specified, (together with link functions and variance functions if necessary) models of the dependent variable can be constructed in a manner similar to multiple linear regression. This offers considerable versatility.

Many widely used disjunct statistical tests can be specified and performed as generalised linear models. Rather than changing tests when minor details of the analysis change, generalised linear modelling makes it possible to accommodate a wide range of tests within a single framework. For example, a simple t-test may sometimes suffice if one wishes only to know whether the value of a variable differs between two samples, but an ANOVA would be necessary if a third sample were involved, and an ANCOVA would be needed to remove the variance caused by another continuous variable if one suspected this was important. These three different tests could however be undertaken within the single analytical framework of generalised linear modelling. Similarly, associations between characteristics of two variables could be analysed with a chi-square test, but a G-test would have to be used if associations between three variables were involved. There is no single test which specifically incorporates four such variables, but associations between any number of variables can be studied by specifying the analysis as a generalised linear model. The flexibility of GENSTAT not only offers the freedom to analyse a wide range of problems, it avoids the need for a vast cumbersome collection of tools for narrow statistical tasks.

The capacity of generalised linear modelling to incorporate several independent variables offers substantial advantages in the analysis of data collected from wild birds. Firstly, confounding variables can be controlled. Thus, two independent variables which appear to affect the dependent variable on their own, may themselves be correlated with each other, and the apparent effect of one may arise spuriously from its

correlation with the other. Secondly, even where independent variables are not correlated with each other, incorporating independent variables with significant effects before testing the significance of the focal variable can serve to reduce the residual variance and thus enhance the power of the test. In this thesis, as a general rule, I have tested the effect of each variable after controlling for the significant effects of others. In GENSTAT, the dependent variable is specified with the command 'MODEL' followed by the name of the dependent variable (the residual distribution, link function, and weighting of observations can be specified at this point). To prepare for the ensuing analysis and to enable calculation of correlations between the independent variables, the command 'TERMS' is then used followed by a list of independent variables. A model can then be fitted with the command 'FIT' followed by a list of independent variables. Independent variables can then be added to or dropped from the model using the commands 'ADD' and 'DROP' respectively, followed by the names of the required independent variables. Testing the significance of variable 'a' where one suspects it is confounded by variable 'b' can be achieved either by 'FIT b' followed by 'ADD a', or else by 'FIT a,b' followed by 'DROP a'.

Three main types of generalised linear model have been used in this thesis. Firstly, where the dependent variable is distributed binomially around the model, I have used the term 'binomial model', or I have said that the dependent variable has been 'modelled assuming binomial errors'. Were none of the independent variables categorical, and were logistic link functions used, the term 'logistic regression' could be used, but since I have used binomial models where these conditions are not necessarily met, I have not generally used the term 'logistic regression'. I have used binomial models particularly widely to analyse the effects of various independent variables on breeding success. I have done this by calculating daily survival rates of eggs and chicks for each nest (full details of this are given in Chapter 2 section 4). GENSTAT provides a 't' statistic (or a 'z' statistics where the residual degrees of freedom exceed 60) for each independent variable and I have quoted this when giving the significance of the test.

Secondly, I have used 'log-linear models' where frequencies of observations are concerned. For example if I wish to examine whether nests with rock ledges are less likely to be destroyed than those without ledges, then I would look at the frequencies of nests which are/ are not destroyed in relation to the frequency of nest sites which do/ do not have adjacent rock ledges. Log-linear models are an expansion of chi-square tests, and allow several independent variables to be built into the analysis. Unlike either multiple linear regression or the binomial models outlined, the dependent variable in a log-linear model is 'frequency' rather than the measured value of a focal dependent variable, and these frequencies are assumed to follow a Poisson (or 'random') distribution. Further, it is not the significance of the independent variables which is usually of interest, but rather the interactions of the independent variables with each other. Thus it would be of little interest or surprise if 'frequency' were significantly influenced by whether or not a nest were destroyed - this simply indicates that the numbers of nests with or without rock ledges are not equal. If 'frequency' is significantly influenced by an interaction between presence/absence of ledges and whether or not the nest is lost, then this indicates that the presence or absence of ledges influences the chances of a nest being lost. Unlike a simple chi-square test, the log-linear modelling makes it possible to add in other nest site characteristics and to determine whether the apparent association of say rock ledges and nest losses is in fact just due to an association of ledges with another characteristic which itself is associated with losses. In such analyses, I have used the term 'associated' where two characters are found together more often than would be expected by chance, and 'dissociated' where they are found together less often than would be expected by chance. In presenting the results of a log-linear model, I have given the 'mean deviance' of the interaction term, which is equivalent to either the 'residual mean deviance' after adding the dependent variables, or the ' δ mean deviance' when the interaction term is added or dropped from the model. These mean deviances follow a chi-square distribution and can be tested as such if the 'dispersion parameter' is known. This dispersion parameter specifies the relationship between the mean and the variance of the dependent variable.

By default, if the values for the dependent variable follow a truly Poisson distribution, then the variance equals the mean, and the dispersion parameter (the ratio of these two) equals one. Thus in a 2 x 2 contingency table with Poisson distributed frequencies, the expected residual mean deviance is one if there is no association between the characteristics - a residual mean deviance much greater than one indicates that there is an association.

Thirdly, I have used generalised linear models where the dependent variable is distributed normally around the model. Where all the independent variables are non-categorical, I have simply called this 'multiple linear regression'. However, I know of no similar simple term to describe such generalised linear models in which some of the independent variables are categorical. They could be considered a form of multiple linear regression with multiple groups, or of ANCOVA (analysis of covariance) though the categories may contain markedly unequal numbers of observations (i.e. the design may be 'unbalanced') and the continuous variable (or 'covariate') rather than the categorical variables (or 'treatments') may be the focus of attention. When presenting results of these multiple linear regression type models, I have provided the 'F' statistic associated with the change in explained variance when the focal independent variable is added to or dropped from the model, and following convention I have given the degrees of freedom as subscripts to the 'F'.

I have also made limited use of a fourth type of generalised linear model in which the dependent variable is assumed to follow a Poisson distribution around the model. In this particular analysis, all the independent variables were continuous and so I have used the term 'Poisson regression'. Although like log-linear models this 'Poisson regression' assumes that the data are distributed randomly around the model, the dependent variable in a Poisson regression is a measure of a biological dependent variable rather than a 'frequency' of a particular characteristic. Apart from Poisson-distributed errors, Poisson regression is otherwise very similar to multiple linear regression or logistic regression. In presenting results, I have provided the change in

the mean deviance when the focal independent variable is added to or dropped from the model, together with the dispersion parameter.

The technique of ordinal logistic regression, used widely in this thesis, could also be considered a form of generalised linear model though it is contained as a separate procedure accessible from the GENSTAT procedure library, and has not been specified using the 'MODEL' statement. Full details of ordinal logistic regression are given in chapter 2 section 5.

Digby, P., Galwey, N., and Lane, P. 1989. Genstat5. A Second Course. Oxford University Press.

GENSTAT5. 1987. Genstat 5 Reference Manual. Oxford Science Publications, Clarendon Press, Oxford.

Lane, P., Galwey, N. and Alvey, N. 1987. Genstat 5. An Introduction. Oxford University Press.

McCullagh, P. and Nelder, J. A. 1983. Generalized linear models. Chapman and Hall, London.

Chapter 2 (Methods), section 4.

Calculating nesting success: some refinements on the Mayfield method

David L. Thomson, Pat Monaghan, and Robert W. Furness.

Applied Ornithology Unit, Zoology Department, Glasgow University G12 8QQ.

Calculating Nesting Success.

Abstract

In calculating breeding success, the Mayfield method incurs errors firstly by pooling unweighted observations from nests differing in vulnerability, and secondly by assuming that the losses occur exactly half way between visits to the nest. We highlight and explore these problems using simple models, and we show that the magnitude of the biases can yield misleading conclusions under practically and biologically realistic circumstances. We introduce an alternative to the Mayfield method in which daily survival rates of nests can be calculated directly and modelled, assuming binomial errors and with a logit link function, in a manner akin to logistic regression with multiple groups. We show that this removes the biases, equalises the weightings and removes the distortions when testing hypotheses. By calculating daily survival rates in different ways to produce a series of 'breeding survival variables', we outline a means of distinguishing breeding losses with differing causes so that these can be analysed separately.

In an analysis of data collected from colonial Kittiwakes, the power and versatility of our 'direct' technique are highlighted by comparing results with those from more conventional analytical approaches wherever these are possible. With the direct technique, seasonal trends in breeding success could be detected. It was further possible to show differences in these trends between years, and to demonstrate that they applied only to certain causes of breeding failure. In analysing the effects of clutch supplements on daily breeding survival variables, it was possible to control for these significant seasonal effects, and to detect effects of the experimental treatment. In a comparable analysis, the Mayfield method pointed to similar biological conclusions regarding clutch manipulations, but the details and the magnitude of the effects were different. A simple analysis of apparent hatching success had lower power than an analysis

involving survival rates. With this more straightforward technique, we failed entirely to detect any effects of clutch manipulations and incurred at least one type II error. We propose that our direct method of calculating nesting survival rates, including the separation of losses according to their cause, offers power, versatility, accuracy, and wide applicability and thus will generally offer appreciable improvements on the more conventional techniques.

Introduction

Biases inherent in simple measures of breeding success led Mayfield (1961, 1975) to develop a refined technique based on abstracted measures of exposure and daily survival rates. Nests have a lower chance of failing during a short monitoring period even if they have the same actual breeding success as those followed for longer. By estimating breeding success using daily survival rates, the Mayfield method aims to avoid this error. Certain difficulties have however been identified in this valuable and widely used method, and although improvements have been made (Green 1977, Miller and Johnson 1978, Johnson 1979), some problems do still remain. Firstly, the Mayfield method makes the inaccurate assumption that losses occur exactly half way between the two visits which flank the loss itself. Secondly, inappropriate weightings are applied when observations from nests differing in vulnerability are pooled to produce estimates of survival. The first problem could be avoided if there were a means of calculating survival directly. In testing hypotheses, the second problem could be removed if there were a method which did not necessitate this pooling of observations.

Here we aim to develop models to explore the magnitude of the errors in the Mayfield method resulting from these problems. We look at how these biases change with survival rate and with the duration of intervals between visits. We show how the central variable of daily survival can instead be calculated directly, how data for each nest need not be pooled, how survival rates for each nest can be modelled assuming binomial errors in a manner akin to logistic regression with multiple groups, and thus how some of the problems and biases can be removed. Rather than having a single measure of daily nest survival which encompasses all types of loss, we show how a series of 'breeding survival variables' which recognise losses differing in cause can be produced and analysed separately. The advantages of our direct technique go beyond a solution of the problems which prompted development of the Mayfield method. We explore these

advantages using data collected from colonial Kittiwakes *Rissa tridactyla*, and where possible we compare the results obtained with those from more conventional techniques.

Methods

The Mayfield method and the assumption about the timing of losses.

In estimating breeding success with daily survival rates, the Mayfield method assumes that nests which failed did so on average half way between the last visit when they were seen to be active and the first visit they were observed to have been lost. Because all survival rates between 0% and 100% will produce patterns akin to exponential decay, losses are more numerous near the start of any period and so the average timing of losses is in fact, on average, some time before the half-way point. The assumption would be valid if there were a linear decline in the number of active nests, but this can not occur when survival rate is constant; only when it is decreasing.

This problem is widely acknowledged, and Miller and Johnson (1978) sought to cope with it by assuming that losses occur, on average, at 40% of the time between visits. Although Johnson(1979) demonstrates that with this improvement the method will often perform well, the modification does serve to *reduce* rather than *remove* the bias. Indeed, where nesting success is high and losses occur on average later than 40% of the time, this adjustment of assumptions could potentially introduce the opposite bias.

The Mayfield method estimates daily survival from the formula:

$$S=1-([Np-Ns]/E)$$

where S :- daily survival rate

Np :- the number of observation periods

Ns :- the number of observation periods where the nest is successful

E :- the sum of the exposure periods (in days)

For each observation period where the nest is not successful, the loss is assumed to occur at the mid-point and so exposure is assumed to equal half the duration. Using these equations and assumptions, we have developed simple theoretical models to quantify the error and to determine how it changes both with the duration between visits and with the severity of the mortality rates.

Biases from pooling unweighted observations.

Further errors can appear in the Mayfield method when observations from several nests differing in vulnerability are pooled into a single estimate of breeding success (Green 1977). Through time, nests with low survival rate disappear more rapidly thus leaving a population in which a greater proportion of nests have a high survival rate. If nests are visited repeatedly, observations from nests with higher survival enter the calculations with greater frequency and distort the overall estimate. In this paper, some analytical problems associated with this phenomenon are examined using simple theoretical models. Klett and Johnson(1982) explain clearly some other implications of variability in nest survival rates and show how the Mayfield and other methods can be adapted to cope with this.

Calculating survival rate directly.

We have devised a more direct technique for calculating nesting success which solves not only the problems which originally prompted the method, but also these two biases which remain. Within each data set, there will exist a series of observations for any nest, from the time breeding has commenced to the time it is expected to be complete. These can be used to determine a series of observation intervals, between the first and the second visits, the second and the third, the third and the fourth, etc. Corresponding to each of these intervals will be 3 pieces of information:

d - whether the nest is active at the start of the interval,

n - whether it is active at the end,

p - the duration of the interval.

For 'd' and 'n', active nests are coded as 1, while nests which have been lost are coded as 0. For each nest, the data set for these 3 variables can be subdivided into groups depending on the duration of the interval. For $i=1 \dots t$ of these groups with particular durations, there are 3 pieces of information:

P_i = the duration of the interval

$D_i = \sum d$, or the sum of the denominators for all cases where $p = P_i$,

$N_i = \sum n$, or the sum of the numerators for all cases where $p = P_i$.

Note that for all intervals after a nest has been lost, d and n will always equal zero and will not contribute to D_i or N_i . Calculations will thus always include only information up until the fate of the nest is determined.

Regarding any one nest, for each set of observations with any particular duration between visits, we can calculate an 's'-value directly as:

$$s_i = \left(\frac{N_i}{D_i} \right)^{\left(\frac{1}{P_i} \right)}$$

If for any group of intervals, D_i equals 0, this means that no observations are represented in this group. 's'-values obviously can not be calculated in the absence of data, so groups of intervals where D_i equals 0 should be excluded. This procedure does not exclude cases where *survival rate* is low, but rather cases where the *abundance of data* is low. This procedure does not bias the estimates and is useful as a means of removing missing values.

Using the individual estimates for each of the intervals represented, an S-value for each nest can be determined from the equation:

$$S = \left(\frac{\sum (S_i \times D_i)}{\sum D_i} \right)$$

These S-values will take values between 0 and 1, and can be modelled assuming binomial errors. The average survival rate of the nests (S_{av}) is simply the arithmetic mean of the S-values for the nests, while the survival rate estimate for the population as a unit (S_{all}) is the S-value obtained by applying the calculations to a pooled set of observations rather than performing the calculations separately for each nest. S_{av} and S_{all} are calculated differently and so will not normally be equal.

Distinguishing different causes of losses using the direct technique.

There are several ways in which effects on breeding success can be mediated. Often it will be desirable to separate losses due to say physical damage, predation, desertion, or chick starvation, or to express specifically the survival rates of individual chicks or eggs. This is easily done if we use direct measures of daily survival rates, but not if simple measures such as hatching or fledging success are used. To separate out the effects, the same framework is readily applied but one must redefine d and n as follows:

Predation

d - whether the nest is active at the start of the interval, *and* is either still active at the end or has specifically been destroyed by a *predator* at the end. e.g. a nest which is active at the start but has been damaged by weather at the end is classed as '0'.

n - whether the nest is active at the end. (The causes of the losses need not be determined when calculating this parameter, because they have already been incorporated into calculations of ' d ').

Partial losses e.g. brood reduction

d - whether the nest contains the full brood at the start of the interval, *and* either still has the full brood at the end or has lost some but *not all* of the chicks by the end. e.g. a nest which has the full brood at the start but has been lost completely by the end is classed as '0'.

n - whether the nest still has the full brood at the end. (Again neither the cause of the losses, nor whether the losses are partial or complete, need be determined when calculating this parameter, because they have already been incorporated into calculations of 'd').

Egg or chick survival rates

d - the number of offspring in the nest at the start of the interval

n - the number of offspring in the nest at the end of the interval,

Calculations of egg or chick survival rates must be calculated on a nest-by-nest basis, because offspring within a nest will not be statistically independent. It is possible to partition egg or chick survival in relation to various factors using the same approach as was used before.

All these techniques can be applied separately to incubation and chick-rearing phases by including in the definition of 'd' and 'n' the condition that the interval must start and end during these separate phases. Intervals which span hatching do not apply exclusively to either period, so can not be included in such calculations.

Background of examples using data collected on Kittiwakes.

In order to examine seasonal patterns of breeding success, and to address questions of incubation costs and clutch size determination (Williams 1991, Godfray *et al.* 1991, Stearns

1992), nests were followed every 2-4 days through the incubation period and clutch sizes were manipulated. In 1992, 32 nests with natural clutch sizes of 2 eggs were supplemented to 3 eggs using donor nests with comparable laying dates. A further 80 nests with 2 eggs were retained as controls. As well as these 112 nests used in the clutch size experiments, a further 167 were followed in 1992, and in 1993 a total of 350 were followed.

Analysis

Using the S-values, the effects on breeding success of laying date and clutch supplements were analysed with the Generalised Linear Modelling facilities of GENSTAT5 (Details of generalised linear modelling theory are given in McCullagh and Nelder 1983, and the execution of these analyses using GENSTAT5 is illustrated and explained in GENSTAT5 1987). By specifying the error distribution and employing an appropriate transformation or 'link function', it is possible to construct models akin to multiple linear regression with multiple groups, even though the errors are not distributed normally. Binomially distributed errors were assumed, the conventional logit link function was used, and the S-values were weighted equally - each being drawn from $n=1$ trials. With these S-values of individual nests as the dependent variable, it was possible to include both 'laying date' and 'experimental treatment' as independent variables, and thus to control first for the effects of each when testing the importance of the other. The technique is thus similar to logistic regression but has greater freedom and can accommodate categorical independent variables.

Using the direct technique, survival rate could be partitioned according to different biologically meaningful causes. Numerous Herring gulls nested sympatrically, and Kittiwakes experienced heavy losses of nests and eggs. Many nests were also physically damaged due to weather, and non-breeders were seen fighting vigorously over sites particularly when these were left unattended. Four measures of survival rate were calculated for the incubation stage. 'Clutch'

survival considered the breeding attempt as being alive until all the eggs or chicks were lost from the nest but the nest itself remained intact. 'Intact clutch' survival recognised death as happening when at least one egg was lost from the nest. 'Egg' survival treated each egg in the nest as an *individual*, but not a statistically *independent* entity; each nest yielded only a single independent observation. 'Nest' survival acknowledged mortality as happening when an active nest was physically destroyed. Where active nests were physically lost, the first 3 survival measures considered the period up to the time immediately before, but not including, this loss.

In order to explore the benefits of using the direct technique instead of more conventional approaches, the conclusions reached regarding clutch size manipulations obtained in 1992 using breeding survival rates were compared with those obtained by application of the Mayfield method *per se* and with those from simple Mann-Whitney U tests on hatching success and hatching brood sizes.

In order to ensure that only completed clutches were used in the experiments, manipulations of clutch size were performed a few days after the onset of incubation. Because of this, the hatching successes observed do not correspond exactly with the theoretical projections of survival rates over the full 27-day incubation period.

Results

1. Models exploring biases

Does the duration between visits affect errors in the Mayfield method?

If 2000 nests, with a convenient survival rate of exactly 50% per day, were found and then revisited every day for 4 days, then 125 will remain on the last visit. There will have been

1000+500+250+125=1875 complete daily observation periods for successful nests, and also the same number for unsuccessful nests. The sum of the exposure periods will be $(1875 \times 1 \text{ day}) + (1875 \times 0.5 \text{ day}) = 2812.5 \text{ days}$ in total. The number of successes will have been 1000+500+250+125 = 1875. The Mayfield estimate of survival is then:

$$S = 1 - ([3750 - 1875] / 2812.5) = 33.3\%$$

but our direct estimate of survival is:

$$S = (1875 / 3750)^{(1/1)} = 50\%.$$

If however the nests were only revisited on the last day, the number of successes is 125. There will have been 125 observation periods of successful nests, and 1875 of unsuccessful ones, giving a summed exposure period of $(125 \times 4 \text{ days}) + (1875 \times [4 \text{ days} / 2]) = 4250 \text{ days}$. The true exposure period can not have changed, but that estimated by the Mayfield method is more than 50% greater. As a consequence, the new estimate of daily survival is markedly greater:

$$S = 1 - ([2000 - 125] / 4250) = 55.9\%$$

By contrast, our direct estimate of survival is:

$$S = (125 / 2000)^{(1/4)} = 50\%$$

A comparable analysis of 51200 nests visited only after 8 days yields 200 successes, and a total period of 409600 days. The Mayfield estimate of survival is:

$$S=1-([51200-200]/([200 \times 8]+[51000 \times 4]))=75.2\%$$

and the direct estimate of survival is:

$$S=(200/51200)^{(1/8)}=50\%.$$

As the duration between the visits increases, the Mayfield estimate increases, but the direct calculations continue to yield the correct answer.

Although the simple and convenient values used in the preceding examples serve to illustrate the problem, they are not biologically realistic. The results of a simulation using the biologically more reasonable daily survival estimate of 95%, are given in Figure 1. It is clear that even with parameters which are biologically reasonable and logistically practical, the errors can be statistically important and the conclusions biologically misleading.

Does the bias change with the intensity of nest mortality?

Assuming a group of 20000 nests with 99% daily survival, a visit after 8 days will find 18455 remaining. The total number of intervals is 20000, and the sum of the periods is $(18455 \times 8 \text{ days}) + (1545 \times 4 \text{ days}) = 153820 \text{ days}$. The Mayfield estimate of survival is:

$$S=1-([20000-18455]/153820)=98.996\%$$

The direct estimate of survival is:

$$S=(18455/20000)^{(1/8)}=99.000\%$$

so the Mayfield method underestimates the daily survival rate by only 0.004% which means that daily mortality is overestimated by 0.4% of what it actually is. The biases are small, and the technique performs well.

If there is 95% daily survival, 13268 nests remain after 8 days. Mayfield survival is:

$$S=1-([20000-13268]/[(13268 \times 8)+(6732 \times 4)])=94.94\%$$

and direct survival is:

$$S=(13268/20000)^{(1/8)}=95.00\%$$

This means that the daily survival is underestimated by 0.063% and daily mortality is overestimated by 1.18% of its actual value, and again the technique performs well.

With 80% daily survival, 3355 nests remain after 8 days. Mayfield survival is:

$$S=1-([20000-3355]/[(3355 \times 8)+(16645 \times 4)])=82.03\%$$

and direct survival is:

$$S=(3355/20000)^{(1/8)}=80.0\%.$$

and so although the daily survival is only overestimated by 2.54%, daily mortality is underestimated by 10.15% of its actual value, and this error is potentially important.

The error does not remain constant but changes as the daily mortality increases. Figure 2 shows a plot of Mayfield survival against actual survival and the %error in Mayfield mortality rates, for a large theoretical set of nests visited after 3,8,12 and 20 days. Under these conditions,

there is convergence of the Mayfield estimate with true survival as these values approach 100%. However, the convergence is not perfect in the range of biologically realistic parameters, and Figure 2b highlights that the errors can be important and misleading.

The errors of the Mayfield method may not always be large for all practical and biologically reasonable situations, but the errors depend on the daily survival rate and the duration between visits. This type of error is uncomfortable and makes it difficult to compare results between studies. Since determining daily survival rate directly removes completely these particular biases while adding little to the complexity of the calculations, it would seem generally worthwhile to use this approach in place of the Mayfield method.

Pooling observations and the problem of weighting.

To explore the role of weightings in pooled estimates, we studied hypothetical survival rates for a population of 20000 nests made up of 2 sub-populations of 10000 nests with daily survival rates of 50% and 80%. After 4 days, the number remaining is

$$N=(10000 \times (0.5)^4) + (10000 \times (0.8)^4) = 4721$$

so the survival rate of the population as a whole over this 4 day period is

$$S_{all} = (4721/20000)^{(1/4)} = 69.70\%$$

This figure is more heavily weighted to 80% than to 50%.

The survival rate of this population was found to increase through time and this has complex implications for the weighting. After 1 day, $(10000 \times 0.8) + (10000 \times 0.5) = 8000 + 5000 = 13000$ nests remain, so the population survival rate over the first day is:

$$S_1=13000/20000=65\%.$$

After 2 days, $(8000 \times 0.8) + (5000 \times 0.5) = 6400 + 2500 = 8900$ nests remain, so the population survival rate from the first to the second day is:

$$S_2=8900/13000=68.46\%$$

and after 3 days, $(6400 \times 0.8) + (2500 \times 0.5) = 5120 + 1250 = 6370$ nests remain, and thus the population survival rate from the second to the third day is:

$$S_3=6370/8900=71.57\%,$$

By similar arguments, $S_4=74.11\%$.

The survival rate can show temporal changes which stem purely from mathematical rather than biological or environmental phenomena. Any method which pools observations from a population in which survival rates are heterogeneous will clearly produce results which vary depending on the duration of the study and the frequency of visits.

In testing hypotheses, it would clearly be desirable to avoid these problems and to forego any pooling of observations. It is possible, with the direct technique, to incorporate the S-values of each nest into the calculations as individual observations. This would result in an analysis where each nest was weighted equally, and would avoid the problem of pooling.

2. Examples using the direct technique

The effects of laying date on Kittiwake breeding success during incubation.

Using the direct technique it was possible to establish that some of the breeding survival measures showed linear declines with laying date in 1993, and to detect additional quadratic components to these relationships in 1992 (Table 1.). By distinguishing different types of losses with the direct technique, we could find no evidence that nest survival varied with laying date. It was thus possible to show that physical nest-damage is rather more stochastic than the other 3 measures which focus on losses of eggs and clutches.

Clutch manipulations and breeding success.

Using the direct technique, we could find effects of clutch size manipulations on some measures of breeding success (Table 2). Where laying dates had significant effects, these were controlled by including them as independent variables in the binomial models. There was no evidence that the survival of either intact clutches or of eggs was influenced by the addition of extra eggs, though the result was marginal for egg survival. Nest survival rate and full clutch survival rate were significantly influenced by manipulation treatment. Projecting the population estimates of S_{all} over the full 27 day incubation period, indicates that the controls will retain 0.879 eggs or chicks, while the experimental group will have 0.996. These figures could be expressed as 43.9% and 33.2% success respectively. The birds with increased clutch sizes had lower percentage success rates, but these higher percentage loss rates were not sufficient to outweigh the larger initial clutches.

Clutch manipulations and the Mayfield survival rates.

By pooling observations within each clutch-manipulation group, it was possible to apply an analogous analysis to these data using the Mayfield method *per se*. The results are given in Table 3. Because the population survival estimates derived from the direct technique and the Mayfield method involve different assumptions, projection of the figures over 27 days gives different results. Projected clutch or brood sizes at 27 days for controls and experimentals are

0.299 and 0.503 respectively. These represent percent-successes of 14.9% and 16.8% respectively. The Mayfield method points to some similar, but by no means identical, biological conclusions. The nature of the losses detected are different (intact clutch survival c.f. clutch and nest survival), and the magnitudes of the differences are not identical. The conclusion would still be drawn that adding eggs depresses breeding survival parameters without reducing the number of eggs reaching hatching. The survival parameters themselves are however different, and though the egg and clutch survival rates are not significantly different, the sample means of the control groups lie above those of the experimentals, and this is at odds with the direct estimates. The patterns of hatching success predicted by the Mayfield method differ markedly from both the predictions of the direct technique and the observed patterns of hatching success (Table 4).

A simple analysis of hatching success.

Because Kittiwake nests can readily be located and monitored, the conventional biases of using simple measures of hatching and fledging success do not apply (Mayfield 1961, 1975). There might then seem no good reason in this case to indulge in the more complex Mayfield method, or to calculate daily survival directly. However, the statistical power of applying a Mann-Whitney U test is low and no significant differences in either hatching success or brood size at hatching can be detected (Table 4). Since the groups started with different clutch sizes, at least one of these parameters must change: the use of a simple non-parametric test on hatching success incurs at least one type II error, and fails to detect the biologically important effects which can be found using the more powerful technique of daily survival rates. Analysing daily survival parameters allows us to separate the different types of loss, and to incorporate more information into the analysis. We know not only whether eggs hatch or fail, but also their survival and we have information on the nature of the failure if it occurs. By using daily survival rates we can incorporate all this information and so increase the power and discrimination of the analysis.

Discussion.

Although the Mayfield method often performs well, and although the Mayfield estimates converge with true survival as both approach 100%, there do exist several feasible combinations of parameters with practical and biological applicability, where misleading biases can occur if the Mayfield method is used. Not only can this distort the results of any particular study, it makes it impossible to use the method in comparisons between studies unless methodology is completely standardised. Even when there is such standardisation, it can be difficult to quantify accurately the differences in daily survival rate between studies because the errors depend on the survival rate itself. There may exist particular situations where the biases are negligible, but since the direct technique does provide a means of removing the problems, it is a preferable technique to use.

Where tests are performed on estimates obtained by pooling observations, distorting results can arise because nests with higher survival rate become more heavily weighted. With the direct technique it is possible to test hypotheses using single equally weighted values for each nest, and thus to avoid the problems associated with pooling.

As is clear from the examples, by calculating daily survival rates directly, by partitioning these according to the nature of the losses, and by using multivariate modelling of the resultant values for each nest, it is possible to reveal biological phenomena with precision where other methods, if available, might involve substantial biases or fail to detect them at all. We were able not only to detect changes in breeding success with laying date, but to gain information on the cause of these patterns, and to demonstrate differences between years.

With the direct technique, it was possible to demonstrate that some measures of breeding success were reduced when clutch size was enlarged. The Mayfield estimates led to broadly similar conclusions, but the details of the losses differed, and the quantitative predictions were

notably different. Simple analyses of hatching success and hatching brood size *per se* gave misleading results. A Mann-Whitney U test on these variables failed to detect the effects of the manipulation and committed a type II error. Misinterpretation of these analyses could potentially lead one to draw conclusions completely opposite to those obtained from the more powerful techniques. The Mayfield method was developed to overcome *biases* in simple calculations of fledging or hatching success, but even when the data overcome these biases, simple measures can inadvertently dispose of information and depress statistical power. When one knows not only the final outcome of a nest, but also its prior performance, then a technique which can make full use of this information is worth using.

Acknowledgements

During the development of this technique, DLT was supported by a postgraduate scholarship from the Carnegie Trust for the Universities of Scotland. Fieldwork undertaken to collect the Kittiwake data used in the examples would have been very much more difficult without the help and support of Rob Barrett (Tromsø Museum) and Geir Gabrielsen (NINA). Dr. James Currall (Statistician, Glasgow University Computing Service) and Dr. Stuart Daldry (Statistician, Aberdeen University) kindly read an earlier draft of this paper and provided comments on the statistical theory.

References

- GENSTAT5. 1987. Genstat 5 Reference Manual. Oxford Science Publications, Clarendon Press, Oxford.
- GLIM. 1993. The GLIM system. Numerical Algorithms Group, Oxford.
- GODFRAY, H.C.J., L. PARTRIDGE, AND P.H. HARVEY. 1991. Clutch size. *Ann. Rev. Ecol. Syst.* 22:409-429.
- GREEN, R. F. 1977. Do more birds produce fewer young? A comment on Mayfield's measure of nest success. *Wilson Bulletin* 89(1):173-175.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *The Auk* 96(4):651-661.
- KLETT, A. T. AND D. H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. *The Auk* 99: 77-87.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73(3):255-261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nesting success. *Wilson Bull.* 87(4):456-466.
- McCULLAGH, P. AND NELDER, J. A. 1983. *Generalized linear models*. Chapman and Hall, London.

MILLER, H. W. AND D. H. JOHNSON. 1978. Interpreting the results of nesting studies.

J. Wildl. Mgmt. 421-471-476

STEARNS, S. C. 1992. The Evolution of Life Histories. Oxford Series in Ecology and Evolution.

Oxford University Press, Oxford.

WILLIAMS, J.B. 1991. On the importance of energy considerations to small birds with

gynelateral intermittent incubation. Acta XX Congerssus Internationalis

Ornithologicii: 1964-1975.

Table 1. Results of analysing breeding survival parameters in relation to laying date. In 1993, there was evidence that laying date had quadratic as well as linear components, in the effects on the survival measures, so models combined these effects.

Year	Survival measure	Statistics
1992	Nest survival	linear: $z=1.05$, $df=85$, ns. quadratic: $z=1.03$, $df=85$, ns.
1992	Intact clutch survival	linear: $z=2.00$, $df=81$, $P<0.05$. quadratic: $z=1.89$, $df=81$, $P<0.1$.
1992	Clutch survival	linear: $z=2.12$, $df=83$, $P<0.05$. quadratic: $z=2.09$, $df=83$, $P<0.05$.
1992	Egg survival	linear: $z=2.04$, $df=83$, $P<0.05$. quadratic: $z=2.00$, $df=83$, $P<0.05$.
1993	Nest survival	linear: $z=0.13$, $df=198$, ns
1993	Intact clutch survival	linear: $z=2.50$, $df=174$, $P<0.05$
1993	Clutch survival	linear: $z=2.73$, $df=176$, $P<0.01$
1993	Egg survival	linear: $z=2.59$, $df=176$, $P<0.01$

Table 2. Daily survival rate group means, and significance of treatment effects. Group means are determined using pooled data from all the nests in each experimental treatment. The binomial analysis was performed on the individual estimates of the S-values for each nest, and the significant quadratic laying date effects were controlled in the model.

Survival measure	Control (2 eggs)	Experiment (2+1eggs)	Significance
Intact Clutch Survival	0.967	0.944	$z=1.51$, $df=108$, ns.
Clutch Survival	0.973	0.967	$z=1.97$, $df=108$, $P<0.05$.*
Egg Survival	0.970	0.960	$z=1.83$, $df=108$, $P<0.1$, ns.
Nest Survival	0.991	0.988	$z=2.41$, $df=108$, $P<0.05$.*

Table 3. Mayfield estimates of survival parameters for control and experimental categories. Significance was tested by two-sample tests, and did not control for laying date.

Survival measure	Control (2 eggs)	Experiment (2+1 eggs)	Significance
Intact Clutch Survival	0.958	0.942	$z=2.08$, $df=110$, $P<0.05$.*
Clutch survival	0.962	0.968	$z=0.967$, $df=110$, ns.
Egg survival	0.932	0.936	$z=0.435$, $df=110$, ns.
Nest survival	0.988	0.988	$z=0.00$, $df=110$, ns.

Table 4. Observed brood sizes at hatching and hatching success, for control and experimental nests, and results of comparing these by Mann-Whitney U test.

	Control (2 eggs).	Experimental (2+1 eggs).	Significance.
Average brood size at hatching.	0.89	1.12	$U_{32,79}=1140$, ns.
Average hatching success.	44.3%	37.5%	$U_{32,79}=1182$, ns.

Captions to figures:

Figure 1. Graph showing how the % error in estimated daily mortality rates changes with the interval between visits. Results were calculated from a large theoretical population of nests with a daily survival rate of 95%. For these particular conditions, the error changes from an overestimate of mortality to an underestimate when the interval increases past 11 days.

Figure 2. Relationship between Mayfield survival and true survival, calculated from a large theoretical population of nests re-visited once after various intervals. Figure 2a shows a simple plot of Mayfield survival against true survival, while figure 2b plots the %error in Mayfield mortality against true survival.

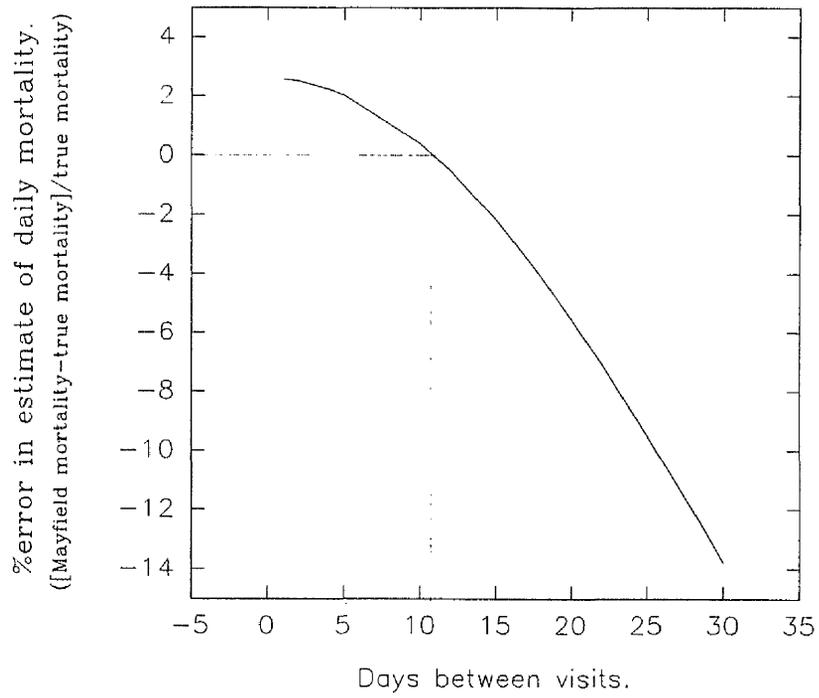
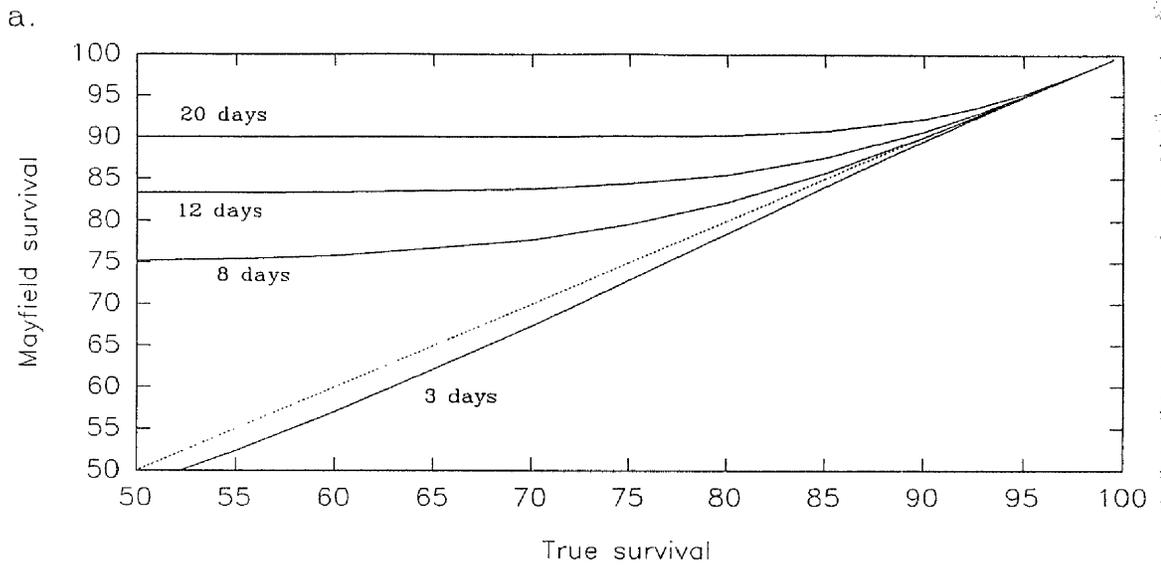


Figure 1.



solid line - observed relationship between Mayfield estimates and true survival.
 dashed line - expected pattern if biases were absent.

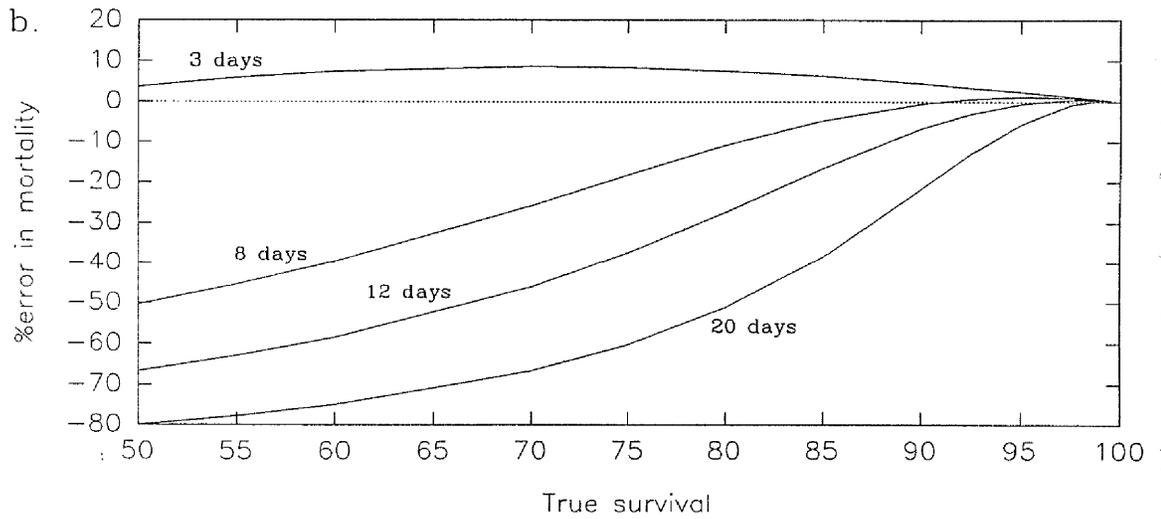


Figure 2.

Chapter 2 (methods), section 5

The technique of ordinal logistic regression for analysing ecological data

D. L. THOMSON, R. W. FURNESS, and P. MONAGHAN

*Applied Ornithology Unit, Division of Environmental and Evolutionary Biology,
Institute of Biomedical and Life Sciences, Glasgow University, G12 8QQ.*

E-mail: gbzv57@udcf.gla.ac.uk

Telephone: 0141 339 8855 ext 8033

Fax: 0141 330 5971

Ordinal logistic regression

Summary

1. In order to assess its potential for analysing ordinal ecological data, ordinal logistic regression (OLR) was compared with the more conventional techniques of poisson regression (PR) and multiple linear regression (MLR) in an analysis of reproductive success in swifts *Apus apus*.
2. Unlike OLR and MLR, the distributional assumptions of PR were violated and PR failed to detect significant effects found using the other two techniques.
3. To interpret the effects of weather, age and long term trends, in terms of lifetime reproductive success, regression models of individual annual breeding success from the three techniques were combined with analogous models of adult survival. Unlike the consistent and realistic interpretations of PR and OLR, MLR produced misleading and impossible interpretations.
4. MLR thus performed well when testing but not when interpreting, while the converse applied to PR.
5. OLR is highly suitable for analysing discontinuous ecological variables such as clutch size, litter size, number of offspring, or else scores of continuous variables such as aggression or body condition. As well as more power and versatility than conventional non-parametric tests, OLR offers better interpretation of results even when the residual distributions permit parametric alternatives.

Key words: generalised linear modelling, ecological regression analysis, discontinuous variables, ordinal, reproductive success.

Introduction

In the analysis of ecological data, specific problems arise repeatedly because critical variables such as clutch size or breeding success are discontinuously distributed (Morgan 1992, Crawley 1993). This commonly necessitates the use of less powerful and less versatile non-parametric methods. The execution of these analyses discards information and lacks power, and the biological interpretation lacks precision. Even if residuals are normally distributed and if linear parametric models can be justified, techniques which do not acknowledge the underlying distribution might lead to unrealistic interpretations outside the range of possible values, and this may result in spurious biological conclusions.

Ordinal logistic regression (OLR) has been in existence for some time (McCullagh 1980), but its potential for analysing such ecological data has rarely been explored. The format of OLR would seem highly suited to the analysis of variables which involve counts or scores, such as clutch size, litter size, number of offspring, aggression scores, body condition scores, or risk exposure. The technique was designed to be used in a manner akin to multiple linear regression (MLR), wherever the data for the dependent variable fall into distinct, ranked categories. Poisson regression (PR) can also be used to analyse such data, but it assumes a poisson distribution which may not always be realistic.

A technique which could test for and interpret ecological effects of several variables on breeding success would be particularly valuable. In long term studies, where not all individuals can be identified and monitored throughout their lives, the ability to explore patterns of lifetime reproductive success ('LRS') indirectly from models of annual breeding success and survival would be useful. The validity of such estimates does however depend on the suitability of the techniques from which they are made.

Using data from a long term study of breeding swifts *Apus apus*, (Douglas-Home 1977, Thomson & Douglas-Home 1993, Thomson *et al.* in press), this paper aims to explore the potential of ordinal logistic regression for analysing ordinal or

interval ecological data. In comparable analyses, the performance of OLR will be compared with the conventional techniques of poisson- and multiple linear- regression.

Firstly, after controlling for other variables, we aim to compare results obtained when testing for effects of breeding age on reproductive success using OLR, PR, and MLR. We interpret the resulting models and examine the frequency of estimates which lie outside the range of possible values.

Secondly, using the three comparable models of breeding success in relation to long term trends, weather and breeding age, we seek separately to combine each with an analogous model of adult survival (Thomson *et al.* in press), and thus to interpret their implications for lifetime reproductive success ('LRS') using a simulation (see Clutton-Brock 1988, Newton 1989). We then look at how evenly reproductive success is divided between individuals in the population and we compare the frequencies of complete lifetime failure. We then compare the variance in LRS explained by breeding lifespan, by mean annual reproductive performance, and by temporal cohort effects. Both MLR and PR can make estimates of breeding success which lie outwith the range of possible values; we examine whether the more realistic distributional assumptions used in making these interpretations from OLR models might lead to more realistic values for LRS.

Methods

THE TECHNIQUE OF ORDINAL LOGISTIC REGRESSION

OLR treats ordinal data as a number of stacked dichotomous variables. Thus, in the case of swift breeding success which can take the values 0,1,2, or 3 chicks, OLR considers the frequency of observations which are 0 or greater, 1 or greater, 2 or greater, etc. The technique then integrates this information and examines any systematic changes in these dichotomous variables to determine, for example, whether swift breeding success changes with an independent variable such as age. Like MLR, it is

possible to incorporate several independent variables, to examine simultaneously, for example, the effects of breeding age and June temperatures, and to examine whether the effect of one variable persists after controlling for another.

Because of different distributional assumptions, the form of the estimates generated by OLR differ markedly from those of MLR. An MLR model can produce a single average estimate with an estimable standard deviation. The data would then be assumed to follow a normal distribution around this estimated value. If data actually follow an ordinal distribution, then MLR estimates can fall between the categories and outside the range of possible values. By contrast, an OLR model yields the probabilities that an observation will lie in any particular category. Though akin to simple logistic regression which examines the probability of an observation lying in each of two categories, OLR permits the use of multiple categories 0,1,2,3....etc. Further, because the categories are stacked rather than simply separated, OLR retains the information that 0 is less than 1 is less than 2 is less than 3 etc.

The computer output from an OLR analysis will depend on the software used. In the analyses reported here, a procedure available from GENSTAT was used (Lane *et al.* 1987, Cole & Lane 1989, Digby, Galwey & Lane 1989). Output from this includes at least four important types of information. Firstly, a value from a t distribution can be used to test the significance of each independent variable. Secondly, regression coefficients with standard errors for each independent variable can be used to examine whether independent variables such as say June temperatures have positive or negative effects on a dependent variable such as breeding success. Thirdly, the mean residual deviance from the full regression model can be used to determine whether data are distributed around the model as expected or whether important interactions are being missed. Lastly, 'cut points' or 'bounds' are used when calculating the probability of observations falling in each category, and are in some ways analogous to intercepts MLR. These cut-points can be used to estimate the relative size and importance of the categories used to describe a truly ordinal dependent variable such as aggression score.

DATA COLLECTION

Annual and lifetime reproductive success are important and widely used ecological variables (Clutton-Brock 1988, Newton 1989) and so were selected in this case study to examine the suitability of OLR for analysing ecological data. The required information was extracted from a long term data set on the breeding success of individually marked swifts at a site in south-eastern Scotland between 1954 and 1993. Full details of the history of this study colony, the fieldwork methods used, and the biological findings, are contained in Douglas-Home (1977), Thomson & Douglas-Home (1993), and Thomson *et al.* (in press). This paper aims not to replicate information published elsewhere, nor to report the biological results of the study, but rather to explore the suitability of OLR using the data available from this source.

Using data available for the nearby Floors Castle meteorological station, Thomson *et al.* (in press) found that adult survival had been affected both by July temperatures and by a further long term non-linear trend. With the standard SURGE4 software (Clobert, Lebreton & Allaine 1987, Pradel 1989, Lebreton *et al.* 1992), they produced a model which could be used to calculate adult survival from details of the year and the weather conditions. Using multiple linear regression, they also found that mean annual breeding success of the colony had been affected by a comparable long term trend, and by June temperatures.

DETECTING SIGNIFICANT EFFECTS USING THE ORDINAL LOGISTIC, POISSON AND MULTIPLE LINEAR REGRESSION

Before comparing the conclusions reached regarding the effects of breeding age on breeding success, all significant independent variables identified by Thomson *et al.* (in press) were first incorporated. The effects on breeding success of breeding-age and breeding-age-squared were thus tested by adding them to models containing mean daily maximum June temperatures, a long term quadratic trend, and an interaction between June temperatures and time.

Breeding age rather than true age was used in this analysis. The true age of breeding birds was not determinable in the study, because most birds were ringed in their first breeding year. Where both members of a pair were identified, the breeding age of the older bird was used.

The assumptions of MLR and PR were checked. Although breeding success itself is not normally distributed, the residuals were consistent with a normal distribution (Kolmogorov-Smirnoff, $X^2_1=5.42$, ns.). The assumptions of PR were however violated and dispersion was not constant.

SIMULATIONS TO COMPARE ESTIMATED REPRODUCTIVE SUCCESS BETWEEN REGRESSION TECHNIQUES

By combining details of the year, the relevant monthly weather data over the period 1954-1993, calculations of breeding age, and the regression models of breeding success, it was possible to estimate the frequencies of birds with particular annual breeding successes. By combining these with comparable models of annual survival, it was then possible to simulate LRS. Twenty four putative cohorts each of 400 birds were thus created for the years 1954-1977, and the fates of all individuals were calculated by building the regression models into GENSTAT programs. From the calculated distributions of breeding success and from the calculated probabilities of any particular breeding success, it was possible to employ random number generators to allocate putative breeding success for each individual. By calculating the probability of survival under the given circumstances, independent random number generators could also be used to determine whether each putative individual then survived to the next breeding season. It was thus possible to total LRS for all individuals in the simulation.

ANALYSING DATA FROM THE SIMULATIONS

These simulations served not to re-test significance but to interpret effects whose significance has already been established. Statistical testing of results generated from simulations would be meaningless but the magnitude of effects and the explained variance can be estimated. Here we aim to compare OLR, PR and MLR in their abilities to elucidate and quantify these effects realistically.

WHICH CALCULATED PATTERNS OF LRS WERE COMPARED BETWEEN THE TECHNIQUES?

The regression techniques differ more in their treatment of variance, than in their average estimates. We therefore first checked that the overall average LRS estimates were similar between the three techniques. The distributions of LRS calculated with the three techniques were then compared, and the implications that any differences might have for the division of reproductive success between individuals of the population were examined. Having thus looked at the contributions made by the most and least productive sections of the populations, the estimated frequencies of birds which failed to produce any offspring were compared. Then, interpretations regarding the relative importance of mean annual breeding success and breeding lifespan were made and compared using the three techniques. Finally, the importance of cohort effects for the determination of LRS was assessed and compared between the three techniques.

Results

TESTING SIGNIFICANCE - A COMPARISON OF REGRESSION TECHNIQUES

Both conventional MLR and ordinal logistic regression identified significant effects of age on breeding success and found these to be best described by a quadratic model including a significant linear component (Table 1). Poisson regression identified only the linear component (Table 1), and further failed to detect the interaction between

June temperatures and time (δ mean deviance=2.1568, $df=1$, dispersion=0.919, ns. Table 1c.). The poisson regression also produced a warning that dispersion was not constant and that the distributional assumptions were violated.

WHAT FRACTION OF ESTIMATES LIE OUTSIDE THE POSSIBLE RANGE OF VALUES FOR ANNUAL BREEDING SUCCESS?

Only OLR produced estimates which were consistently within the range of possible values (0,1,2 or 3 chicks) (Table 2.). Because MLR assumes that breeding success has a continuous and unbounded distribution, it produced highly variable estimates of annual breeding success. 38.1% of these MLR estimates were below zero or above three, and most estimates were fractional rather than whole numbers. Poisson regression assumes that estimated values can not fall below zero and that they are whole numbers. However even with this technique, 9.3% of estimates were greater than 3 young and therefore beyond the maximum possible.

THE DISTRIBUTION OF LIFE TIME REPRODUCTIVE SUCCESS

The three simulations produce estimates of average lifetime reproductive success which are similar (Table 2). The main discrepancies do not so much arise with the means as with the distributions where MLR is strikingly different (Figure 1.). In particular, because of unrealistic treatment of variance around the MLR model, over a quarter (25.9%) of the birds are estimated to have negative lifetime reproductive success (Table 3). With PR, all estimates are whole numbers, no birds have negative LRS, and although estimates of annual productivity exceed the natural maximum in 9.3% of breeding attempts, the final distribution of LRS is similar to that of OLR.

The OLR models estimate that the most productive 20% of the population will produce 53% of all the offspring, while the top 10% will produce 32% (Table 2). These figures are well mirrored by the poisson regression model but MLR model is markedly different and estimates that the least productive 20% of the population produce -21.8%

of the offspring...this negative percentage is clearly unrealistic(!) and highlights the lack of realism in the MLR model, contrasting with the other techniques.

HOW MANY BIRDS FAIL COMPLETELY IN THEIR LIFE TIME REPRODUCTIVE CAREERS?

According to the OLR models, 8.8% of birds which have at least one breeding attempt fail to produce any offspring during their lives. PR similarly estimates that 7.6% of birds fail completely, but according to the MLR model, only 0.07% fail in their LRS though 28.7% produce fewer than 0.5 offspring (Table 3.). The results produced by MLR are sufficiently different to cause concern. Since the OLR models have a more realistic distributional basis, and since they yield tenable interpretations, greater faith in their accuracy is justified.

20.8% of individual annual breeding attempts were observed to fail. Both the PR and OLR models suggest that the life history strategy of high survival and repeated breeding serve to reduce the frequency of lifetime failure. MLR suggests that the frequency of lifetime failure is actually higher than the frequency of annual failure! This result is not only biologically unrealistic, it is mathematically impossible.

WHICH IS MORE IMPORTANT IN DETERMINING LRS - BREEDING SUCCESS OR SURVIVAL?

The OLR models estimate that 88.6% of the variance in LRS is attributable to breeding lifespan, and 18.5% can be accounted for by mean annual breeding success (Table 4). (Breeding performance improves with age and the variables which influence lifespan and breeding success are correlated - this is why the two factors seem to account for a total variance in excess of 100%.) PR similarly estimated that breeding lifespan could account for 83.1% of the variance while mean annual breeding success accounted for 22.1%. MLR suggests that breeding lifespan accounts for only 18.7% of the variance and mean annual breeding success for 40.3%.

HOW MUCH OF THE VARIANCE IN LRS IS DUE TO COHORT EFFECTS?

Under the OLR models, 14.2% of the variance in lifetime reproductive success is due to the temporal effects of individual cohorts (Table 4). PR similarly estimates that 14.6% of the variance is due to cohorts but MLR models suggest this figure is only 2.9%.

Discussion

In terms of distributional assumptions, both OLR and MLR were appropriate for testing the effects of age on annual breeding success, and both detected the same effects. By contrast, the assumptions of PR were violated and the technique failed to detect effects identified with OLR and MLR.

By contrast, although all techniques generated similar average estimates of LRS, the biological interpretations of LRS made with MLR were impossible and were markedly different from those made by OLR and PR. OLR offers the opportunity to explore the division of LRS between individuals in a way which is much more realistic than can be achieved with the conventional technique of MLR.

Similarly, the MLR-estimated frequency of birds which fail to produce any offspring is impossible while the PR- and OLR-estimates are feasible and similar. Both OLR and PR suggest that high survival and repeated breeding serve to buffer the birds and protect them from complete failure. MLR suggests that the frequency of lifetime failure is actually higher than the frequency of failure in any single year!

Consistent with many empirically established results (Newton 1989), OLR and PR suggest that breeding lifespan is more important than mean annual breeding success for determining LRS. MLR, by contrast, would lead us to the opposite conclusion. Because MLR does not recognise the limited range of values which can be taken by breeding success, it overestimates the residual variance in breeding success. The higher the errors in MLR, the greater the residual variance in calculated mean annual breeding success and the greater the estimated influence of breeding success in explaining the variance in LRS. This is a statistical artefact with biologically misleading implications.

The problem can be removed by using OLR which adopts a more realistic treatment of variance in breeding success. PR recognises the lower limit and the discontinuous distribution of breeding success, but does not recognise the upper limit. The treatment of variance by PR is thus not as realistic as OLR but is better than MLR.

The overestimates of residual variance made by MLR also have important analytical implications when quantifying the importance of environmental effects. The higher the noise due to spurious variance in breeding success, the lower is the apparent importance of other factors. This problem can be removed by using OLR.

Even when parametric techniques are justified, ordinal logistic regression, which acknowledges the underlying distribution of the data, can point to biologically realistic implications, while conventional multiple linear regression can involve misleading distortions. Unlike poisson regression which was inappropriate and which performed poorly, both OLR and MLR provided comparable tests, and both detected the significance of particular variables. However, when considering what the models meant, ordinal logistic regression avoided important errors. Not only does ordinal logistic regression provide the opportunity to perform appropriate and powerful analyses on data whose residuals are distributed non-normally, it produces interpretations from ordinal data which are more realistic than those from parametric techniques. Even when normally distributed residuals permit the use of parametric tests on ordinal data, there are advantages of employing ordinal logistic regression.

Acknowledgements

The analysis of these data was funded by the Carnegie Trust for the Universities of Scotland. For collecting, collating, and providing data, and for enabling visits to the birds, we acknowledge the late Henry Douglas Home, Lady Caroline Douglas Home, W.Murray, A.MacMillan, S.da Prato, A.Kerr, C.Badenoch, the late R.J.Robertson, R.Tabony, Meteorological Office. J.Buchanan and M.Partridge provided help and advice with computing. Dr. J.Currall, C.Donnelly, Prof.C.M.Perrins and

Dr.R.H.McCleery all contributed help or advice regarding analysis, and in particular J.Currall kindly read an earlier draft. Having begun his study of swifts in 1954, Henry Douglas-Home sadly died many years before the results of his work could be seen.

References

- Clobert, J., Lebreton, J-D., & Allaine, D. (1987) A general approach to survival rate estimation by recaptures or resightings of marked birds. *Ardea* 75, 133-142.
- Cole, T.J. & Lane, P.W. (1989) Procedure ORDINALLOGISTIC. Genstat 5. Procedure Library Manual. (eds. Payne, R.W. and Arnold, G.M.) Lawes Agricultural Trust, Rothamsted Experimental Station, NAG, Oxford.
- Clutton-Brock, T.H. (1988) *Reproductive Success*. University of Chicago Press, Chicago.
- Crawley, M.J. (1993) *GLIM for ecologists*. Blackwell Scientific Publications, Oxford.
- Digby, P., Galwey, N., & Lane, P. (1989) *Genstat5. A Second Course*. Oxford University Press.
- Douglas-Home, H. (1977) *The Birdman. Memories of birds*. Collins, London.
- Lack, D & Lack, E. (1951) The Breeding Biology of the Swift *Apus apus*. *Ibis* 93, 501-546.

- Lane, P., Galwey, N. & Alvey, N. (1987) *Genstat 5. An Introduction*. Oxford University Press.
- Lebreton, J-D., Burnham, K.P. , Clobert, J., & Anderson, D.R. (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67-118.
- McCullagh, P. (1980) Regression Models for Ordinal Data. *Journal of the Royal Statistical Society B.* **42**, 109-142.
- Morgan, B.J.T. (1992) *The analysis of quantal response data*. Chapman and Hall, London.
- Newton, I. (1985) Lifetime reproductive output of female sparrowhawks. *Journal of Animal Ecology* **54**, 241-253.
- Pradel, R. (1989) *User's Manual for Program SURGE4. Version 4.0*.
C.E.P.E./C.N.R.S. BP5051 34033 MONTPELLIER-Cedex, France.
- Thomson, D.L & Douglas-Home, H. (1993) Long term changes in weather and in the breeding schedule of Common Swifts *Apus apus*. *Recent advances in the study of the Apodidae*. (eds. G. Malacarne, C. T. Collins & M. Cucco), pp. 199-202. Avocetta 17, Turin.
- Thomson, D.L., Douglas-Home, H., Furness, R.W., & Monaghan, P. (in press). A long term study of the effects of weather on the breeding success and survival of common swifts *Apus apus*. *Journal of Zoology*.

Table 1a. Variables used in ordinal logistic regression models of individual annual breeding success. Note that multiple linear regression (Table 1b) identifies the same effects, but that poisson regression (Table 1c) fails to find some.

	Ordinal	Logistic	Regression
Residual		df	deviance
		215	584.2
			mean deviance
			2.573
		estimate	s.e.
			t
bound[1]		-4.792	1.8492
bound[2]		-5.717	1.8590
bound[3]		-7.640	1.8897
Breeding age		0.331	0.1213
Breeding age squared		-0.022	0.0097
Mean daily max June T(°C)		0.782	0.2500
Year		0.701	0.2482
Year squared		-0.014	0.0049
June temperature by year		-5.951	2.6995

Table 1b. Variables used in multiple linear regression models of individual annual breeding success.

	Multiple	Linear	Regression	
		df	sum of squares	mean square
Regression		6	36.3	6.0421
Residual		225	218.1	0.9694
Total		231	254.4	1.1012
		estimate	s.e.	t
Breeding age		0.189	0.0635	2.97
Breeding age squared		-0.013	0.00507	-2.61
Mean daily max June T(°C)		0.443	0.131	3.38
Year		0.391	0.131	2.99
Year squared		-0.0076	0.0026	-2.95
June temperature by year		-5.951	1.43	-2.34

Table 1c. Variables used in poisson regression models of individual annual breeding success. Non-significant effects were retained to enable meaningful comparison of results with the other two regression techniques. Note that the analysis yielded a warning that dispersion was not constant and that the data did not follow a poisson distribution.

Poisson Regression			
	df	deviance	mean deviance
Regression	6	21.8	3.632
Residual	220	200.9	0.913
Total	226	222.7	0.985

	estimate	s.e.	t
Breeding age	0.119	0.0530	2.25
Breeding age squared	-0.009	0.00442	-1.93
Mean daily max June T(°C)	0.255	0.101	2.54
Year	0.224	0.102	2.18
Year squared	-0.0044	0.0020	-2.15
June temperature by year	-1.85	1.14	-1.62

Table 2. Estimates of i.) the frequency of out-of-range estimates of annual breeding success, ii.) average lifetime reproductive success, and iii.) the relative productivities of the most successful sections of the population.

Type of regression used to simulate breeding success	% estimates out of range	Estimated average lrs	% of total lrs produced by most productive 20%	% of total lrs produced by most productive 10%
Ordinal logistic	0.0%	7.65	53%	32%
Multiple linear	38.1%	8.54	85%	59%
Poisson	9.3%	7.91	54%	33%

Table 3. The frequencies of birds which experience lifetime reproductive failure or have apparently negative LRS, as calculated from the 3 simulations.

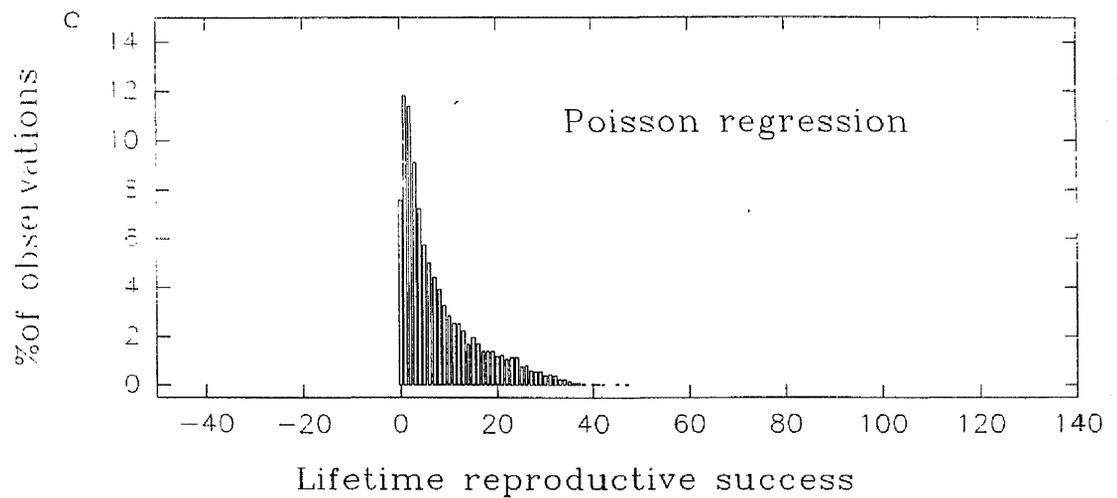
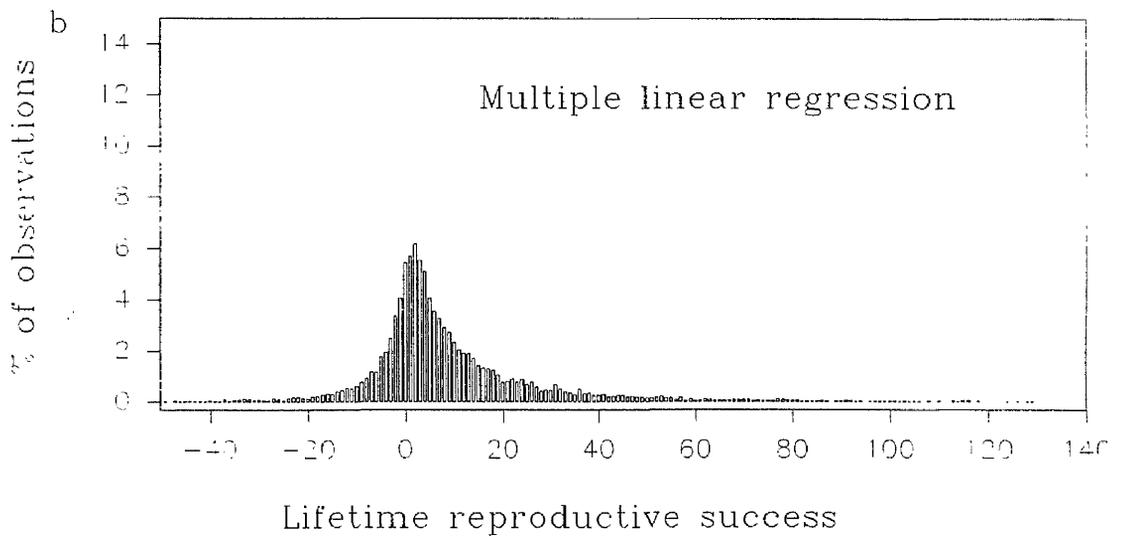
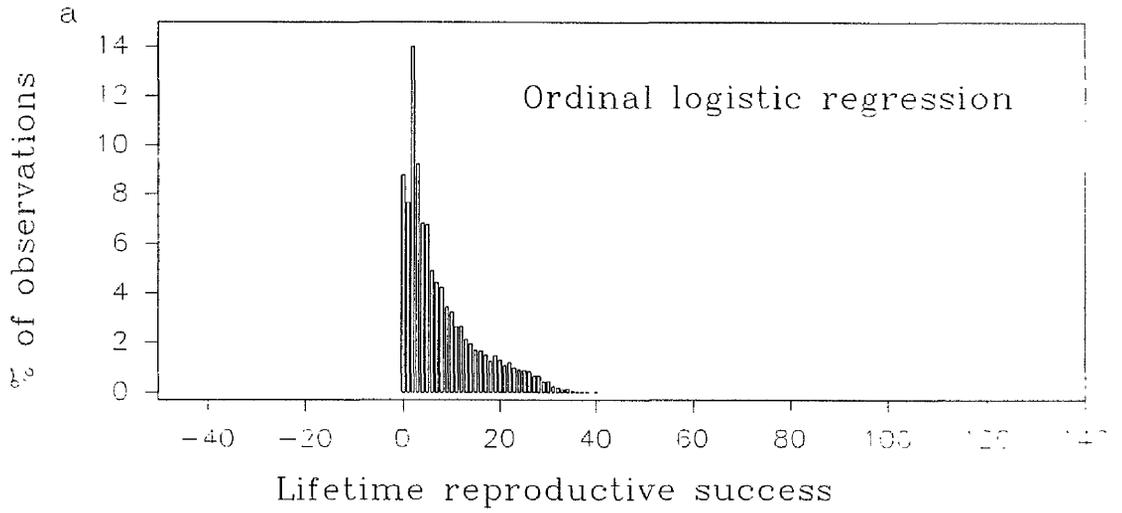
Type of model used to simulate breeding success	% with zero LRS	% with LRS<0.5	% of birds with negative LRS
Ordinal logistic regression	8.8%	8.8%	0.0%
Multiple linear regression	0.07%	28.7%	25.9%
Poisson regression	7.6%	7.6%	0.0%

Table 4. Comparison between the simulations, of the importance of breeding lifespan, mean annual breeding success, and temporal cohort effects, in accounting for the variance in lifetime reproductive success.

Type of regression model	% lrs variance explained by longevity	% lrs variance explained by mean annual breeding success	% lrs variance explained by cohort effects
Ordinal logistic	88.6%	18.5%	14.2%
Multiple linear	18.7%	40.3%	2.9%
Multiple linear	83.1%	22.1%	14.6%

Captions to Figures:

Figure 1. Distributions of lifetime reproductive success as generated from simulations where breeding success is modelled with a.) Ordinal logistic regression, b.) Multiple linear regression, and c.) Poisson regression.



Chapter 2 (methods)

Section 6. Direct and indirect approaches.

In approaching questions of clutch size determination, I have employed both direct empirical and indirect theoretical approaches. With the first of these, a hypothesis can be tested by direct observation. With the second, the hypothesis is tested indirectly by exploring the implications of assumptions which may themselves be derived from observations. Both approaches involve simplifying the problem, and both have their values and their drawbacks. I aim here to discuss these within the context of clutch size determination and thereby to indicate why each was chosen under the respective circumstances. I aim not to advocate the use of any one approach, but to weigh up the merits of each.

If problems are tackled only from an indirect theoretical perspective, then unrealistic assumptions may persist and there may be undue emphasis on some things but neglect of others. Based on indirect heat budget models, King(1973) argued that there should be no metabolic cost of incubation, but in chapter 4, I present a review indicating that there commonly is a metabolic cost of incubation. I use indirect models myself in chapter 3, and question the hypothesis that clutch size is shaped principally by natural selection during the chick-rearing phase (c.f. Van der Werf 1992, Roff 1992). However, with these models, falsification would depend on critical assumptions which have not been tested. Instead of adopting these as untested assumptions, I instead acknowledge these as key variables which should be collected in order to resolve the problem. Although the model serves to identify these key variables, the validity of the main hypothesis is thus best tested not with the model alone but by reviewing the empirical record (Chapter 4) or by looking at the behaviour of the focal study species (Chapter 5). Similarly, the relevant models which predict age-related increases in reproductive effort make the assumption that senescence is a fixed trait (Gadgil and Bossert 1970, Charlesworth and Leon 1976). While it is possible to explore indirectly

the implications of relaxing this assumption (Chapter 11), I acknowledge that the accuracy of the predictions and the validity of the assumptions can ultimately be tested only directly.

However, despite such shortcomings, indirect theoretical approaches can offer insights where direct empirical solutions are impractical. For example, looking directly at the relationship between reproductive effort and age is difficult especially in long-lived species because long term studies are required (e.g Hamer and Furness 1991) and because reproductive effort can be difficult to measure (Taylor 1991). Yet conditions for the evolution of increasing reproductive effort can be identified indirectly using mathematical models (chapter 11, Gadgil and Bossert 1970, Charlesworth and Leon 1976).

Similarly, even with long term studies, lifetime reproductive success may not be determinable if individuals are not monitored in all their breeding attempts. In chapters 8 and 9 I tackle this problem by constructing models of annual breeding success and inter-annual survival and thence examine the lifetime reproductive success of swifts indirectly using simulations. The only direct way round the problem empirically would be to repeat the 40 years of data collection and increase the intensity of observations. I would argue that the more indirect approach, despite its analytical complexity, is simpler and more efficient, and yields insights where a direct approach is infeasible.

The choice of approach may also depend on whether the patterns or the processes are of principal interest. If the patterns themselves are the focus of interest, then direct observations using an empirical approach are preferable. An indirect theoretical approach is only of any value under these circumstances if it yields clear reliable predictions. If however the processes underlying the patterns are of greater interest, then a more indirect theoretical approach is likely to be both necessary and more revealing. If the principal interest is in the processes then the superficial patterns are of ancillary interest and are only useful if they shed light on these underlying processes. For example, if thermal physiology and heat budgets are of greater interest than the gross metabolic costs of incubation, then heat budget models are more valuable

than direct measurements. In this thesis however, the actual metabolic costs of incubation and their implications for clutch size determination are of greater interest so a direct approach is preferable (chapters 3-6). Yet, by contrast, although the evolutionary understanding of clutch size sought in this thesis could be used to predict clutch size indirectly, if the real interest lay in the superficial patterns of clutch size, then direct observations would be by far the more productive approach. It is easy to observe how many eggs different kittiwakes lay, but I want to investigate what regulates clutch size and why individuals differ (Chapters 5 and 7).

Both indirect and direct approaches can be employed in the falsification of hypotheses, and each has its merits. By comparing direct observations with either predictions or assumptions it may be possible to highlight discrepancies. In chapter 4 I use a direct empirical review to test the hypothesis that the demands of incubation are of negligible importance for the regulation of clutch size. I argue that the hypothesis is not justified given the empirical record and suggest that incubation is in fact often important.

Yet falsification can also be achieved indirectly by examining the logical structure of hypotheses. It may be possible to identify flaws, and by exploring the implications of altering assumptions, and it may be possible to assess whether a model is robust or whether the simplifying assumptions limit its value. In environments where breeding success fluctuates, bet-hedging of lifetime reproduction can be achieved by preserving high survival (Boyce and Perrins 1987, Boyce 1988). However, in chapter 9 I test whether this is sensitive to the assumption that survival shows less inter-annual variance than breeding success. I use a simulation model to explore whether the high adult survival of swifts insures their breeding success in a fluctuating environment. Although breeding success varies with weather conditions which change from season to season, I demonstrate that the survival does not insure the birds against bad years. The prediction that the birds can hedge their bets is thus sensitive to the assumption that survival is less variable than breeding success.

However, falsification might not always be justified by isolated observations. Discrepancies between direct observations and predictions need to be placed indirectly within a wider context if their importance is to be quantified. Except for mathematical errors, there is no such thing as a model which is wrong, only one which is inappropriate (Parker and Maynard Smith 1990), and so discovery of discrepancies need not necessarily justify the rejection of a model. In chapter 8 I start with the null hypothesis that individual birds do not differ consistently in their performance. I then reject this upon finding that some individuals are consistently better breeders than others, but upon exploring indirectly the implications of these differences, I find that they are of little importance in determining lifetime reproductive success. Theoretical insights which reveal deficiencies in the hypotheses may not only provide better grounds for rejection, they bypass the effort of making potentially difficult direct observations. Rectification and improvement also follows more readily if problems are identified with the theory, and discrepancies can be placed within a wider framework. Detection of isolated discrepancies between predictions and observations merely indicates that 'something' is wrong with the model and need not point clearly to any means of improvement.

Boyce, M.S. and Perrins, C.M. 1987. Optimizing Great Tit clutch size in a fluctuating environment. *Ecology* 68:142-153.

Boyce, M.S. 1988. Bet Hedging in Avian Life Histories. *Proc XIX Int. Orn. Congr.*: 2131-2139.

Charlesworth, B. and Leon, J.A. 1976. The relation of reproductive effort to age. *Am. Nat.* 110:449-459.

Gadgil, M. and Bossert, W.H. 1970. Life historical consequences of natural selection. *Am. Nat.* 104:1-24.

- Hamer, K.C. and Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in great skuas Catharacta skua.
J. Anim. Ecol. 60: 693-74.
- King, J.R. 1973. Energetics of reproduction in birds. In 'Breeding Biology of Birds'
Farner, D.S. (ed.). 78. Nat Acad. Sci. Washington D.C.
- Parker, G. and Maynard Smith, J. 1990. Optimality theory in evolutionary biology.
Nature 348:27-33.
- Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman
and Hall, New York.
- Rose, M. 1991. Evolutionary biology of aging. Oxford University Press, Oxford.
- Taylor, P. 1991. Optimal Life Histories with Age Dependent Trade off Curves.
J.Theor.Biol. 148:33-48.
- Van der Werf, E. 1992. Lack's clutch size hypothesis: an examination of the
evidence using meta-analysis. Ecology 73:1699-1705.

Chapter 2 (methods)

Section 7. The Kittiwake as a study species.

Many of the chapters report studies performed with Kittiwakes *Rissa tridactyla* on the island of Hornoya in North-East Norway where it is logistically feasible to live and to study the birds during the breeding season. This study species offers numerous advantages and I aim here to outline why it was chosen. Further background biology of kittiwakes is given in Cramp and Simmons 1983, Coulson and Thomas 1985, Lloyd *et al.* 1991.

Roughly 20 000 pairs of kittiwakes nest on Hornoya (Barrett *pers comm.*), and I was able to work on 279 nests in 1992 and 350 nests in 1993 (together with a further 192 nests which were visited only once during 1993). All kittiwake nests were accessible, either directly or with a ladder, and all nests in the study plots could be checked regularly using a mirror mounted on a 30' bamboo pole. Study plots were located at the low cliffs and rocky outcrops on the north-eastern side of the island. Most nests were accessible in this area, unlike many of those on the higher cliffs of the western side. The abundance and accessibility of these breeding kittiwakes were valuable characteristics for the studies outlined in chapters 5, 7, and 9. In chapter 5, I report a study in which clutch and brood size were manipulated by moving eggs and chicks between nests. Numerous synchronous accessible nests are required for this. In chapter 7, I look at whether there are areas of the colony where breeding success is consistently good and I look at whether this is related to the quality of the nest site. For this, it is necessary to monitor breeding performance at numerous individual nests and to record details of the nest sites. In chapter 9, I examine whether clutch size might be constrained by the space available at the nest. This also involved manipulating nest contents, recording nest site characteristics, and following breeding performance through the season.

Kittiwakes can lay 1, 2 or 3 eggs. Questions of clutch size determination would be more difficult to tackle in a species which does not vary its clutch size. By increasing clutches or broods from 2 to 3, it is possible to study how birds would perform if they employed a different, but feasible and realistic, reproductive strategy (chapter 5). Manipulations which present birds with unnaturally large clutches may have little ecological meaning. As well as facilitating manipulations of clutch size, natural variance in clutch size creates the opportunity for individual optimisation and for effects of adult quality (chapter 7) on clutch size.

Using a noose mounted on a long rod, kittiwakes can be captured and recaptured feasibly. This has made them popular subjects (Gabrielsen et al. 1987) for the doubly labelled water technique employed in measuring metabolic rates (chapter 6). The ability to capture and recapture individual birds is also a requirement for looking at changes in adult body mass and for ptilochronology. In the course of fieldwork, I also developed a noose-trap which could be mounted at the nest site and in which birds would become caught when they returned to the nest. This proved valuable when birds could not be approached with the long rod. The noose-trap consisted of a piece of semi-rigid wire (c. 50cm) twisted into a loop at one end and tied securely to a length of guy chord (c:20m). The other end of the guy chord was then tied to a heavy or immobile object such as a ladder. A series of chord nooses were attached along the wire so that they hung down c.5-10cm. The untied end of the main wire was twisted into a loop to prevent the nooses sliding off, and both sharp ends were then covered with tape to avoid the risk of injury. The wire could be bent into an appropriate shape so that the nooses were suspended round the edge of the nest at the bird's head height, reminiscent of curtains draped from a curved rail. Adhesive tape or small piece of flexible wire (of the type used to twist-seal polythene bags) could be used to keep the loops of the nooses open until the bird became entangled. I would wait c.30m from the nest until the bird had returned to the nest. When the bird was approached, it would then fly off the nest carrying the wire with it. Since the bird could fly only as far as the guy chord permitted, it could then be extracted and processed.

For reasons of safety and practicality, it was not possible to stay and undertake fieldwork alone on Hornoya and so the periods of fieldwork (8th May - 20th July 1992 and 15th June - 28 July 1993) were constrained by the dates when others were present.

Coulson, J.C. and Thomas, C.S. 1985. Changes in the biology of the Kittiwake

Rissa tridactyla: a 31 year study of a breeding colony.

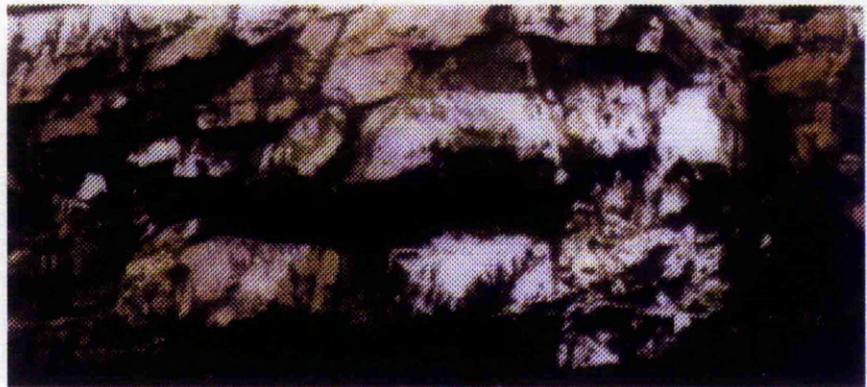
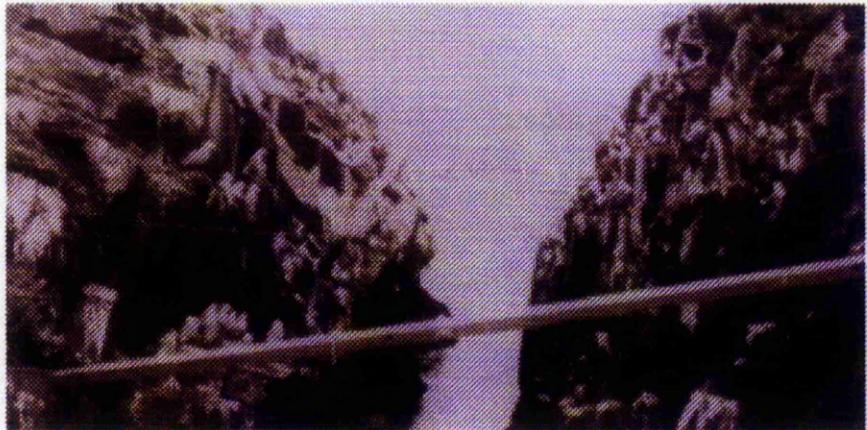
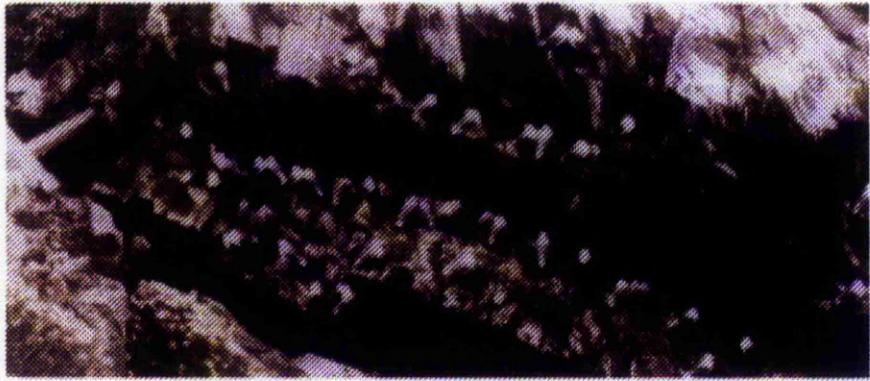
J. Anim. Ecol. 54:9-26

Cramp, S. and Simmons, K.E.L. (eds) 1983. Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Volume III. Waders to Gulls. Oxford University Press, Oxford.

Gabrielsen, G.W., Mehlum, F., and Nagy, K. 1987. Daily energy expenditure and energy utilization of free-ranging Black-legged Kittiwakes.

Condor 89: 126-132.

Lloyd, C., Taşker, M.L. and Partridge, K. 1991. The Status of Seabirds in Britain and Ireland. Academic Press Inc., San Diego.



Kittiwake nesting areas on Hornoya. Note that chicks from some sites can move from the nest onto space created either by adjacent rock ledges or by the fusion of nests. Nests in the gully (first 2 photos) face north and south and offer the opportunity to study the effects of aspect on performance.



1. Incubating kittiwake - note the yellow dye mark from which the bird can be identified.
2. Kittiwake egg - note the red spots produced by fleas.
3. Thermometer used to monitor air temperature on Hornoya.



Chapter 2 (methods)

Section 8a. The swift as a study species.

Although the kittiwake was a good species for studying intensively within the time span of a PhD, it was not possible to collect longer term data. The benefits of the swift in this particular case arose mainly because of a data set which had accumulated over the period since 1954, and which thus presented the opportunity to look at breeding success, survival, and thence lifetime reproductive success of marked individuals over a longer period. The study colony consists only of 15 nest boxes situated on a private residence which can be visited only infrequently. A readable account of how the study developed is given in Douglas-Home (1977). The experiments performed on the kittiwakes could not have been done on the swifts, and long term data available from the swifts could not have been collected from the kittiwakes. General background biology of swifts is given in Lack and Lack 1951, Lack 1956, Cramp 1985 and also in section 8b. I aim here to outline the reasons for using this species, to give some details of the field techniques employed, and to consider some of the errors which can arise in this type of long term study.

As aerial feeders, swifts occupy an environment which fluctuates with weather. They have small clutches of 1-3 eggs and high adult survival rates of around 80% (Perrins 1971, section 8b). There have been few studies of how low clutch sizes and high survival may be a form of bet-hedging strategy in a fluctuating environment (Boyce and Perrins 1987). Swifts would seem to be an ideal study species in this respect, especially when a long term study of marked individuals offers the opportunity to estimate lifetime performance (chapter 11).

Repeated observations of marked individuals offer the opportunity to look at whether individuals differ consistently in their annual breeding success, whether

competent breeders also have higher survival, and at whether differences in adult quality can account for differences in lifetime reproductive success (chapter 8).

The nestboxes are situated beneath the windows of the Hirsel - a large country house located on a private estate near Coldstream in the eastern scottish borders. Data have been collected by qualified ringers each year since 1954, except 1963 and 1964. Using information supplied by local observers, the ringers have timed the visit to coincide with the presence of large feathered young in the boxes. By leaning out of the windows, placing a piece of card or cloth over the entrance hole of the nestbox and reaching inside through the lid, it has been possible to capture roosting adults and their chicks. The identity of marked adults has then been established, unmarked adults and chicks have been given metal rings, and the number of chicks has been recorded.

In long term studies of marked individuals, there is always uncertainty as to whether an individual which is not observed breeding is either dead, or alive and breeding but not detected, or alive but not breeding, or alive and breeding elsewhere. This applies even when marked birds are followed intensely. This uncertainty can create errors in measures of survival and lifetime reproductive success and these could compromise the answers to certain questions.

If breeding birds disperse out of the study population and do not return, then adult survival will be underestimated and measures of lifetime reproductive success will fail to include offspring produced at other breeding sites. This is a standard problem about which often little can be done. The error is however absent from survival estimates derived from the age-structure of ringed birds found dead, and so in the study of swifts, I checked that the calculated survival rates were similar to these estimates (Thomson *et al. in press*). Had there been a large difference, this would suggest that errors of this type may be considerable. At least some swifts returned to breed in the study colony year after year, and one bird even had a breeding lifespan of 16 years.

If birds breed intermittently at other sites, then studies which try to observe lifetime reproductive success directly will incur underestimates, but the simulation techniques used here will not commit this error - they assume instead that breeding

success at the remote colony will follow the same patterns as the study colony. If birds take years of non-breeding outwith the colony, then the simulation techniques will overestimate lifetime reproductive success. If birds breed in the study colony but evade detection, direct estimates will underestimate lifetime reproductive success but the simulation techniques will not.

Boyce, M.S. and Perrins, C.M. 1987. Optimizing Great Tit clutch size in a fluctuating environment. *Ecology* 68:142-153.

Cramp, S. (ed.) 1985. Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Volume IV. Terns to woodpeckers. Oxford University Press, Oxford.

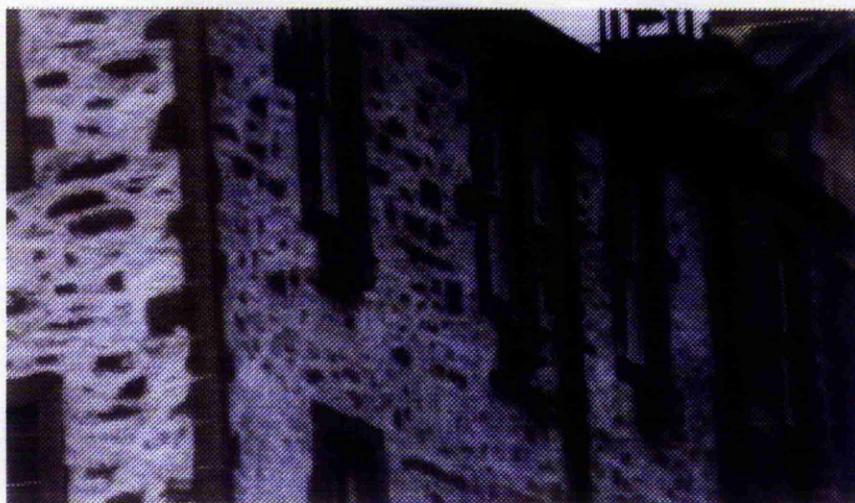
Douglas-Home, H. 1977. The Birdman. Memories of birds. Collins, London.

Lack, D. and Lack, E. 1951. The Breeding Biology of the swift Apus apus. *Ibis* 93:501-546.

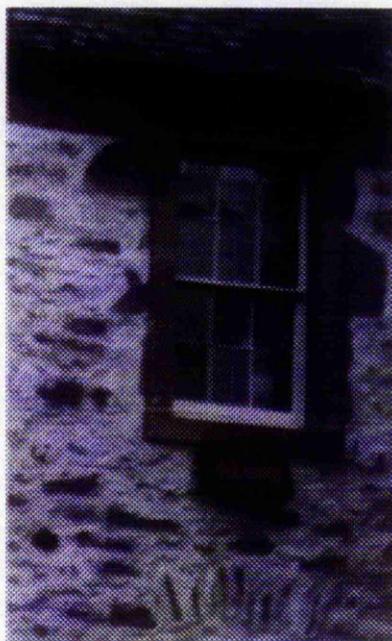
Lack, D. 1956. Swifts in a tower. Methuen and Co., London.

Perrins, C. 1971. Age of First Breeding and Adult Survival Rates in the Swift. *Bird Study* 18:61-70.

Thomson, D.L., Douglas-Home, H., Furness, R.W., and Monaghan, P. (*in press*). Breeding success and survival in the common swift Apus apus: a long term study on the effects of weather. *Journal of Zoology*, London.



The Hirsell, near Coldstream in the Scottish Borders. Note the swift nest boxes beneath the windows.





Checking swift nest boxes at the Hirsel. The first photo shows the inside of a nest box, the second photo shows a swift being ringed, and the third photo shows an adult swift in the hand.

Chapter 2 (methods), section 8b

This manuscript has been accepted by Journal of Zoology,
London, and is currently 'in press'.

Breeding success and survival in the common swift Apus apus: a long term study on the effects of weather.

David L. Thomson, Henry Douglas-Home, Robert W. Furness, Pat Monaghan.

Applied Ornithology Unit, Division of Environmental and Evolutionary Biology,
Institute of Biomedical and Life Sciences, Glasgow University, G12 8QQ.

Swift ecology and weather

Synopsis

In an analysis of data collected between 1954 and 1993, the breeding success of swifts *Apus apus* was found to have been positively related to temperatures in June, especially in recent years. Adult survival until the next breeding season, by contrast, was found to have been more vulnerable to low temperatures in July, at the end of the breeding season. In addition to the effects of changes in June and July temperatures, both breeding success and survival have shown further long term trends, increasing and then decreasing through the study period. A simulation integrating all these effects suggests that lifetime reproductive success ('LRS') is influenced more by changes in lifespan than annual breeding success, and so fluctuations in July temperatures, but not June temperatures, would have more important effects.

Contents

Introduction

Methods

Study site and fieldwork

Weather records

Analyses

Simulation to investigate the implications for lifetime reproductive success

Results

Empirical results

Factors affecting annual reproductive success

Factors affecting annual survival rates

Simulation results

Will changes in weather have affected lifetime reproductive success?

The potential implications of longevity and annual breeding success for
lifetime reproductive success.

Discussion

Acknowledgements

References

Introduction

While environmental change clearly influences the behaviour and population ecology of birds (e.g. Furness and Greenwood, 1993), the biological effects of long term changes in weather patterns may be difficult to evaluate (Marquiss and Newton, 1990). Aerially feeding birds, such as swifts *Apus apus*, are unusually sensitive to weather changes (Lack and Lack, 1951; Bryant, 1975; Martins and Wright, 1993c). Over five years, Lack and Lack (1951) found that chick survival had been poor in the years when the breeding season had been cold, wet, windy or overcast. Over a shorter time scale, they found higher chick growth rates on warm, sunny, dry, or calm days. In a three year study, Martins and Wright (1993a,b,c) enlarged broods, but in only one year of harsh weather did they find greater brood reduction or depressed body condition of adults or of chicks. They also found different effects at distinct stages of the breeding season. Brood reduction happened soon after hatching while critically low adult body condition occurred later in the breeding season. Swifts suffer higher predation during harsh weather and particularly at the end of the breeding season (Kuhk, 1948; Klass, 1953).

Many of these results have been inferred from studies of relatively short duration. To date, it has not been possible either to follow the effects of long term weather changes nor to ascertain whether the different effects of weather at different stages in the season persist over several separate years. No studies have looked directly at the effects of weather on adult survival, or explored the implications of weather change for lifetime reproductive success. Using the results of a study of breeding swifts commenced in 1954 (Douglas-Home, 1977; Thomson and Douglas-Home, 1993), we examine the effects of weather on breeding success and survival and consider whether each might be affected at different periods in the season. We look at whether other factors have produced further long term trends ('temporal effects') in breeding success and survival. By combining the statistical regression models derived from these analyses, we explore the influence of these weather factors on lifetime reproductive success ('LRS').

Methods

Study site and fieldwork

With a view firstly to marking and identifying individuals, and secondly to measuring their breeding performance, fifteen nest boxes located near Coldstream, Southern Scotland (Douglas-Home 1977, Thomson and Douglas-Home 1993), were visited once annually in all years from 1954 to 1993 except 1963 and 1964. These visits generally took place in July, and were timed to coincide with the late chick rearing stage. Adult swifts often roost nocturnally in their nestboxes and can thus commonly be caught by hand. Not all breeding birds were caught each year, however, and individuals were trapped in only just over 50% of the years between their first and last capture. When caught, the identity of ringed adults was noted, and metal rings were attached to unmarked adults. Breeding success is defined as the number of large feathered young present, and ringed, in each nest at the time of the visit, and the data base covers 236 breeding attempts over 38 years. Though adults were not caught in all years, survival rate was determined from the patterns of captures and recaptures following standard methods (Clobert *et al.*, 1987; Pradel, 1989; Lebreton *et al.*, 1992).

Weather records

In order to examine the effects of weather on both chick production and adult survival, we analysed records of temperature and rainfall collected from the Floors Castle station, 13 km from the study site. Temperature and rainfall have been found to be important for breeding performance in other studies, and although there is some evidence that other meteorological variables can also have effects (Lack and Lack 1951, Gory 1987, Cucco *et al.* 1992), records of local sunshine and wind speed are not available here, and data from more distant stations are not representative. For each of the three months of the breeding season (May, June, and July) we used two standard

meteorological variables. We considered firstly the monthly means of daily maximum temperature, and secondly the number of days each month with rainfall in excess of 1mm. Long term trends in these variables have been found (Thomson and Douglas-Home, 1993).

Analyses

The analysis sought firstly to test which weather variables affected breeding performance and adult survival. We further looked for additional temporal changes in breeding and survival that might indicate other unidentified environmental changes. Having tested the significance of each of the effects, we constructed regression models of breeding success and adult survival which contained all the significant effects. Using a simulation, we then combined these two regression models and examined the implications of the weather variables for lifetime reproductive success.

Environmental factors such as weather have simultaneous effects on large numbers of birds, so individuals breeding under the same conditions can not be assumed to yield statistically independent observations. Thus, using *mean annual* breeding success as the dependent variable, we tested the significance of temporal effects and weather variables in a multiple linear regression. We examined the change in the variance accounted for when each independent variable was dropped from the regression model containing all the other significant variables. Having thus established which variables were significant, we then went on to build a model describing 'individual' rather than 'mean annual' breeding performance.

Because studies of LRS have often found effects of experience on survival and annual breeding performance (Clutton-Brock, 1988; Newton, 1989), it was important to take these into account. Although breeding age could be measured, it was not possible to determine true age because age of first breeding was estimable for only 12 birds which returned to breed in the natal colony and there was no fixed age of first breeding. Five birds were first recorded breeding at age 1 year, 1 at 2, 2 at 3, 1 at 4, 1

at 5, and 2 at 6. We did not attempt to estimate true age, but focussed instead on breeding age. An adult caught breeding for the first time was given a breeding age 'one', etc. Where both adults of a pair were caught, we used the age of the older bird. Individual breeding success increased and then decreased with breeding age, and could be described by a quadratic equation (ordinal logistic regression: $z=2.73$, $df=227$, $p<0.01$ for the linear component, and $z=2.41$, $df=227$, $p<0.02$ for the quadratic component). This significant effect of age on breeding success persisted after controlling for the weather and temporal effects and was therefore incorporated into the simulation. Conversely, the other effects also persisted after controlling for the effects of age. Long term changes in the performance of the colony were not due to changing age-structure, even though average breeding age was inevitably lower during the early years of the study.

Although repeated observations of individual birds were used in the analysis, this did not violate assumptions regarding the independence of data. All variables being tested were characteristics of particular years or particular breeding ages. Any individual can breed only once in any particular year or at any particular age. Spurious associations between the consistent performance of individuals and the particular conditions of any year or age do not therefore arise.

Because individual breeding performance is a discontinuous variable, the technique of ordinal logistic regression (McCullagh, 1980; Cole and Lane, 1989), rather than multiple linear regression, was used in the final analysis of individual breeding success. This is analogous to logistic regression but the dependent variable can take more than 2 ordinal values. It is also similar to multiple linear regression, but acknowledges that individual breeding success can take only whole numbers rather than being continuous. With this technique, it was possible to determine the probabilities of producing 0, 1, 2, or 3 chicks, given the year, the weather conditions and the bird's breeding age. The ability to make these predictions using ordinal logistic regression is clearly preferable to making predictions from a multiple linear regression model in which breeding performance is assumed to be continuously and normally

distributed. Ordinal logistic regression could not however be used to examine the effects of annual conditions on mean annual performance because mean annual performance is a continuous, not an ordinal, variable.

Regression models of adult survival rate were constructed using the SURGE4 technique (Clobert *et al.*, 1987; Pradel, 1989; Lebreton *et al.*, 1992). The significance of weather-, temporal- and age- effects could be tested, combining and controlling each as independent variables in a manner akin to multiple regression analysis. The technique estimates both survival rate and capture rate simultaneously by integrating all the information from captures and recaptures and so has more power than conventional techniques (Cormack, 1964; Jolly, 1965; Seber, 1972; and see North, 1987). With the SURGE4 regression model, and with information on the year and weather conditions, it was possible to calculate the probability of an individual surviving to the next year.

Although several variables were found to affect survival rate, none were found to affect capture rate as well, and there was no evidence that capture rate was affected by the weather during the month of the visit. Accordingly, except for the years 1963 and 1964 where no field records were available and where capture rate was therefore fixed to zero, capture rate was otherwise assumed to be constant in the final analysis.

Simulation to investigate the implications for life-time reproductive success.

Since individual breeding adults were captured in only just over 50% of their breeding years, LRS could not be studied directly but only indirectly by means of a simulation based on the regression models of breeding success and adult survival. After establishing the statistical significance of the weather, temporal and age effects on survival and annual reproductive success, the biological importance of each was examined by considering the relative impact on LRS, and by looking at whether LRS would itself show long term temporal trends under the conditions of the simulation. The simulation was not performed to *test* the significance of the various effects, but to

explore their possible implications. It provided a means of estimating the numerical magnitude of the effects and the fractions of variance accounted for. It could thus be used as a way of quantifying the biological importance of effects whose significance had already been established.

For the simulation, a GENSTAT program (Lane *et al.*, 1987) was used to follow 24 putative cohorts each of 400 birds starting breeding in the years 1954-1977. We set the maximum breeding lifespan to 16 years (the highest recorded in this colony), thus necessitating the omission of cohorts commencing breeding during 1978-1993. In the simulation, we followed the effects of conditions around the study site in the years 1954-1993. Real values for all the significant weather, temporal and age variables were thus known for each individual throughout the simulation period.

In the simulation, each bird commencing breeding was randomly assigned a breeding success of either 0, 1, 2 or 3 chicks using the probabilities generated from the ordinal logistic regression model. With the analogous probabilities derived from the regression models of survival rate, each bird was then randomly assigned either survival to the next year or mortality. The same procedure was then repeated successively for the birds which survived each time, and a lifetime total of reproductive success was determined for each individual by summing the assigned annual successes. For each cohort, the mean breeding lifespan, the mean annual breeding success, and the mean lifetime reproductive success were determined by averaging the values for the individuals.

In order to compare the importance of factors affecting annual breeding success and adult survival, the results of the simulation were analysed in two ways. Firstly, we examined the fractions of variance in LRS which could be accounted for by mean annual breeding success and breeding lifespan. Secondly we looked at whether the different components of the weather in the first breeding year influenced LRS via effects on either mean annual reproductive success or breeding lifespan.

Results

1. Empirical results

Factors affecting annual reproductive success

On average, throughout the study period and for all age classes, the birds produced an average of 1.63 (\pm s.e.=0.069) large feathered young per breeding attempt.

Mean daily maximum June temperatures were positively related to mean annual reproductive success (regression coefficient=0.613, $F_{1,34}=8.51$ $p<0.01$, $R^2=0.23$, Figure 1a.), and there was a significant interaction between June temperatures and time such that June temperatures have become more important for breeding success in recent years ($F_{1,34}=6.68$, $p<0.05$, $R^2=0.16$, Figs 1b and 1c). June will generally have coincided with the first stages of chick rearing. There was no evidence that annual reproductive success was influenced by mean daily maximum temperatures during the months of May or July, nor by the number of days with rainfall in excess of 1mm, in any of the months of the breeding season.

After controlling for June temperature effects, there was a significant temporal effect. The residual breeding success increased before it decreased and could be described by a quadratic equation ($F_{1,34}=7.73$, $p<0.01$, $R^2=0.20$, for the linear component, and $F_{1,34}=7.54$, $p<0.01$, $R^2=0.20$, for the quadratic component) (Figure 2.). The cause of this temporal effect is not clear, but it may be due to weather variables which were not measured at the station or to other factors influencing the abundance of aerial insects.

All the significant effects persisted when each of the others was first controlled, and remained when the average fitted annual productivity, predicted from the age function, was used as a term to contend with possible changes in the age structure of the population. Any correlations between the independent variables themselves could not therefore produce spurious effects.

Factors affecting annual adult survival rates.

Overall the average annual adult survival was estimated at 76.16% (95% confidence interval ('C.I.') =72.21%-79.70%).

At the end of the breeding season in any one year, increasing July temperature significantly improved the chances of swifts surviving to the following year (regression coefficient=0.653, 95% C.I.=0.2834-1.0224, $p<0.05$). No significant effects of any other weather variables or age on survival could be detected. A significant temporal effect, resembling that shown by breeding success, was detected; after controlling for the other effects, residual survival rate increased before decreasing (regression coefficient for linear component=0.176, 95% C.I. =0.0461-0.306, $p<0.05$, and for regression coefficient for quadratic component = -0.00456, 95% C.I.= -0.00764 - -0.00149, $p<0.05$). Each significant effect persisted even when the others were controlled.

2. Simulation results

Will changes in weather have affected lifetime reproductive success?

The simulation indicated that lifetime reproductive success would not be constant, but would show long term changes. The trend in cohort average lifetime reproductive success indicated by the simulation could be described by a long term sine model, and this accounted for 52% of the variance(Figure 3a). Under this scenario, birds commencing breeding at the peak of the trend would have over twice the lifetime reproductive success of birds starting in the trough. The most productive cohort in the simulation had an average reproductive success of 11.58 (sd=8.345) offspring while the least productive achieved only 3.04 (sd=5.052). Cohort effects could account for 14.2% of the variance in simulated individual LRS.

The potential implications of longevity and annual breeding success for lifetime reproductive success.

Figure 3b shows that the long term trends in breeding lifespan are strikingly similar to those of LRS shown in 3a. Figure 3c shows long term trends in mean annual reproductive success for comparison. Although both survival and breeding success were influenced by similar temporal effects, their potential implications for LRS might differ partly because each was influenced by different weather variables. In the simulation, after allowing for the effects of mean annual breeding success, 81.5% of the variance in LRS could be uniquely accounted for by the number of breeding years. By contrast, mean annual breeding success was much less important and accounted uniquely for only 11.4% of the variance after allowing for the number of breeding years. A further 7.1% of the variance which was shared between the two variables because mean annual breeding success is correlated with number of breeding years and because annual breeding success changes with age.

Although mean daily maximum June temperatures had a significant effect on breeding success in any year, the simulation indicates that June temperatures in the first breeding year would have no detectable effect on the average annual breeding success of a cohort ($F_{1,22}=0.0167$, ns.). Clearly then, the results also indicate that June temperature would have no detectable effect on the average LRS of a cohort ($F_{1,22}=0.559$, ns).

By contrast, under the conditions of the simulation, July temperature in the first breeding year could account for 16.6% of the variance in breeding lifespan ($F_{1,22}=5.56$, $p<0.05$), and this has clear implications for LRS, accounting for 11.8% of the variance. Through their effects on adult survival, conditions in July at the end of the breeding season would have an appreciable influence on lifetime performance.

Discussion

Lack and Lack (1951) suggested that chick mortality was higher in poor weather, and that chick growth rates and feeding rates were influenced by temperature, rainfall, wind speed and sunshine. Thomson and Douglas-Home (1993) found that the timing of fledging was affected by both temperature and rainfall in all months of the breeding season. Here however, only temperatures during June, the period of hatching and early chick rearing, were found to have any significant influence on the number of large feathered chicks ultimately produced by swifts. These results are consistent with Martins' and Wright's (1993a) suggestion that breeding success is strongly influenced by brood reduction soon after hatching. Weather throughout the season clearly has marked effects on the breeding patterns of swifts. However, apart from brood reduction which may tailor brood size to annual weather conditions and food abundance, swifts have a suite of responses which serve to buffer breeding success from the effects of weather. These include plasticity in laying dates, incubation duration, chick growth rates and the allocation of food between parents and chicks (Lack and Lack, 1951; Martins and Wright, 1993a,b,c).

In contrast to breeding success, it is the temperature in July at the end of the breeding season that most influences adult survival to the next year. This may be because body condition is low at that time and the birds may be more susceptible to weather and to predators (Kuhk, 1948; Klass, 1953; Lack and Lack, 1951; Martins and Wright, 1993a,b,c). The percentage of swifts in the diet of predatory birds can increase by more than ten-fold at the end of breeding seasons or after harsh weather (Kuhk, 1948; Klass 1953). This shows that both the strain of breeding and harsh weather expose the birds to predation. Martins and Wright (1993b,c) showed that in poor weather food was limited and that parents allocated food to their brood and sacrificed their own self-feeding. Towards the end of the breeding season, this led to vulnerable adults in critically low body condition. Conditions in July at the end of breeding may also influence the birds' ability to prepare for and cope with migration,

though Martins and Wright (1993b) found that adults could quickly recover body condition after they stopped feeding chicks.

Both annual breeding success and adult survival showed long term trends during the period 1954-1993, increasing before decreasing. Although the cause is unclear, this indicates that, in addition to the effects of the measured weather variables, other changes in the aerial environment around the study site may have occurred. These may have been due to factors such as other weather variables not measured around the study site, or changes in levels of aerial pollution. That both survival and breeding success have shown comparable trends suggests that conditions around the study site, rather than in the wintering areas or on migration, are important. Long term trends in adult survival could arise through changes in wintering or migration conditions, and could reflect climate change, changing land-use, desertification, or other processes that influence the abundance and availability of aerial insects.

The results indicate that different components of the weather differ in their importance for LRS. Swifts are long-lived birds with relatively low annual reproductive output (Perrins, 1971), and LRS appears to be influenced more by breeding lifespan than by average annual reproductive performance. Our simulation thus shows that the temperatures in July towards the end of the breeding season will have been more important for LRS than temperatures in June during the earlier stages of the chick rearing period. Weather affecting adult survival is more important than weather affecting annual breeding success. Though survival was marginally lower than for other populations (Perrins, 1971; Baillie and Green, 1987; Lebreton *et al.*, 1992), our estimate of 76.16% translates into an average breeding lifespan of 4.47 years, and this opportunity to breed in several years may lessen the impact of poor breeding conditions in any one year.

Acknowledgements

This work was supported by the Carnegie Trust for the Universities of Scotland. We acknowledge the help of W.Murray, A.MacMillan, S.da Prato, A.Kerr, C.Badenoch, the late R.J.Robertson, and staff at the Meteorological Office in collecting, collating and providing data, Lady Caroline Douglas Home for help and access to the birds, J.Buchanan and M.Partridge for help and advice with computing. J.Currall offered statistical advice, as did C.Donnely. Prof. C.M.Perrins and Dr.R.M.McLeery offered help with analysing survival rates. R.Tabony discussed long term weather trends. Dr. J.Currall and an anonymous referee gave comments on the manuscript. Having begun the study in 1954, Henry Douglas-Home sadly died many years before the results of his work could be seen.

References

- Baillie, S.R. and Green, R.E. (1987). The importance of variation in recovery rates when estimating survival rates from ringing recoveries. In: North, P.M.(ed.). Ringing Recovery Analytical Methods. Acta. Orn. **23**: 41-60.
- Bryant, D.M. (1975). Breeding biology of House Martins in relation to aerial insect abundance. Ibis **117**: 180-216.
- Clobert, J., Lebreton, J-D., and Allaine, D. (1987). A general approach to survival rate estimation by recaptures or resightings of marked birds. Ardea **75**: 133-142.
- Cole, T.J. and Lane, P.W. (1989). Procedure ORDINALLOGISTIC. in Payne, R.W. and Arnold, G.M.(eds.). Genstat 5. Procedure Library Manual. Lawes Agricultural Trust, Rothamsted Experimental Station, NAG, Oxford.

- Cormack, R.M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* **51**: 429-438.
- Cucco, M., Malacarne, G., Orrechia, G., and Boano, G. (1992). Influence of weather conditions on pallid swift *Apus pallidus* breeding success. *Ecography* **15**: 184-189.
- Douglas-Home, H. (1977). *The Birdman. Memories of birds*. Collins, London.
- Furness, R.W. and Greenwood, J.J.D. (1993). *Birds as monitors of environmental change*. Chapman and Hall, London.
- Gory, G. (1987). Influence du climat mediterranean sur la reproduction du martinet noir (*Apus apus* L.). *Oiseau et Rev. Francais. Ornith.* **57**: 69-84.
- Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration - Stochastic model. *Biometrika* **52**: 225-247.
- Klaas, C. 1953. Zur Ernährung des Baumfalken. *Vogelwelt* **74**: 48-49.
- Kuhk, R. 1948. Wirkung der Regen- und Kalteperiode 1948 aut den Mauersegler, *Micropus apus* (L.). *Vogelwarte* **1**: 28-30.
- Lack, D and Lack, E. (1951). The Breeding Biology of the Swift *Apus apus*. *Ibis* **93**: 501-546.
- Lane, P., Galwey, N. and Alvey, N. (1987). *Genstat 5. An Introduction*. Oxford University Press.

- Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**: 67-118.
- Martins, T.L.F. and Wright, J. (1993a). Brood reduction in response to manipulated brood sizes in the common swift (*Apus apus*). *Behavioural Ecology and Sociobiology* **32**: 61-70.
- Martins, T.L.F. and Wright, J. (1993b). Cost of reproduction and allocation of food between parent and young in the swift (*Apus apus*). *Behav. Ecol.* **4**: 213-223.
- Martins, T.L.F. and Wright, J. (1993c). Patterns of food allocation between parent and young under differing weather conditions in the Common Swift (*Apus apus*). In: Malacarne, G., Collins, C.T. and Cucco, M. (eds). *Recent advances in the study of the Apodidae*. *Avocetta* **17**: 147-156.
- McCullagh, P. (1980). Regression Models for Ordinal Data. *J.R. Statist. Soc. B.* **42**: 109-142.
- Marquiss, M. and Newton, I. (1990). Effects on Animals: Birds. In Cannell, M.G.R. and Hooper, M.D. (eds.). *The Greenhouse effect and terrestrial ecosystems of the UK*. Institute of Terrestrial Ecology, NERC, HMSO, London.
- North, P.M. (ed.) (1987). Ringing Recovery Analytical Methods. Proc. Euring Technical Conf. and Meeting of Mathematical Ecology Group of the Biometric Society (British Region) and British Ecological Society. *Acta Ornithologica* **23**(1).

- O'Connor, R.J. (1979). Egg weights and brood reduction in the European Swift (*Apus apus*). *Condor* **81**: 133-145.
- Perrins, C. (1971). Age of First Breeding and Adult Survival Rates in the Swift. *Bird Study* **18**: 61-70.
- Pradel, R. (1989). User's Manual for Program SURGE4. Version 4.0.
C.E.P.E./C.N.R.S. BP5051 34033 MONTPELLIER-Cedex, France.
- Seber, G.A.F. (1972). Estimating survival rates from bird band returns. *J. Wildl. Mgt.* **36**: 405-413.
- Thomson, D.L. and Douglas-Home, H. (1993). Long term changes in weather and in the breeding schedule of Common Swifts *Apus apus*. In *Recent advances in the study of the Apodidae*: 199-202. Malacarne, G., Collins C.T. and Cucco, M (Eds.) Turin, *Avocetta* **17**: 199-202.

Captions to Figures:

Figure 1. a). The relationship between mean daily maximum June temperatures and breeding success. b). The relationship between mean daily maximum June temperatures and breeding success in the period 1954-1974. c). The relationship between mean daily maximum June temperatures and breeding success in the period 1975-1993.

Figure 2. a). Long term quadratic temporal trend in annual breeding success, after controlling for the effects of June temperatures.

Figure 3. Long term trends in: a). average cohort lifetime reproductive success; b). breeding lifespan; and c). cohort mean annual breeding success, as determined from the simulation.

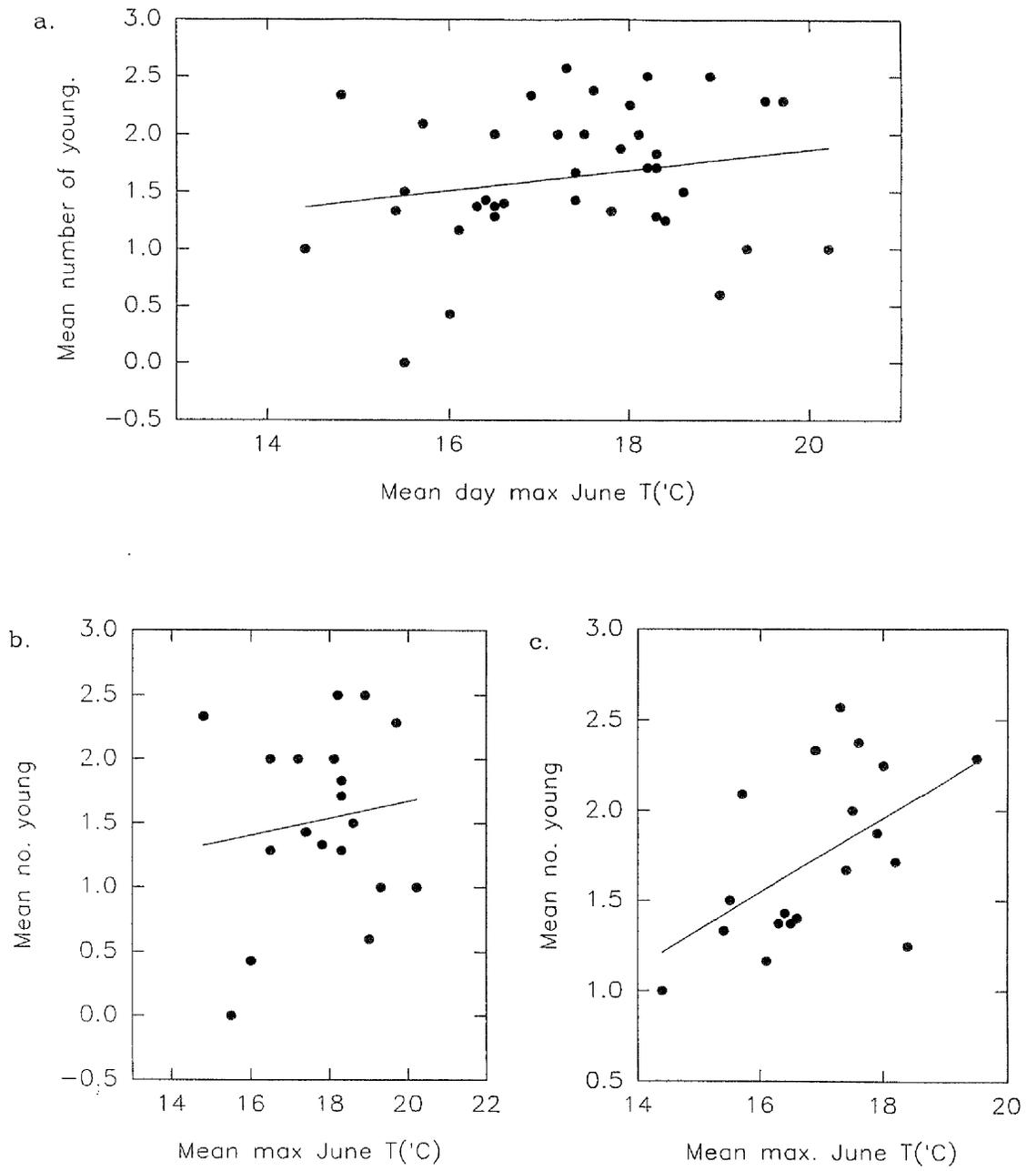


Figure 1.

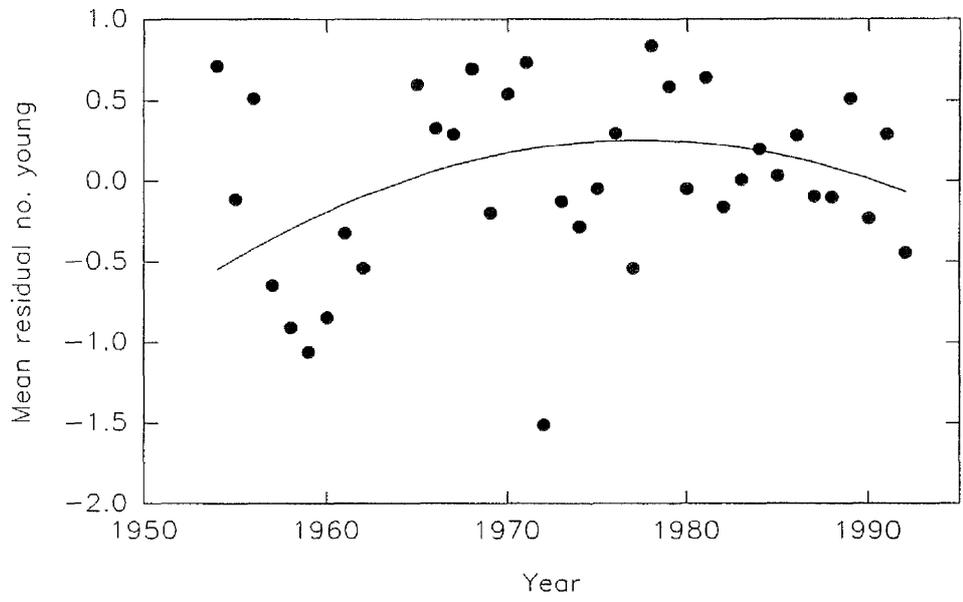


Figure 2.

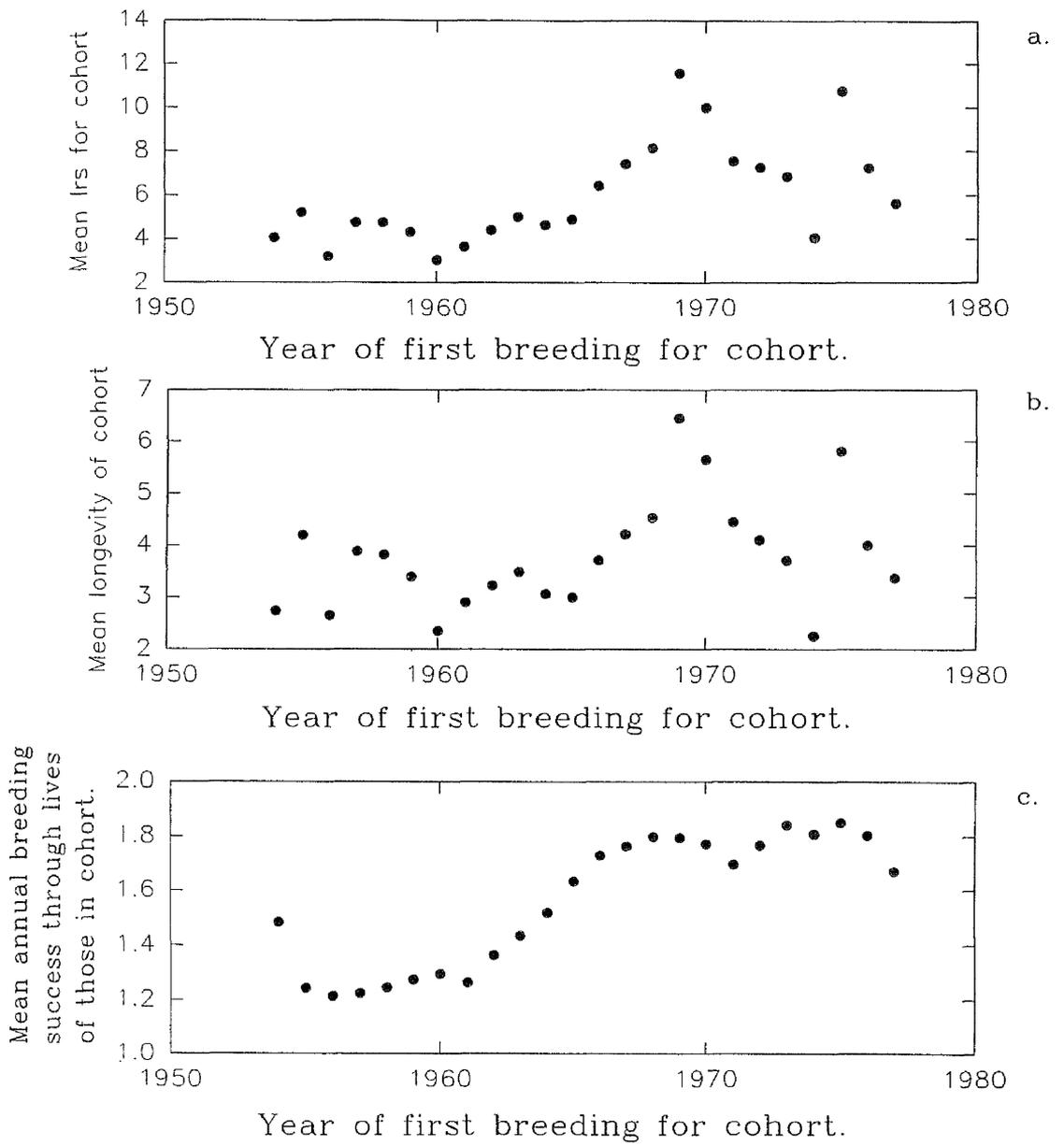


Figure 3.

Results

Chapter 3

Are there bottlenecks on avian reproduction? Clutch size and the temporal distribution of reproductive demands.

David L. Thomson, Pat Monaghan, Robert W. Furness.

Applied Ornithology Unit, Division of Environmental and Evolutionary Biology,
Institute of Biomedical and Life Sciences, Glasgow University. G12 8QQ.

Introduction

It has been common to tackle questions about clutch size evolution by hunting for a single critical period, such as chick rearing or egg formation, when resources are stretched or when natural selection acts most strongly on clutch size (Lack 1947, Weeks 1978, Nur 1984, Winkler 1985, Lessells 1986, Murphy and Haukioja 1986, Weathers and Sullivan 1989). The widespread use of brood-size manipulations as phenotypic approximations of clutch size mutations, betrays a common view that genes determining clutch size are exposed to natural selection principally during the chick rearing phase (Partridge 1989, Dijkstra *et al.* 1990, Van der Werf 1992). Some have however found evidence that clutch size may be shaped at other stages (Moreno *et al.* 1989, 1991, Bolton *et al.* 1992, Williams 1991, Weathers and Sullivan 1989). We here explore whether these many apparently conflicting results are mutually exclusive, and examine whether there are ways in which natural selection on clutch size could operate in concert over several stages. We ask whether bottlenecks on clutch size occur if birds are able to spread the demands of reproduction over several periods. By constructing a simple mathematical framework we seek to identify which variables should be collected in order to test whether there is a single reproductive bottleneck or whether natural selection on clutch size operates over several stages.

Methods

The currency of energy as a proximate determinant of fitness.

With a simple discrete-time linear model we sought to describe the processes which determine, at each stage of the breeding season, the level of resources which can be allocated to fitness-enhancing activities such as staying alive and breeding. Such resources may be nutritional or energetic. Thus, from equations combining food requirements and nutritional intake, we sought to describe the processes dictating the threat of emaciation and the need to sacrifice either breeding or survival.

Food has been shown to influence the number of offspring which birds can rear (Cody 1966, Drent and Daan 1980, Martin 1987, Godfray *et al.* 1991, Stearns 1992), and so a nutritional or energetic currency for fitness would seem appropriate in this model. Other factors such as predation (Lima 1987, Slagsvold 1982a), parasitism (Moller 1993), and space (Slagsvold 1982b, 1989a, 1989b, Van Balen 1984, Slagsvold and Amundsen 1991), have received less attention (Godfray *et al.* 1991), but could easily be incorporated into our framework by changing the proximate currency of fitness.

Using an energetic currency, we constructed models assuming that birds must be able to attain sufficient food to balance their own energy budget and to cover the costs of producing and maintaining their offspring (Bryant and Tatner 1988a). Failure to do this involves a reduction of either reproductive success or adult survival. We assumed that birds which can lay and tend the biggest clutch size and yet still preserve energetic solvency may maximise reproductive output.

Income and Expenditure

There are two components to balancing the energy budget - income and expenditure, and we therefore sought to build energy intake into our model even though it is difficult to measure directly. Expenditure has proved easier to measure and has received the greater amount of attention (Drent and Daan 1980, Bryant and Tatner 1991, Tatner and Bryant 1993). Expenditure can be measured using either respirometry on captive or inactive birds (Gabrielsen *et al.* 1988, Brown 1984, 1988, Biebach 1981, 1984) or doubly labelled water on free living individuals (Lifson and McLintock 1966, Speakman and Racey 1987, Tatner and Bryant 1989). Income may be calculated indirectly from expenditure (Bryant and Tatner 1988a), or estimated crudely from abundance (Perrins 1965, Bryant 1975, Wijnandts 1984, Masman *et al.* 1986). Natural food availability is meaningless for captive birds and is difficult to quantify in wild birds.

Despite extensive information on energy expenditure during avian reproduction, there currently exists no operational theory of clutch size determination based on expenditure alone. Although the probability of energy deficit might reasonably increase with energy expenditure (Bryant and Tatner 1988a), there is little evidence either for a relationship between brood size and energy expenditure or for a simple association between energy expenditure and reproductive costs (Bryant 1988). Both these missing pieces would seem to be key components of a theory relating clutch size regulation to energy expenditure alone, and this gap prompts the incorporation of energy income, at least at the level of theory. Birds observed with high energy expenditure need not be energetically challenged - a human being who is observed spending large sums of money need not be, and indeed is even unlikely to be, a human being who is financially stressed. From a purely methodological perspective, there may often be little which can be done to incorporate energy income more fully, but there is no reason to exclude it from theoretical developments.

In particular, birds are often implicitly assumed to work hardest during the chick rearing phase (Lack 1947) - a view which has sometimes been supported by application of the doubly labelled water technique (Tatner and Bryant 1993). Yet, without complementary measurements of income and without integration of all the necessary variables, it may be unsatisfactory to adopt or retain the assumption that this high expenditure necessarily implies either a bottleneck on reproductive output or strong natural selection on clutch size.

How could reproductive demands be spread over several stages?

In constructing our model, we assume that reproductive demands can be spread over several stages of the breeding season and that the balance of income and expenditure at one stage can affect the balance at another. The prevalence of mechanisms by which this can be achieved offers justification of this assumption.

Firstly, within a currency of energy, reproductive demands are not incurred simply by high expenditure, but by a high probability of an intolerable deficit. Where

different phases of the breeding cycle entail different levels of energy expenditure, the timing of breeding seasons may be adjusted so that the phases of high energy expenditure coincide with the phases of high energy availability (Perrins and Birkhead 1983). Yet this timing of breeding also implies that the abundant resources are removed from the less 'critical' phases. Not only is the maximum energy income shifted to match the maximum energy expenditure, lower energy income is shifted to the period of lower energy expenditure. If this shifting and timing were unconstrained then surely it would stabilise only when the probability of energy deficit was equal at all times. The phase of lowest energy expenditure would then be as critical as the phase of highest expenditure. Because of this interdependence of stages, it is as logical to look for clutch-size regulation during phases of low energy income, as to look for it during phases of maximum energy expenditure.

Secondly, during less 'critical' phases, it may be possible to prepare for the 'critical' stages by storing resources, whether in fat deposits, in eggs, or even in caches. Clearly there are limits to the extent to which this can be done, but the levels of stored resources depend on the 'spare' energy during the less critical phases. Not only does the performance at the 'critical' stage then become dependent on the performance during the less 'critical' stage, but any reduced income or heightened expenditure during the non-critical stage will affect overall performance. The birds might be accumulating credit during the less 'critical' phases, but even then, overall performance could be dependent on energy balance during this stage. Birds may be less likely to complete incubation or chick rearing successfully if they have depleted their resources during egg formation, and they may be less able to cope with the breeding season if they have not laid down resources during the pre-breeding period (Ankney and MacInnes 1978).

Thirdly, even if it is not possible to store resources, it may be possible to defend them. Before the breeding attempt or in the early stages, birds may compete for territories which pay-off later in the year. Like the storing of resources, this constitutes a means of investment, and again, the overall performance may be dependent on the maintenance or attainment of capital during the supposedly less demanding phases. The

higher the expenditure or the lower the income during these phases, the lower the opportunity for investment and the poorer the prospects for overall performance.

With such mechanisms at their disposal, birds might be expected to spread reproductive demands between stages until demands were equal at all points. The patterns of demands themselves might follow a trajectory towards such an optimal situation, but attainment of such a hypothetical 'ideal free' distribution of reproductive demands depends on the ability of the birds to spread demands between stages. Complete freedom to do this would seem unlikely, but there is evidence that even over considerable time scales, reproduction at one point can influence performance at a later date (Bell and Koufopanou 1986, Nur 1988, Roff 1992). The demands incurred by a first clutch can influence a bird's ability to reneest that season. Wandering albatrosses (*Diomedea exulans*) and royal albatrosses (*D. epomophora*) which breed successfully in one year are unlikely to breed in the next (Warham 1991). Elevated reproductive demands in one year can depress reproductive performance the following year (Roskaft 1985, Gustafsson and Sutherland 1988). It has been conventional to consider these costs of reproduction as operating between distinct reproductive bouts, and to view elevated current reproductive effort as a phenomenon which depresses future performance. It is however as fair to look for similar costs of reproduction which operate between stages of single reproductive bouts, and to consider tempered reproductive effort as a means of shouldering the demands of reproduction at a later stage. Increasing reproductive effort from say 'RE' to 'RE+c' may make birds less able to cope with 'N' offspring the next year, but similarly, one way in which a bird can cope with 'N' offspring the next year is to reduce current reproductive effort from 'RE+c' to 'RE'. The energetic strains of breeding can not be borne during breeding alone, but they can in part be borne some considerable time before. When birds can spread demands over such large time scales, it would seem reasonable that they could also spread them over stages within a single reproductive attempt.

Results

A basic model.

In this model, I assume that at all points 't' in the breeding season, birds hold a quantity of resources 'R_t' which can be allocated to fitness enhancing activities such as staying alive or producing/caring for offspring. If these critical fitness resources are nutritional or energetic, then 'R_t' could be equated roughly with body reserves. I propose that there is a critical level of resources below which it is not possible to drop without jeopardising adult survival. At any time 't', the level of resources held 'R_t' is a function of previous resources 'R_{t-1}', income (I_t), and expenditure (E_t), and can be described by a simple discrete-time linear model:

$$R_t = R_{t-1} + I_t - E_t \dots\dots\dots (1)$$

For breeding birds, I assume that income is independent of the number of offspring, but dependent on the time of year and the stage of the breeding season. Thus even if E_t is particularly high, then resource levels can still be sustained by timing the breeding attempt so that I_t is at its highest level. This of course has the consequence that I_{t-1} and I_{t+1} are lower and so less likely to offset E_{t-1} and E_{t+1}. Under these circumstances, resources would be more likely to drop to a critical level during 't-1' and 't+1', even though such problems are less likely during 't'.

If resources fall towards a critical level even when breeding is well timed, then expenditure must be cut back to preserve adult survival. Expenditure can be described as a function involving 3 components: the essential expenditure incurred were the bird not breeding at time 't' (E_{e,t}), the increment above this required for a minimal level of breeding at 't' (E_{b,t}), and an increasing function of the number of offspring at each stage (OF_t) with gradient 'k_t'. 'k_t' is the amount by which expenditure should increase to meet the requirements of each additional offspring:

$$E_t = E_{e,t} + E_{b,t} + (k_t \times OF_t) \dots\dots\dots (2)$$

These 2 equations can then be combined:

$$R_t = R_{t-1} + I_t - [E_{e,t} + E_{b,t} + (k_t \times OF_t)] \dots\dots\dots (3)$$

Thus if at any point in time, resources are approaching a critically low level, then the birds would be forced to cut back on the expenditure involved in breeding, and thus to reduce or neglect their clutch or brood. So, if there is a cost of breeding at any stage, and if the costs increase with the number of offspring, then the optimal clutch size will in part be an adaptation to the capacities of the parents during this stage.

During the next stage 't+1', it follows from equation (1) that the resource level at time t+1 is:

$$R_{t+1} = R_t + I_{t+1} - E_{t+1} \dots\dots\dots (4)$$

and from equations 2 and 3, this equates to:

$$R_{t+1} = R_t + I_{t+1} - [E_{e,t+1} + E_{b,t+1} + (k_{t+1} \times OF_{t+1})] \dots\dots\dots (5)$$

but further, from equation 3, we know that this equates to:

$$R_{t+1} = \{ R_{t-1} + I_t - [E_{e,t} + E_{b,t} + (k_t \times OF_t)] \} + I_{t+1} - [E_{e,t+1} + E_{b,t+1} + (k_{t+1} \times OF_{t+1})] \dots\dots\dots (6)$$

Thus, the level of resources held at time t+1 is a function not only of the number of offspring at time t+1 but also of the number of offspring at time t. So, unless energy expenditure is independent of the number of eggs incubated (i.e. $k_t = 0$), then the likelihood that resources will drop to a critically low level during chick-rearing depends not only on the number of chicks reared but on the number of eggs tended. Similarly the costs a bird can afford to incur during incubation depend on the costs it anticipates to suffer during chick rearing. Thus if $k_t > 0$ at several stages, then demands are spread over time and no one bottleneck exists.

Discussion

When are the demands truly clutch-size-dependent?

If the shifting of demands were unconstrained, and if it stopped only when the probability of intolerable deficit were equal at all stages, then it might at first seem that genes determining clutch size would be exposed to natural selection at all stages and that clutch size might become an adaptation to the capacities of the parents to produce or care for their offspring throughout the breeding season. If however the income and expenditure at any stage are both fully independent of clutch size, then even though the birds might face difficulties balancing their resource budgets at these times, there can be no selection on clutch size during that stage and clutch size can not become an adaptation to the parents' capacities during that stage. Physiologists formerly advocated no energetic cost to incubation (King 1973, Grant 1984), which would also imply the absence of clutch-size specific changes in incubation costs. Yom-Tov and Hilborn (1981) presented a theoretical model that identified incubation as an energetic bottleneck, but suggested that this bottleneck was independent of clutch size. More recently, energetic costs of incubation (Croxall 1982, Gabrielsen et al. 1991) and their dependence on clutch size (Biebach 1981, 1984, Haftorn and Reinertsen 1985, Coleman and Whittall 1988) have been found. Direct evidence of elevated expenditure with increased brood-sizes remains elusive (Bryant and Tatner 1988b, Bryant 1988) but since chick rearing entails the measurable maintenance and growth costs of chicks (Ricklefs and White 1981, Gabrielsen et al. 1992, Klaasen *et al.* 1992), it is not unreasonable to assume that energetic demands exist and that these depend on brood size. Recently, the brood size dependent costs of post-fledging care have been found to be important (Weathers and Sullivan 1989). Egg formation also entails measurable costs (Walsberg 1983, Grau 1984), though it may be possible to prolong egg formation itself and thus to maintain low demands at any point in time.

More measurements of the clutch-size-specific energy costs of egg formation, incubation, chick rearing, and post-fledging care would be useful, though these are by no means easy to obtain.

Addition of further variables to this model may improve realism but only at the price of intractability - especially since the model already presents 9 components which require empirical estimation. The two most important components of the model are: the ability of birds to spread demands over several stages; and the functions relating reproductive expenditure to the number of offspring at each stage. Observations which shed light on these two components would offer insights into the importance of different stages in the determination of avian clutch size. That many studies have found costs of reproduction indicates that reproductive effort at one stage can influence performance at a later date and that birds are often capable of spreading the demands of reproduction over several stages. Thus, if birds can spread these demands of reproduction over several stages - or if demands are 'ideally free' to move - so that resources held at one stage are strongly dependent on the resources held and the income/expenditure of resources at other stages, then the role of different stages in regulating clutch size depends largely on the way demands change with the number of offspring tended at that stage.

Acknowledgements

This work was supported by a Carnegie Postgraduate Scholarship to DLT.

References

- Ankney, C.D. and MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female lesser Snow Geese. *Auk* 95: 459-471.
- Bell, G. and Koufopanou, V. 1986. The cost of reproduction. *Oxford Surveys in Evolutionary Biology*. Vol 3. Eds. Dawkins, R. and Ridley, M. pp 83-131. Oxford University Press, Oxford.
- Bolton, M., Houston, D.C. and Monaghan, P. 1992. Nutritional constraints on egg formation in the lesser black backed gull: an experimental study. *J. Anim. Ecol.* 61:521-532.
- Biebach, H. 1981. Energetic cost of incubation on different clutch sizes in Starlings (*Sturnus vulgaris*). *Ardea* 69:141-142.
- Biebach, H. 1984. Effect of clutch size and time of day on the energy expenditure of incubating starlings *Sturnus vulgaris*. *Physiol. Zool.* 57:26-31.
- Brown, C.R. 1984. Resting metabolic rate and energetic cost of incubation in Macaroni Penguins *Eudyptes chrysopholus* and Rockhopper Penguins *E. chrysocome*. *Comp. Biochem. Physiol. A.* 77:345-350.
- Brown, C.R. 1988. Energy expenditure during incubation in four species of sub-antarctic burrowing petrels. *Ostrich* 59:67-70.
- Bryant, D.M. 1975. Breeding biology of house martin *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117: 180-216.

- Bryant,D.M. and Tatner,P. 1988a. Energetics of the annual cycle of Dippers *Cinclus cinclus*. Ibis 130:17-38.
- Bryant,D.M. and Tatner,P. 1988b. The costs of brood provisioning: effects of brood-size and food supply. Proc. Int. Orn. Congr. 364-379.
- Bryant,D.M. 1988. Energy expenditure and body mass changes as measures of reproductive costs in birds. Functional Ecology 2:23-34.
- Bryant,D.M. and Tatner,P. 1991. Intraspecies variation in avian energy expenditure: correlates and constraints. Ibis 133:236-245.
- Cody,M.L. 1966. A general theory of clutch size. Evolution 20:174-184.
- Coleman,R.M. and Whittall,R.D. 1988. Clutch size and the cost of incubation in the Bengalese finch (*Lonchura striata var. domestica*). Behav. Ecol. Sociobiol. 23:367-372.
- Croxall,J.P. 1982. Energy costs of incubation and moult in petrels and penguins. J.Anim.Ecol. 51:177-194.
- Dijkstra,C., Bult,A., Bijlsma,S., Daan,S., Meijer,T. and Zijlstra,M. 1990. Brood size manipulations in the Kestrel (*Falco tinunculus*): effects on offspring and adult survival. J.Anim.Ecol. 59:269-285.
- Drent,R.H. and Daan,S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.

- Freed, L.A. 1981. Loss of mass in breeding wrens: stress or adaptation?
Ecology 62:1179-1186.
- Gabrielsen, G.W., Mehlum, F., and Nagy, K. 1987. Daily energy expenditure and energy utilization of free-ranging Black-legged Kittiwakes.
Condor 89:126-132.
- Gabrielsen, G.W., Mehlum, F. and Karlsen, H.E. 1988. Thermoregulation in four species of arctic seabirds. J. Comp. Physiol. B 157: 703-708.
- Gabrielsen, G.W., Mehlum, F., Karlsen, H.E., Andresen, O., and Parker, H. 1991. Energy cost during incubation and thermoregulation in the female Common Eider *Somateria mollissima*. Norsk Polarinstitutt Skrifter 195:51-62.
- Gabrielsen, G.W., Klaassen, M. and Mehlum, F. 1992. Energetics of Black-legged Kittiwake *Rissa tridactyla* chicks. Ardea 80:29-40.
- Godfray, H.C.J., Partridge, L. and Harvey, P.H. 1991. Clutch size.
Ann Rev. Ecol. Syst. 22:409-429.
- Grant, G.S. 1984. Energy cost of incubation to the parent bird. in Whittow, G.C. and Rahn, H. (eds). Seabird Energetics. Plenum Press, New York.
- Grau, C.R. 1984. Egg formation. in Whittow, G.C. and Rahn, H. (eds). Seabird Energetics. Plenum Press, New York.
- Gustafsson, L. and Sutherland, W.J. 1988. The cost of reproduction in the Collared Flycatcher *Ficedula albicollis*. Nature 335:813-815.

- Haftorn, S. and Reinertsen, R.E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in free-living blue tits *Parus caeruleus*. *Auk* 102:470-478.
- King, J.R. 1973. Energetics of reproduction in birds. In 'Breeding Biology of Birds' Farner, D.S. (ed.). 78. Nat Acad. Sci. Washington D.C.
- Klaasen, M., Zwaan, B., Heslenfield, P., Lucas, P., and Luijckx, B. 1992. Growth rate associated changes in the energy requirements of tern chicks. *Ardea* 80:19-28.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89:302-352.
- Lessells, C.M. 1986. Brood size in Canada Geese: a manipulation experiment. *J. Anim. Ecol.* 55:669-689.
- Lifson, N. and McClintock, R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* 12:46-74.
- Lima, S.L. 1987. Clutch size in birds: a predation perspective. *Ecology* 68:1062-1070.
- Masman, D., Gordijn, M., Daan, S., and Dijkstra, C. 1986. Ecological energetics of the European Kestrel: Field estimates of energy intake through the year. *Ardea* 74: 24-39.
- Martin, T.E. 1987. Food as a limit on breeding birds: a life history perspective. *Ann. Rev. Ecol. Syst.* 18:453-487.

- Moller,A.P. 1993. Ectoparasites increase the costs of reproduction in their hosts.
J.Anim.Ecol. 62:309-322.
- Moreno,J. and Carlson,A. 1989. Clutch size and the cost of incubation in the Pied
Flycatcher *Ficedula hypoleuca*. *Ornis scand.* 20:123-128.
- Moreno,J., Gustafsson,L., Carlson,A. and Part,T. 1991. The cost of incubation
in relation to clutch-size in the Collared Flycatcher *Ficedula albicollis*.
Ibis 133: 186-193.
- Nur,N. 1984. The consequences of brood size for breeding blue tits: II.
Nestling weight, offspring survival and optimal brood size. *J. Anim.*
Ecol. 53: 497-517.
- Nur,N. 1988. The cost of reproduction in birds: An examination of the evidence.
Ardea 76:155-168.
- Partridge,L. 1989. Lifetime Reproductive Success and Life-history Evolution. in
Newton,I.(ed). *Lifetime Reproduction in Birds*. Academic Press,London.
- Perrins,C.M. 1965. Population fluctuations and clutch size in the great tit, *Parus*
major L. *J.Anim.Ecol.* 34:601-647.
- Perrins,C.M. and Birkhead,T.R. 1983. *Avian Ecology*. Blackie, Chapman and
Hall, New York.
- Ricklefs,R.E. and White,S.C. 1981. Growth and energetics of chicks of the Sooty
Tern (*Sterna fuscata*) and Common Tern (*S. hirundo*). *Auk* 98: 361-378.

- Roff,D.A. 1992. The Evolution of Life Histories. Theory and Analysis. Chapman and Hall, New York.
- Roskaft,E. 1985. The effect of enlarged brood-size on the future reproductive potential of the Rook. *J. Anim. Ecol.* 54:255-260.
- Slagsvold,T. 1982a. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54: 159-169.
- Slagsvold,T. 1982b. Clutch size, nest size, and hatching asynchrony in birds: experiments with the fieldfare (*Turdus pilaris*). *Ecology* 63:1389-1399.
- Slagsvold,T. 1989a. On the evolution of clutch size and nest size in passerine birds. *Oecologia* 79: 300-305.
- Slagsvold,T. 1989b. Experiments on clutch size and nest size in passerine birds. *Oecologia* 80: 297-302.
- Slagsvold,T. and Amundsen,T. 1992. Do great tits adjust hatching spread, egg size and offspring sex ratio to changes in clutch size?
J. Anim. Ecol. 61: 249-258.
- Speakman,J.R. and Racey,P.A. 1988. The doubly labelled water technique for measurement of energy expenditure in free-living animals.
Sci. Prog. Oxford 72: 227-237.
- Stearns,S.C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

- Szekely, T., Karsai, I., and Williams, T.D. 1994. Determination of clutch-size in the Kentish Plover *Charadrius alexandrinus*. *Ibis* 136:
- Tatner, P. and Bryant, D.M. 1989. The doubly labelled water technique for measuring energy expenditure. In Bridges, C.R. and Butler, P.J. (eds). *Techniques in Comparative Respiratory Physiology*. pp77-112. Cambridge University Press, Cambridge.
- Tatner, P. and Bryant, D.M. 1993. Interspecific variation in daily energy expenditure during avian incubation. *J.Zool.* 231(2):215-232.
- Van Balen, J.H. 1984. The relationship between nest-box size, occupation and breeding parameters of the great tit *Parus major* and some other hole-nesting birds. *Ardea* 72:163-175.
- Van der Werf, E. 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. *Ecology* 73:1699-1705.
- Walsberg, G.E. 1983. Avian Ecological Energetics. in Farner, D.S., King, J.R., and Parkes, K.C. (eds.). *Avian Biology*, vol VII. Academic Press, New York.
- Warham, J. 1991. *The petrels: their ecology and breeding systems*. Academic Press, London.
- Weathers, W.W. and Sullivan, K.A. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monog.* 59:223-246.

- Weeks,H.P. 1978. Clutch size variation in the eastern phoebe in Southern Indiana.
Auk 95:656-666.
- Wijnandts,H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*).
Ardea 72:1-92.
- Winkler,D.W. 1985. Factors determining a clutch size reduction in California Gulls
(*Larus californicus*): a multi-hypothesis approach. Evolution 39:667-677.
- Williams,J.B.1991. On the importance of energy considerations to small birds
with gynelateral intermittent incubation. Acta XX Congressus Internationalis
Ornithologici: 1964-1975.
- Yom-Tov,Y. and Hilborn,R. 1981. Energetic constraints on clutch size and time of
breeding in temperate zone birds. Oecologia 48:234-243.

Chapter 4

AVIAN CLUTCH SIZE AND THE DEMANDS OF INCUBATION

BY DAVID L. THOMSON, PAT MONAGHAN, AND
ROBERT W. FURNESS

*Applied Ornithology Unit,
Graham Kerr Building,
Glasgow University,
Glasgow G12 8QQ,
U.K.*

Clutch size and incubation demands

CONTENTS

- I. Introduction
- II. Methods
- III. Results
 - (1) The metabolic demand of incubation
 - (2) Does increased clutch size carry penalties during incubation?
 - (a) Clutch size and hatching success
 - (b) Clutch size and the duration of incubation
 - (c) Clutch size and adult energy expenditure
 - (d) Clutch size and parental body condition
- IV. Discussion
 - (1) The metabolic demand of incubation
 - (2) Clutch size and incubation demands
- V. Conclusions and implications of current data for further research
- VI. Summary
- VII. Acknowledgements
- VIII. References

I. INTRODUCTION

While avian clutch size may in part be adapted to the number of young the adults can feed (Lack, 1947a), other factors must be involved since enlarged broods can commonly be raised (Dijkstra *et al.*, 1990; Godfray *et al.*, 1991; Van der Werf, 1992). Clutch size-dependent demands incurred prior to the chick rearing period may influence the optimal clutch size (Nur, 1984, 1988; Partridge, 1989; Moreno *et al.*, 1991; Williams, 1991; Bolton *et al.*, 1992; Tatner & Bryant, 1993; Monaghan *et al.*, 1995), but earlier stages such as incubation have received relatively little attention.

The energetic demands of incubation could be important for clutch size, but previous reviews of physiological studies have reported only minor energetic demands of incubation under thermoneutral conditions, and it has been suggested that the insulation provided by the nest is so good that the metabolic rate of incubating birds (IMR) will often not exceed that of resting non-incubating birds (RMR) (King, 1973; Grant, 1984). If the relevant energetic demands really are so low then the incubation phase is unlikely to be of importance in the determination of clutch size. Results are however equivocal and important demands of incubation under the thermal conditions of the natural environment have recently been reported (Williams, 1991; Tatner & Bryant, 1993).

The purpose of this paper is therefore to review the literature on the metabolic demands of incubation and to examine the evidence that these demands can influence the evolution of avian clutch size. We look also for ecological and methodological factors which may account for discrepancies and contradictory results, and in bringing together the data available to date, we seek also to identify areas where more research would be valuable.

We have focused on two main issues. Firstly we assess the proportion of studies finding metabolic demands of incubation and we quantify the magnitude of these demands. Secondly, we review the evidence that an increase in the number of eggs incubated influences parental energy expenditure, body condition, incubation period, or the hatching success of the eggs.

II. METHODS

The results of 115 physiological and ecological studies were examined. By looking at whether incubation metabolic rate (IMR) was raised above the resting metabolic rate of non-incubating birds, we assessed the proportion of studies finding metabolic costs of incubation. We then assessed the magnitude of these metabolic demands in terms of basal metabolic rate (BMR), and looked at whether unusually high or low demands were peculiar to particular taxonomic, methodological or ecological circumstances.

To examine whether ambient temperature affected the energetic demands of incubation, we distinguished studies performed under strictly thermo-neutral conditions from those where temperature was less narrowly defined. Using studies involving a sufficient range of ambient temperatures, we also examined whether incubating birds showed normal patterns of thermoregulation or whether metabolic rate was elevated before temperatures dropped below the conventional lower critical temperature. Lastly, because indirect heat budget modelling makes assumptions about how different demands such as incubation and thermoregulation substitute or complement each other (e.g. Walsberg & King, 1978a,b; Mugaas & King, 1981) we compared results from these methods with those from more direct methods such as respirometry or doubly labelled water.

In examining whether the number of eggs incubated affected parental energy expenditure, hatching success, incubation duration, or parental mass loss, we used only studies which manipulated clutch size and thus removed potentially confounding effects of adult quality (Partridge, 1989; Roff, 1992). Birds may be physically incapable of covering unnaturally large clutches, and so we compared results obtained from manipulations of clutch size within the natural range with those where abnormally large clutches were created.

As well as varying with the methods employed, the importance of incubation demands may vary among particular groups of birds, depending on aspects of their ecology or phylogeny. Williams (1991) suggested that uniparental incubators unaided by their partners ('gynelateral intermittent incubators') may endure substantial metabolic demands of incubation. Moreno (1989) has demonstrated that species with self-feeding young are more likely to sacrifice body condition during incubation and would thus seem more willing to invest in incubation than those which must feed their young after hatching. Hole-nesting birds may be better insulated and have lower energy expenditure during incubation. Species with relatively heavier clutches may find them more costly to incubate. We therefore examined whether biologically important incubation demands might exist only under some of these specific circumstances.

We established the taxonomic order and family of each study species using Howard & Moore (1984). Where possible, we extracted the remaining information from the papers themselves, from the authors, or from standard reference works (Cramp & Simmons, 1977). Information conforming to Williams's (1991) strict definition of 'gynelateral intermittent incubation' was not always available and so we classified incubation habits as 'uniparental' or 'biparental'. We calculated 'relative clutch mass' by multiplying the average egg mass by the average clutch size, and dividing the product by the average mass of incubating birds.

We present results using each study as a single unit of observation, but provide also pooled results where multiple studies were performed on particular species. In no case did conclusions differ when pooled data were used. Different species were used in each study of hatching success and incubation duration, so no pooling was necessary in these cases.

III. RESULTS

The collated data are given in appendix I.

(1) *The metabolic demand of incubation*

On average, IMR was over 60% above basal metabolic rate (Table 1.). Under thermo-neutral conditions, IMR was little above BMR, but it was more than 70% greater than BMR where measurements were made under a wider range of temperatures (Table 1). From the data currently available, there is no evidence that relative clutch mass affects IMR ($F_{1,21}=0.59$, ns [data pooled for each species]). There were no other marked effects of either methodology or ecology on IMR/BMR, though all studies yielding estimates of IMR/BMR were performed on species where the adults feed the young (Table 1, Appendix I). Measures of IMR/BMR are available from four taxonomic orders - sphenisciforms (n=6 studies), procellariiforms (n=21), charadriiforms (n=1), and passeriforms (n=2). There is no evidence that either taxonomic order or taxonomic family account for any of the variance in IMR/BMR ($F_{2,25}=0.39$, ns; $F_{4,23}=0.66$, ns. [After controlling for whether measurements were made in the thermoneutral zone]).

Contrary to predictions (King, 1973), 15 of 38 studies reported incubation metabolic rates (IMR) in excess of the metabolic rate of resting non-incubating birds (RMR). [These elevated values averaged $1.25 \times \text{RMR}$ (s.e.=0.05) and so were not trivial]. Of the six studies carried out under strictly thermo-neutral conditions, none found IMRs in excess of RMR. IMRs above RMR were found across five taxonomic orders - sphenisciforms (n=6 out of 8 studies), procellariiforms (n=1/17), falconiforms (n=2/2), galliforms (n=2/2), and passeriforms (n=4/7). Taxonomic order had a significant impact (log-linear residual mean deviance=7.509, $df=2$, $P<0.05$) and in particular procellariiforms would seem to have an unusual incubation strategy compared with the other groups since 16 out of the 17 studies of procellariiforms found IMR below RMR. Otherwise the results are not markedly influenced by the methods used or by the ecology of the study species (Table 2), and there was no evidence that relative

clutch mass affected the probability that IMR was elevated above RMR (binomial $t_{22}=0.73$, ns.[data pooled for each species]).

Metabolic rates began to increase before the ambient temperature fell below the lower end of the conventional thermo-neutral zone in all of the six studies which looked at incubation demands over a sufficient range of temperatures. Elevated demands of thermoregulation within the conventional thermoneutral zone indicated that the lower critical temperature was elevated in incubating birds.

(2) Does increased clutch size carry penalties during incubation?

(a) Clutch size and hatching success

Of the 16 studies where clutch size was enlarged, nine reported a significant reduction in the percentage of eggs hatching. We know of no studies which have increased clutch size experimentally and found an increase in the percentage of eggs hatching. Reductions in hatching success were found in four orders: procellariiforms (n=1/1 study), pelecaniiforms (n=1/2), charadriiforms (n=1/1), and passeriforms (n=3/6). There was no evidence that relative clutch mass was particularly high in those studies where hatching success was reduced, indeed it was non-significantly lower. Significant reductions in hatching success were found even where clutches were manipulated within the natural range and were found among studies irrespective of the ecological factors considered (Table 3).

(b) Clutch size and the duration of incubation

Of the seven studies that considered the relationship between clutch size and the duration of incubation, six found that larger clutches took longer to incubate. These effects were found across three taxonomic orders - pelecaniiforms, charadriiforms, and passeriforms.

(c) Clutch size and adult energy expenditure

Larger clutches were not accommodated effortlessly. Out of nine studies, eight have reported evidence of elevated energy expenditure with increased clutch size. (All these studies used clutch sizes within the natural range.) All nine studies were performed on passerines, and so more work on the clutch-size-specific demands of incubation in a wider range of species would be valuable. Seven species were represented in these studies, and effects of clutch size on adult expenditure were found at least once in each species.

(d) Clutch size and parental body condition

Only three studies on only two passerines considered the influence of clutch size on adult body condition, but two found higher loss of condition with bigger clutches. In both species, effects of clutch size on condition were found at least once.

IV. DISCUSSION

(1) *The metabolic demand of incubation*

In accord with others who have focused specifically on the physiological demands of incubation (King, 1973; Grant, 1984), the results we reviewed indicated only minor demands within the thermoneutral zone. Under thermo-neutral conditions, IMR is only just above the basal metabolic rate, and is either equal to or below the metabolic rate of resting non-incubating birds.

However, for ecological questions about clutch size evolution, the emphasis is less physiological and the relevant demands are markedly higher. When the metabolic rates of incubating birds were measured in a more natural environment rather than under strictly thermo-neutral conditions, there was a highly significant nine-fold difference in the increment above basal levels, and contrary to physiological predictions (King, 1973) a number of studies found IMR elevated above resting levels. King's prediction was borne out under thermo-neutral conditions, and in the special case of

procellariiforms which have unusually low temperatures of incubation (Warham, 1991), but not for other taxonomic groups under wider conditions.

The demands of incubation and the demands of thermoregulation may be closely connected with each other as well as with ambient temperature. The data indicate that in incubating birds, the lower critical temperature is shifted upwards, and elevated expenditure is required even at temperatures that would normally fall within the thermo-neutral zone. The most ecologically meaningful setting for measuring the demands of incubation is the natural environment, and important discrepancies may arise if narrowly defined conditions are used instead.

(2) *Clutch size and incubation demands*

Even within the natural range of clutch sizes and across species with diverse ecologies, there is evidence that the percentage of eggs hatching can decline significantly with increasing clutch size. We were unable to determine why half the studies found no relationship between clutch size and hatching success, while the other half found that hatching success was reduced when clutch size was enlarged. The data indicate that often the demands of incubation are neither negligible nor independent of clutch size.

The precise cause of reduced hatching success is not clear from the data available and several proximate factors may be involved. Results reviewed here indicate that energy expenditure generally increases with clutch size during incubation. The results also indicate that the demands of larger clutches can depress adult body condition. In combination with the longer period required to incubate larger clutches, these increased demands, depressed condition, and prolonged exposure, may entail greater risks of nest predation and higher chances of failure.

V. CONCLUSIONS AND IMPLICATIONS OF CURRENT DATA FOR FURTHER RESEARCH

Results available to date point to various unanswered questions, and to groups of birds which might merit greater attention. Although we have identified some significant methodological and ecological variables, it would be valuable to know more about why incubation appears to be costly under some circumstances but not under others. Since all studies of both the clutch-size-specific metabolic demands of incubation and the effects of clutch size on body condition have been performed on passerines, it may be instructive to look at other taxonomic groups. More measurements of IMR/BMR among uniparentally incubating species and among species with self-feeding young may be illuminating. More studies of whether IMR exceeds RMR, particularly among species with self-feeding young, might permit the identification of other factors which influence this.

The data also indicate that results obtained under one set of conditions or among one set of birds can not necessarily be extrapolated to wider circumstances. In particular, studies performed in the thermoneutral zone have little relevance to species which commonly incubate outwith the thermoneutral zone, and results obtained from procellariiforms may be anomalous.

The most important implication of the results currently available stems from our overall conclusion that the demands of incubation can be important in the determination of clutch size.

VI. SUMMARY

We reviewed information on the demands of incubation to examine whether these could influence the optimal clutch size of birds. The results indicate that there are commonly appreciable metabolic costs of incubation, and that the incubation of enlarged clutches imposes penalties on birds.

Contrary to physiological predictions, incubation metabolic rate (IMR) was elevated above the metabolic rate of resting non-incubating birds (RMR) in 15 of 38 studies, and was often substantially above basal metabolic rate (BMR), averaging $1.64 \times$ BMR. Of six studies performed under thermo-neutral conditions, none found IMR to be in excess of RMR, and IMRs measured exclusively within the thermo-neutral zone averaged only $1.08 \times$ BMR contrasting with the much higher figure of $1.75 \times$ BMR under wider conditions. 16 of 17 studies on procellariiforms found IMR below RMR, indicating a significant difference between this and other orders. We could find no other methodological, ecological, or taxonomic factors which had clear effects on IMR.

Where clutch size was adjusted experimentally during incubation, larger clutches were associated with: significantly lower percentage hatching success in eight of 15 studies; longer incubation periods in six of seven studies; greater loss of adult body condition in two of three studies; and higher adult energy expenditure in eight of nine studies.

We propose that the demands of incubation can be appreciable and can influence the optimal clutch size of birds.

VII. ACKNOWLEDGEMENTS

This work was supported by a Postgraduate Scholarship from the Carnegie Trust for the Universities of Scotland to DLT. Bernie Zonfrillo and Phil Whitfield helped us with information about the species considered.

VIII. REFERENCES

- ANDERSSON, M. (1976). Clutch size in the Long-tailed Skua *Stercorarius longicaudus*: some field experiments. *Ibis* **118**, 586-588.
- BALTZ, M. E. & THOMPSON, C. F. (1988). Successful incubation of experimentally enlarged clutches by house wrens. *Wilson Bulletin* **100**, 70-79.
- BIEBACH, H. (1981). Energetic cost of incubation on different clutch sizes in Starlings (*Sturnus vulgaris*). *Ardea* **69**, 141-142.
- BIEBACH, H. (1984). Effect of clutch size and time of day on the energy expenditure of incubating starlings *Sturnus vulgaris*. *Physiological Zoology* **57**, 26-31.
- BIEBACH, H. (1986). Energetics of rewarming a clutch in Starlings (*Sturnus vulgaris*). *Physiological Zoology* **59**, 69-75.
- BLAGOSKLONOV, K. N. (1977). Experimental analysis of the rhythm of incubation in the pied flycatcher (*Ficedula hypoleuca*). *Soviet Journal of Ecology* **8**, 340-344.
- BOLTON, M., HOUSTON, D. C. & MONAGHAN, P. (1992). Nutritional constraints on egg formation in the lesser black backed gull: an experimental study. *Journal of Animal Ecology* **61**, 521-532.
- BRISKIE, J. V. & SEALY, S. G. (1989). Determination of clutch size in the Least Flycatcher. *Auk* **106**, 269-278.

- BROWN, C. R. & ADAMS, N. J. (1984). Basal metabolic rate and energy expenditure during incubation in the Wandering Albatross *Diomedea exulans*. *Condor* **86**, 182-186.
- BROWN, C. R. (1984). Resting metabolic rate and energetic cost of incubation in Macaroni Penguins *Eudyptes chrysopholus* and Rockhopper Penguins *E. chrysocome*. *Comparative Biochemistry and Physiology A*. **77**, 345-350.
- BROWN, C. R. (1988). Energy expenditure during incubation in four species of sub-antarctic burrowing petrels. *Ostrich* **59**, 67-70.
- BRYANT, D. M. & TATNER, P. (1988). The costs of brood provisioning: effects of brood-size and food supply. *Acta XIX Congressus Internationalis Ornithologici* 364-379.
- BRYANT, D. M. & TATNER, P. (1988). Energetics of the annual cycle of Dippers *Cinclus cinclus*. *Ibis* **130**, 17-38.
- COLEMAN, R. M. & WHITTALL, R. D. (1988). Clutch size and the cost of incubation in the Bengalese finch (*Lonchura striata var. domestica*). *Behavioural Ecology Sociobiology* **23**, 367-372.
- CRAMP, S. & SIMMONS, K. E. L. (ed.). (1977). *Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Vol. I. Ostrich to Ducks*. Oxford University Press.
- CROXALL, J. P. (1982). Energy costs of incubation and moult in petrels and penguins. *Journal of Animal Ecology* **51**, 177-194.

- CROXALL, J. P. & RICKETTS, C. (1983). Energy cost of incubation in the Wandering Albatross *Diomedea exulans*. *Ibis* **125**, 33-39.
- DIJKSTRA, C., BULT, A., BIJLSMA, S., DAAN, S., MEIJER, T. & ZIJLSTRA, M. (1990). Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and adult survival. *Journal of Animal Ecology* **59**, 269-285.
- DAAN, S., DIJKSTRA, C., DRENT, R., & MEIJER, T. (1988). Food Supply and the Annual Timing of Avian Reproduction. *Acta XIX Congressus Internationalis Ornithologici* 392-407.
- ETTINGER, A. D. & KING, J. R. (1980). Time and energy budgets of the Willow Flycatcher (*Empidonax traillii*) during the breeding season. *Auk* **97**, 533-546.
- FLINT, E. N. & NAGY, K. A. (1984). Flight energetics of free-living Sooty Terns. *Auk* **101**, 288-294.
- FREDRICKSON, L. H. (1969). An experimental study of clutch-size of the American Coot. *Auk* **86**, 541-550.
- GABRIELSEN, G. W., MEHLUM, F., KARLSEN, H. E., ANDRESEN, O., & PARKER, H. (1991). Energy cost during incubation and thermoregulation in the female Common Eider *Somateria mollissima*. *Norsk Polarinstitutt Skrifter* **195**, 51-62.
- GABRIELSEN, G. W. & UNANDER, S. (1987). Energy cost during incubation in Svalbard and Willow Ptarmigan hens. *Polar Research* **5**, 59-69.

- GALES, R. & GREEN, B. (1990). The annual energetics cycle of little penguins *Eudyptula minor*. *Ecology* **71**, 2297-2312.
- GESSAMAN, J. A. & FINDELL, P. R. (1979). Energy cost of incubation in the American Kestrel. *Comparative Biochemistry and Physiology A* **63**, 57-62.
- GODFRAY, H. C. J., PARTRIDGE, L. & HARVEY, P. H. (1991). Clutch size. *Annual Review of Ecology and Systematics* **22**, 409-429.
- GRANT, G. S. (1984). Energy cost of incubation to the parent bird. in *Seabird Energetics* (ed. G. C. Whittow and H. Rahn). Plenum Press, New York.
- GRANT, G. S. & WHITTOW, G. C. (1983). Metabolic cost of incubation in the Laysan Albatross and Bonin Petrel. *Comparative Biochemistry and Physiology A* **74**, 77-82.
- HAMILTON, K. L. & GESSAMAN, J. A. (1981). Energetic cost of incubation of the Barn Owl: a preliminary report. *American Zoologist* **21**, 964.
- HARRIS, M. P. (1964). Aspects of the breeding biology of the gulls *Larus argentatus*, *L. fuscus*, and *L. marinus*. *Ibis* **106**, 432-456.
- HAFTORN, S. & REINERTSEN, R. E. (1985). The effect of temperature and clutch size on the energetic cost of incubation in free-living blue tits *Parus caeruleus*. *Auk* **102**, 470-478.
- HEPP, G. R., KENNAMER, R. A., & HARVEY, W. F. IV. (1990). Incubation as a reproductive cost in female Wood Ducks. *Auk* **107**, 756-764.

- HILDEN, O. (1964). Ecology of Duck populations in the island group of Valassaaret, Gulf of Bothnia. *Annales Zoologici Fennici* **1**, 153-277.
- HILLS, S. (1980). Incubation capacity as a limiting factor of a shorebird clutch size. *American Zoologist* **20**, 774.
- HILLS, S. (1983). *Incubation capacity as a limiting factor of shorebird clutch size*. Msc Thesis, University of Washington.
- HOWARD, R. & MOORE, A. (1984). *A complete checklist of the Birds of the World*. Macmillen, London.
- JARVIS, M. J. F. (1974). The ecological significance of clutch size in the South African gannet *Sula capensis* (Lichtenstein). *Journal of Animal Ecology* **43**, 1-17.
- JONES, G. (1987). Time and energy constraints during incubation in free-living Swallows (*Hirundo rustica*): an experimental study using precision electronic balances. *Journal of Animal Ecology* **56**, 229-245.
- KING, J. R. (1973). Energetics of reproduction in birds. In *Breeding Biology of Birds* (ed. D. S. Farner). p.78. National Academy of Sciences. Washington D.C.
- LACK, D. (1947a). The significance of clutch size. *Ibis* **89**, 302-352.
- LACK, D. (1947b). The significance of clutch size in the partridge (*Perdix perdix*). *Journal of Animal Ecology* **16**, 19-25.

- MASMAN, D., DAAN, S. & BELDHUIS, H. J. A. (1988). Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly-labelled water methods. *Ardea* **76**, 65-81.
- MERTENS, J. A. L. (1977). The energy requirements for incubation in great tits, *Parus major* L. *Ardea* **65**, 184-196.
- MERTENS, J. A. L. (1980). The energy requirements for incubation in great tits and other bird species. *Ardea* **68**, 185-192.
- MONAGHAN, P., BOLTON, M. & HOUSTON, D.C. (1995). Egg production constraints and the evolution of avian clutch size. *Proceedings of the Royal Society of London, Series B.* **259**, 189-191.
- MORENO, J. (1989). Strategies of mass change in breeding birds. *Biological Journal of the Linnean Society* **37**, 297-310.
- MORENO, J. & CARLSON, A. (1989). Clutch size and the cost of incubation in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis scandinavica* **20**, 123-128.
- MORENO, J., GUSTAFSSON, L., CARLSON, A. & PART, T. (1991). The cost of incubation in relation to clutch-size in the Collared Flycatcher *Ficedula albicollis*. *Ibis* **133**, 186-193.
- MORENO, J. & SANZ, J. J. (1994). The relationship between the energy expenditure during incubation and clutch size in the Pied Flycatcher *Ficedula hypoleuca*. *Journal of Avian Biology* **25**, 125-130.

- MUGAAS, J. N. & KING, J. R. (1981). *Annual variation of Daily Energy Expenditure in the Black-billed Magpie: A Study of Thermal and Behavioural Energetics*. Studies in Avian Biology No.5. Cooper Ornithological Society.
- NELSON, J. B. (1964). Factors influencing clutch-size and chick growth in the north Atlantic gannet *Sula bassana*. *Ibis* **106**, 63-77.
- NORMAN, F. I. & GOTTSCH, M. D. (1969). Artificial twinning in the short-tailed shearwater *Puffinus tenuirostris*. *Ibis* **111**, 391-393.
- NUR, N. (1984). The consequences of brood size for breeding Blue Tits II. Nestling weight, offspring survival and optimal brood size. *Journal of Animal Ecology* **53**, 497-517.
- NUR, N. (1988). The consequences of brood size for breeding blue tits. III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. *Evolution* **42**, 351-362.
- OBST, B. S., NAGY, K. A. & RICKLEFS, R. E. (1987). Energy utilization by Wilson's Storm-Petrel (*Oceanites oceanicus*). *Physiological Zoology* **60**, 200-210.
- PARTRIDGE, L. (1989). Lifetime Reproductive Success and Life-history Evolution. In *Lifetime Reproduction in Birds*. (ed. Newton, I.). Academic Press, London.
- PARTRIDGE, L. (1992). Measuring Reproductive Costs. *Trends in Ecology and Evolution* **7**, 99-100.
- PAYNTER, R. A. (1949). Clutch size and the egg and chick mortality of Kent Island Herring Gulls. *Ecology* **30**, 146-166.

- PIERSMA, T. & MORRISON, R. I. G. (1994). Energy expenditure and water turnover of incubating ruddy turnstones: high costs under high arctic climatic conditions. *Auk* **111**, 366-376.
- PETTIT, T. N., NAGY, K. A., ELLIS, H. T. & WHITTOW, G. C. (1988). Incubation energetics of the Laysan Albatross. *Oecologia* **74**, 546-550.
- REZNICK, D. (1985). Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**, 257-267.
- REZNICK, D. (1992). Measuring the Costs of Reproduction. *Trends in Ecology and Evolution* **7**, 42-45.
- RICKLEFS, R. E. & WILLIAMS, J. B. (1984). Daily energy expenditure and water turnover rate of adult European starlings (*Sturnus vulgaris*) during the nesting cycle. *Auk* **101**, 707-716.
- RICKLEFS, R. E., ROBY, D. D., & WILLIAMS, J. B. (1986). Daily energy expenditure by adult Leach's Storm Petrels during the nesting cycle. *Physiological Zoology* **59**, 649-660.
- SIKAMAKI, P. (1995). Are large clutches costly to incubate - the case of the Pied Flycatcher. *Journal of Avian Biology* **26**, 76-80.
- SMITH, H. G. (1989). Larger clutches take longer to incubate. *Ornis Scandinavica* **20**, 156-158.
- SNOW, D. W. (1958). The breeding of the Blackbird, *Turdus merula*, at Oxford. *Ibis* **100**, 1-30.

- SZEKELY, T., KARSAI, I., & WILLIAMS, T. D. (1994). Determination of clutch-size in the Kentish Plover *Charadrius alexandrinus*. *Ibis* **136**, 341-248.
- TARBURTON, M. K. (1987). An experimental manipulation of clutch and brood size of White-rumped Swiftlets *Aerodramus spodiopygius* of Fiji. *Ibis* **129**, 107-114.
- TATNER, P. & BRYANT, D.M. (1993). Interspecific variation in daily energy expenditure during avian incubation. *Journal of Zoology* **231**, 215-232.
- VAN DER WERF, E. (1992). Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. *Ecology* **73**, 1699-1705.
- VLECK, C. (1981). Energetic cost of incubation in the zebra finch. *Condor* **83**, 229-239.
- WALSBERG, G.E. & KING, J.R. (1978a). The energetic consequences of incubation for two passerine species. *Auk* **95**, 644-655.
- WALSBERG, G.E. & KING, J.R. (1978b). The heat budget of incubating mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. *Physiological Zoology* **51**, 92-103
- WARHAM, J. (1991). *The petrels: their ecology and breeding systems*. Academic Press, London.
- WEATHERS, W. W. (1985). Energy cost of incubation in the canary. *Comparative Biochemistry and Physiology A*. **81**, 411-413.

- WEATHERS, W. W. & SULLIVAN, K. A. (1989). Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs* **59**, 223-246.
- WESTERTERP, K. R. & BRYANT, D. M. (1984). Energetics of free-existence in Swallows and martins (Hirundinidae) during breeding: a comparative study using doubly labelled water. *Oecologia* **62**, 376-381.
- WESTERTERP, K. R. & DRENT, R. H. (1985). Energetic costs and energy saving mechanisms in parental care of free-living passerine birds as determined by the D₂¹⁸O method. *Acta XVIII Congressus Internationalis Ornithologicii*. pp. 392-399. (ed. Ilyichev, V.D. and Gavrilov, V.M.). Moscow, Nauka.
- WILLIAMS, J. B. (1987). Field metabolism and food consumption of Savannah Sparrows during the breeding season. *Auk* **104**, 277-289.
- WILLIAMS, J. B. (1988). Field metabolism of tree swallows during the breeding season. *Auk* **105**, 706-714.
- WILLIAMS, J. B. (1991). On the importance of energy considerations to small birds with gynelateral intermittent incubation. *Acta XX Congressus Internationalis Ornithologicii*: 1964-1975.
- WILLIAMS, J. B. (1993). Energetics of incubation in free-living orange-breasted sunbirds in South Africa. *Condor* **95**, 115-126

Table 1. Incubation metabolic rate in terms of basal metabolic rate, splitting results according to methodology and species ecology. Results are not split according to whether the young are self-feeding because all studies presenting IMR in terms of BMR were performed on species where the adults feed the young after hatching. Results from pooling data for each species are given in square brackets.

	IMR/BMR	Statistics
All studies	1.636 (n=30, se=0.08) [1.606 (n=26, se=0.08)]	
Temperature within thermoneutral zone.	1.080(n=5, se=0.08) [1.000(n=4, se=0)]	F _{1,27} =13.84, p<0.001 [F _{1,23} =15.18, p<0.001]
Costs measured over a wider range	1.753(n=24, se=0.08) [1.720(n=21, se=0.08)]	
Costs determined directly	1.618(n=28, se=0.08) [1.594(n=25, se=0.08)]	F _{1,28} =0.72, ns [F _{1,24} =0.54, ns]
Costs calculated from heat budget models	1.895(n=2) [1.895(n=1)]	
Uniparental incubation	1.717(n=3) [1.625(n=2)]	F _{1,28} =0.14, ns [F _{1,24} =0.03, ns]
Biparental incubation	1.627(n=27, se=0.08) [1.604(n=24, se=0.09)]	
Cavity-nester	1.622(n=17, se=0.13) [1.551(n=15, se=0.13)]	F _{1,28} =0.42, ns [F _{1,22} =0.03, ns]
Open-nester	1.655(n=13, se=0.07) [1.681(n=11, se=0.08)]	

Table 2. Frequencies of studies which have found a metabolic cost of incubation above resting levels. Results are split according to the methodology of the study and the ecology of the species. Results pooling data for each species are shown in square brackets.

	Frequency of IMR>RMR	Frequency of IMR<=RMR
All studies	15 [15]	23 [19]
Costs measured in thermoneutral zone	0 [0]	6 [3]
Costs measured under wider thermal conditions	15 [15]	17 [16]
Costs calculated from heat budget models.	1 [1]	3 [3]
Costs calculated directly	14 [14]	20 [16]
Self-feeding young	2 [2]	1 [1]
Young fed by parents	13 [13]	22 [18]
Uniparental	6 [6]	5 [4]
Biparental	9 [9]	18 [15]
Cavity-nester	4 [4]	11 [11]
Open-nester	11 [11]	12 [8]

Table 3. Frequencies of studies which have reported a reduction in the percentage of eggs hatching, when clutch size is enlarged. The data are further split according to the experimental technique and various ecological aspects of the study species. The fifteen studies concerned were all performed on different species, so no pooled values for individual species are given.

	% hatching success significantly reduced in enlarged clutches.	No difference detected in % hatching success.
All studies	8	7
Clutch enlarged within natural range	2	3
Clutch enlarged above natural max.	6	4
Uniparental incubation	2	3
Biparental incubation	6	4
Self-feeding chicks	3	2
Chicks fed by parents	5	5
Cavity nesting species	2	3
Open nesting species	6	4

Appendix I.

Results of the following studies are set out under the following column headings:

1. Whether the study used natural variance(2), clutch size manipulations(1), or whether there was no consideration of clutch size(0).
2. Whether hatching success declined with increased clutch size(-1), showed no detectable difference(0), or increased with clutch size(1).
3. Whether metabolism increased with clutch size(1) or not(0).
4. Whether ambient temperature was exclusively within the thermo-neutral zone(1) or not(0).
5. Sample size.
6. Incubation metabolic rate(IMR) as a multiple of BMR
7. IMR as a multiple of RMR.
8. Field metabolic rate during incubation(FIMR) as a multiple of BMR.
9. FIMR as a multiple of RMR.
10. Whether incubation is uniparental(1) or biparental(2).
11. Whether study was performed in the natural thermal environment(1) or not(0).
12. Whether the thermoneutral zone showed a shift due to incubation(1) or not(0).
13. Whether the duration of incubation increases with clutch size(1) or not(0).
14. Whether declining adult body condition is greater with increasing clutch size(1) or not(0).
15. Whether costs were calculated directly(1) or indirectly(2).
16. Whether clutch size was(1) or was not(0) increased above the natural maximum.
17. Whether chicks are fed by the adults(1) or not(0).
18. Whether the species is a cavity-nester(1) or an open nester(0).
19. Mean body weight
20. Mean clutch size
21. Relative clutch mass (Clutch mass/body mass).
22. Reference.

<i>Aptenodytes patagonica</i>	0	*	*	0	31	2.03	1.56	*	*	2	1	*	*	1	1	0	12662.0	1.0	0.02	Croxall 1982
<i>Aptenodytes forsteri</i>	0	*	*	0	1	1.36	1.17	*	*	1	1	*	*	1	1	0	24800.0	1.0	0.02	Croxall 1982
<i>Fygoscalis papua</i>	0	*	*	0	10	2.10	1.38	*	*	2	1	*	*	1	1	0	6290.0	2.0	0.04	Croxall 1982
<i>Fygoscalis adeliae</i>	0	*	*	0	92	1.75	1.07	*	*	2	1	*	*	1	1	0	3970.0	2.0	0.06	Croxall 1982
<i>Fygoscalis antarctica</i>	0	*	*	0	25	1.97	1.18	*	*	2	1	*	*	1	1	0	*	2.0	*	Croxall 1982
<i>Eudyptes chrysolophus</i>	0	*	*	0	38	1.67	1.03	*	*	2	1	*	*	1	1	0	3779.0	2.0	0.08	Croxall 1982
<i>Eudyptes chrysolophus</i>	0	*	*	1	5	*	0.69	*	*	2	0	*	*	1	1	0	3820.0	2.0	0.08	Brown 1984
<i>Eudyptes chrysocome</i>	0	*	*	1	5	*	0.74	*	*	2	0	*	*	1	1	0	*	2.0	*	Brown 1984
<i>Eudyptula minor</i>	0	*	*	0	3	*	*	2.00	1.15	2	1	*	*	1	1	1	960.0	2.0	0.11	Gales & Green 1990
<i>Diomedea exulans</i>	0	*	*	0	19	1.60	0.80	*	*	2	1	*	*	1	1	0	7686.0	1.0	0.06	Croxall & Ricketts 1983
<i>Diomedea exulans</i>	0	*	*	1	5	1.40	*	*	*	2	1	*	*	1	1	0	7686.0	1.0	0.06	Brown & Adams 1984
<i>Diomedea exulans</i>	0	*	*	0	19	1.55	1.10	*	*	2	1	*	*	1	1	0	7686.0	1.0	0.06	Croxall 1982
<i>Diomedea immutabilis</i>	0	*	*	1	4	*	<1.0	*	*	2	0	*	*	1	1	0	2990.0	1.0	0.10	Grant & Whitton 1983
<i>Diomedea immutabilis</i>	0	*	*	1	8	*	1.00	*	*	2	1	*	*	1	1	0	2990.0	1.0	0.10	Pettit et al. 1988
<i>Diomedea immutabilis</i>	0	*	*	0	77	1.39	0.80	*	*	2	1	*	*	1	1	0	2990.0	1.0	0.10	Croxall 1982
<i>Diomedea melanophris</i>	0	*	*	0	213	1.55	0.94	*	*	2	1	*	*	1	1	0	3694.0	1.0	0.07	Croxall 1982
<i>Diomedea chrysostoma</i>	0	*	*	0	216	1.53	0.92	*	*	2	1	*	*	1	1	0	3624.0	1.0	0.08	Croxall 1982
<i>Pterodroma macroptera</i>	0	*	*	1	5	1.00	*	*	*	2	1	*	*	1	1	1	555.0	1.0	0.15	Brown 1988
<i>Pterodroma macroptera</i>	0	*	*	0	41	1.03	0.44	*	*	2	1	*	*	1	1	1	555.0	1.0	0.15	Croxall 1982
<i>Pterodroma inexpectata</i>	0	*	*	0	1	1.42	0.54	*	*	2	1	*	*	1	1	1	329.0	1.0	0.19	Croxall 1982
<i>Lugensa brevirostris</i>	0	*	*	1	3	1.00	*	*	*	2	1	*	*	1	1	1	331.0	1.0	0.17	Brown 1988
<i>Pterodroma phaseopygia</i>	0	*	*	0	1	2.38	0.92	*	*	2	1	*	*	1	1	1	425.0	1.0	*	Croxall 1982
<i>Pterodroma hypoleuca</i>	0	*	*	1	2	*	<1.0	*	*	2	0	*	*	1	1	1	176.0	1.0	0.22	Grant & Whitton 1983
<i>Pterodroma pycrofti</i>	0	*	*	0	1	1.50	0.51	*	*	2	1	*	*	1	1	1	183.0	1.0	0.17	Croxall 1982
<i>Halobaena caerulea</i>	0	*	*	1	2	1.00	*	*	*	2	1	*	*	1	1	1	202.0	1.0	0.19	Brown 1988
<i>Procellaria aequinoctialis</i>	0	*	*	1	2	1.00	*	*	*	2	1	*	*	1	1	1	1280.0	1.0	0.10	Brown 1988
<i>Puffinus tenuirostris</i>	1	-1	*	20	*	*	*	*	*	2	1	*	*	1	1	1	634.0	1.0	0.14	Norman & Gottsch 1969
<i>Puffinus puffinus</i>	0	*	*	0	62	1.76	0.70	*	*	2	1	*	*	1	1	1	469.0	1.0	0.12	Croxall 1982
<i>Puffinus lherminieri</i>	0	*	*	0	1	2.07	0.68	*	*	2	1	*	*	1	1	1	163.0	1.0	0.18	Croxall 1982
<i>Oceanites oceanicus</i>	0	*	*	0	4	2.62	0.70	*	*	2	1	*	*	1	1	1	40.0	1.0	0.28	Croxall 1982
<i>Oceanites oceanicus</i>	0	*	*	0	5	2.20	*	3.20	*	2	1	*	*	1	1	1	40.0	1.0	0.28	Obst et al. 1987
<i>Fregata tropica</i>	0	*	*	0	6	1.90	0.53	*	*	2	1	*	*	1	1	1	56.5	1.0	0.27	Croxall 1982
<i>Oceanodroma castro</i>	0	*	*	0	1	1.71	0.40	*	*	2	1	*	*	1	1	1	41.8	1.0	0.20	Croxall 1982

Oceanodroma leucorhoa	0	*	*	0	12	1.19	*	*	*	2	1	*	*	*	1	*	1	1	44.9	1.0	0.20	Ricklefs et al. 1986
Sula capensis	1	-1	*	*	149	*	*	*	*	*	2	1	*	*	*	0	1	0	2660.0	1.0	0.04	Jarvis 1974
Sula bassana	1	0	*	*	17	*	*	*	*	*	2	1	*	*	1	1	0	3067.0	1.0	0.03	Nelson 1964	
Aix sponsa	2	*	*	*	150	*	*	*	*	*	*	1	1	*	*	0	1	469.0	12.0	*	Hepp et al. 1990	
Aythya fuligula	2	-1	*	0	111	*	*	*	*	*	*	1	1	*	*	*	0	680.0	9.5	0.74	Hilden 1964	
Aythya marila	2	-1	*	0	62	*	*	*	*	*	*	1	1	*	*	*	0	883.0	9.5	0.66	Hilden 1964	
Somateria mollissima	0	*	*	1	2	*	<1.0	*	*	*	1	0	*	*	1	*	0	1915.0	3.0	0.17	Gabrielsen et al. 1991	
Falco sparverius	0	*	*	0	3	*	1.20	*	*	*	2	0	*	*	1	*	1	117.0	4.5	*	Gessaman&Findell 1979	
Falco tinnunculus	0	*	*	0	2	*	1.23	*	*	*	1	1	*	*	2	1	0	193.0	3.8	0.32	Masman et al. 1988	
Lagopus lagopus lagopus	0	*	*	0	5	*	1.21	*	*	*	1	1	1	*	*	0	0	517.0	9.8	0.42	Gabrielsen&Unander1987	
Lagopus mutus hyperboreus	0	*	*	0	4	*	1.16	*	*	*	1	1	1	*	*	0	0	461.0	6.6	0.34	Gabrielsen&Unander1987	
Fulica americana	1	0	*	0	384	*	*	*	*	*	2	1	*	*	*	1	1	0	*	9.0	*	Fredrickson 1969
Charadrius hiaticula	0	*	*	0	4	*	*	6.55	*	*	2	1	*	*	*	1	0	0	63.6	3.8	0.72	Tatner & Bryant 1993
Charadrius alexandrinus	1	0	*	*	72	*	*	*	*	*	2	1	*	1	*	1	0	0	47.1	3.0	0.57	Szekely et al. 1994
Calidris mauri	1	-1	*	0	36	*	*	*	*	*	2	1	*	*	*	1	0	0	25.6	4.0	1.17	Hills 1983
Calidris pusilla	1	0	*	0	12	*	*	*	*	*	2	1	*	*	*	1	0	0	26.0	4.0	1.06	Hills 1983
Calidris alpina	1	-1	*	0	12	*	*	*	*	*	2	1	*	*	*	1	0	0	43.2	4.0	0.93	Hills 1983
Limnodromus scolopaceus	1	-1	*	0	9	*	*	*	*	*	2	1	*	*	*	1	0	0	105.0	4.0	*	Hills 1983
Actitis hypoleucos	0	*	*	0	3	*	*	3.71	*	*	2	1	*	*	*	1	0	0	50.0	4.0	0.96	Tatner & Bryant 1993
Arenaria interpres	2	*	*	0	8	*	*	4.12	*	*	2	1	*	*	*	1	0	0	144.0	3.8	0.48	Piersma & Morrison 1994
Stercorarius longicaudus	1	-1	*	*	14	*	*	*	*	*	2	1	*	1	*	1	0	0	313.0	2.0	0.26	Andersson 1976
Larus argentatus	2	1	*	*	220	*	*	*	*	*	2	1	*	*	*	*	1	0	813.0	3.0	0.33	Harris 1964
Larus argentatus	2	1	*	*	100	*	*	*	*	*	2	1	*	*	*	*	1	0	813.0	3.0	0.33	Paynter 1949
Larus fuscus	2	1	*	*	79	*	*	*	*	*	2	1	*	*	*	*	1	0	755.0	2.7	0.29	Harris 1964
Sterna fuscata	0	*	*	*	9	1.62	*	*	*	*	2	1	*	*	*	1	1	0	190.0	1.0	*	Flint & Nagy 1984
Tyto alba	0	*	*	0	*	*	1.00	*	*	*	1	1	*	*	*	1	1	1	392.0	5.7	0.31	Hamilton&Gessaman1981
Aerodramus spodiopygius	1	*	*	*	90	*	*	*	*	*	2	1	*	*	*	*	0	1	0	*	*	Tarburton 1987
Merops viridis	0	*	*	0	9	*	*	2.13	*	*	2	1	*	*	*	1	1	1	35.4	4.5	*	Tatner & Bryant 1993
Empidonax traillii	0	*	*	0	10	*	0.82	*	*	*	1	1	*	*	*	2	1	0	*	3.5	*	Walsberg & King1978a
Empidonax traillii	0	*	*	0	13	*	*	3.45	*	*	2	1	*	*	*	2	1	0	*	3.5	*	Ettlinger & King 1980
Empidonax minimus	1	-1	*	*	122	*	*	*	*	*	1	1	*	0	*	0	1	0	10.0	4.0	*	Briskie & Sealy 1989
Tachycineta bicolor	*	*	*	0	9	*	*	4.00	*	*	1	1	*	*	*	1	1	1	22.6	5.7	*	Williams 1988
Riparia riparia	0	*	*	0	3	*	*	3.57	*	*	2	1	*	*	*	1	1	1	13.6	4.8	0.49	Westerterp&Bryant1984
Riparia riparia	0	*	*	0	3	*	*	3.60	*	*	2	1	*	*	*	1	1	1	13.6	4.8	0.49	Westerterp & Drent 1985
Hirundo rustica	0	*	*	0	1	*	*	4.06	*	*	1	1	*	*	*	1	1	0	18.7	4.4	0.45	Westerterp&Bryant1984
Hirundo rustica	1	*	*	0	2	*	*	*	*	*	1	1	*	*	1	0	1	0	18.7	4.4	0.45	Jones 1987
Hirundo rustica	0	*	*	0	1	*	*	4.03	*	*	1	1	*	*	*	1	1	0	18.7	4.4	0.45	Westerterp & Drent 1985

Hirundo tahitica	0	*	*	0	*	*	0	*	2.31	*	1	1	*	*	1	*	1	1	14.7	*	Tatner&Bryant 1993
Delichon urbica	0	*	*	0	*	2.89	*	2	1	*	*	1	*	1	*	1	1	19.7	4.1	0.35	Westerterp&Bryant1984
Delichon urbica	0	*	*	0	3	2.94	*	2	1	*	*	1	*	1	*	1	1	19.7	4.1	0.35	Westerterp & Drent 1985
Cinclus cinclus	0	*	*	0	8	3.17	*	1	1	*	*	1	*	1	*	1	1	67.0	5.0	0.34	Bryant & Tatner 1988
Tragodytes aedon	1	0	*	0	229	*	*	1	1	*	1	*	0	1	1	1	1	9.7	7.7	*	Baltz & Thompson 1988
Erithacus rebeccula	0	*	*	0	3	2.62	*	1	1	*	*	1	*	1	0	1	0	16.7	5.0	0.72	Tatner&Bryant 1993
Turdus merula	2	0	*	347	*	*	*	1	1	*	*	*	*	1	0	1	0	97.1	3.9	0.29	Shov 1958
Ficedula hypoleuca	1	0	0	65	*	3.50	*	1	1	*	1	1	1	0	1	1	1	13.2	6.3	0.81	Moreno & Carlson 1989
Ficedula hypoleuca	1	*	0	9	*	*	*	1	1	*	*	2	0	1	1	1	1	13.2	6.3	0.81	Blagcklohnv 1977
Ficedula hypoleuca	1	*	1	0	18	*	*	1	1	*	0	1	0	1	1	1	1	13.2	6.3	0.81	Moreno & Sanz 1994
Ficedula hypoleuca	1	-1	0	204	*	*	*	1	1	*	1	0	0	1	1	1	1	13.2	6.3	0.81	Siikamaki 1995
Ficedula albicollis	1	-1	1	75	*	3.30	*	1	1	*	*	1	0	1	1	1	1	16.0	6.0	0.60	Moreno et al. 1991
Parus major	2	*	1	0	1	2.29	*	1	1	*	*	2	1	1	1	1	1	17.5	9.9	0.96	Mertens 1980
Parus major	1	*	1	0	4	1.50	*	1	1	*	*	2	0	1	1	1	1	17.5	9.9	0.96	Mertens 1977
Parus caeruleus	0	*	*	0	4	*	3.15	*	1	0	1	*	2	0	1	1	1	10.7	11.0	1.13	Tatner&Bryant 1993
Parus caeruleus	1	*	1	0	1	1.70	*	1	1	*	*	1	0	1	1	1	1	10.7	11.0	1.13	Haftorn & Reinhertsen1985
Parus caeruleus	1	0	*	0	20	*	*	1	1	*	1	*	0	1	1	1	1	10.7	11.0	1.13	Smith 1989
Parus caeruleus	0	*	*	0	4	*	3.48	*	1	1	*	*	1	1	1	1	1	10.7	11.0	1.13	Westerterp & Drent 1985
Nectarinea violacea	0	*	*	0	10	*	6.50	*	1	1	*	*	1	1	1	1	1	*	*	*	Williams 1993
Zonotrichia leucophrys oriantha	0	*	*	0	*	0.80	*	1	1	*	*	2	1	0	1	0	1	27.2	4.0	*	Walsberg & King 1978b
Junco phaeonotus	0	*	*	0	14	*	2.61	*	1	1	*	*	1	1	1	1	1	19.9	3.6	*	Weathers & Sullivan 1989
Passerculus sandwichensis	*	*	*	0	3	*	2.64	*	1	1	*	*	1	1	1	1	1	20.4	4.0	*	Williams 1987
Agelaius phoeniceus	0	*	*	0	10	*	0.84	*	1	1	*	*	2	1	0	1	0	56.7	3.4	*	Walsberg & King1978a
Serinus canaria	1	*	1	0	4	1.10	*	1	0	1	*	1	0	1	0	1	0	13.3	*	*	Weathers 1985
Poephila guttata	0	*	*	0	10	1.20	*	2	0	*	*	1	1	1	1	1	1	11.5	*	*	Vleck 1981
Lonchura striata	1	1	1	7	*	*	*	2	0	*	*	1	0	1	0	1	0	10.3	6.5	*	Coleman & Whittall 1988
Sturnus vulgaris	1	1	0	8	1.50	*	*	2	0	1	*	*	1	0	1	1	1	82.0	5.0	*	Biebach 1984
Sturnus vulgaris	0	*	*	0	6	*	2.36	*	2	1	*	*	1	0	1	1	1	82.0	5.0	*	Westerterp & Drent 1985
Sturnus vulgaris	0	*	*	4	*	2.72	*	2	1	*	*	1	1	1	1	1	1	82.0	5.0	*	Ricklefs & Williams 1984
Sturnus vulgaris	1	1	0	*	*	*	*	2	0	1	*	*	1	0	1	1	1	82.0	5.0	*	Biebach 1981
Sturnus vulgaris	1	*	*	0	20	*	*	2	0	*	*	1	0	1	1	1	1	82.0	5.0	*	Biebach 1986
Pica pica	0	*	*	0	2	1.85	*	1	1	*	*	2	1	0	1	0	1	237.0	5.5	0.22	Muyias & King 1981

Chapter 5

Clutch size determination in Kittiwakes *Rissa tridactyla*: an experimental study of incubation and chick rearing stages

David L. Thomson, Robert W. Furness, Pat Monaghan

Applied Ornithology Unit, Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, Glasgow University, G12 8QQ, UK.

Abstract

In order to study the relationship between clutch size and reproductive demands during the multiple stages of incubation and chick rearing, we enlarged the clutches and broods of Kittiwakes at different stages in the season and then examined whether these birds experienced lower breeding success and greater physiological stress than control birds where clutch and brood size were unaltered. Where the number of eggs was increased at the onset of incubation, a greater proportion of clutches was lost. This did not however depress the absolute average number of chicks hatching because more chicks could hatch from those enlarged clutches which did survive until hatching. Neither during incubation nor during the subsequent chick rearing phase was there any evidence that the adults with these enlarged clutches suffered greater loss of body condition, or slower rates of feather regrowth. There was no evidence that chicks had slower growth rates in nests where clutch size had been enlarged, but chicks grew more slowly in nests where brood size was still large at hatching. Where brood size, rather than clutch size, was enlarged, the adults were more likely than controls to lose chicks in the days following the manipulation. This was true regardless of whether broods with newly hatched or older chicks were manipulated; there was no evidence that the severity of the reduction in breeding success was greater when older broods were manipulated. We propose that clutch size may be shaped not by any single bottleneck in the season but rather by the demands experienced over several stages.

Introduction

In studies of clutch size evolution, the widespread use of experimental brood size manipulations indicates a common view that clutch size evolves mostly in response to the chick-rearing capacities of parents, rather than to their capacities during other stages of the season (Lack 1947, Dijkstra et al. 1989, Godfray et al. 1991, Van der Werf 1992). There does however exist evidence that these other stages may be important for the evolution of avian clutch size (Partridge 1989, Weathers and Sullivan 1989, Williams 1991, Bolton et al 1992), and the phase of incubation has received recent attention. When the clutch size of Collared Flycatchers *Ficedula albicollis* was enlarged during incubation, Moreno et al. (1991) found a reduction in hatching success and an elevation of parental metabolic rate. Although it is difficult to include all stages of the season or to perform the perfect experimental manipulation (Partridge 1989, 1992), the incubation stage can easily be incorporated by adjusting the number of eggs after laying and its importance readily compared with the stages of chick-rearing.

By enlarging clutches and broods at different stages in the season, we aim here to study the importance of demands during the multiple stages of both incubation and chick rearing for shaping clutch size of Kittiwakes *Rissa tridactyla*. In order to assess whether parental capacities are stretched by additional offspring at these different stages, we examine whether increased clutch sizes reduce breeding success, depress adult body condition and inhibit the regrowth of feathers during incubation and chick rearing. We measure chick growth rates to examine whether adults are capable of feeding bigger broods adequately.

Methods

Manipulation technique

By checking 279 Kittiwake nests every 2-4 days between 8th May and 20th July 1992 on the island of Hornoya, North-East Norway (70°N 31°E), it was possible to determine clutch size and clutch completion date, and thereby to select suitable nests for experimental alteration of clutch size. After clutch completion was confirmed (no change in clutch size over a period of at least 4 days), we increased the clutches from 2 eggs to 3 eggs in 32 nests. Another 80 comparable nests with 2 eggs were similarly visited and disturbed so that they could be used as controls. Groups of nests with similar clutch completion dates were used in each block of experimental, control, and donor nests. We continued to check all nests every 2-4 days to follow losses.

We checked that this experimental procedure itself did not interfere with the behaviour of the birds. Between 31st May and 14th June 1994, on the Isle of May, Eastern Scotland, we similarly added an egg to 25 nests with 2 eggs and observed these birds intensively for one and a half hours, comparing their behaviour with that of neighbouring unmanipulated controls in order to look for signs that birds might recognise and reject the foreign eggs or respond unnaturally to the manipulation. All birds returned to their nests and incubated their clutches, and no birds were seen to reject eggs or to be visibly stressed. Birds with extra eggs were not significantly more likely to delay returning to the nest (GLIM of 2 categories with binomially distributed errors: $t_{48}=0.89$, ns) nor to delay settling after returning (GLIM of 2 categories with binomially distributed errors: $t_{48}=0.00$, ns), and nor did they show a higher frequency of standing and interrupting incubation after settling (GLIM of 2 categories using logarithmic transformation and normally distributed errors: $F_{1,48}=0.01$, ns.).

Between 15th June and 28th July 1993 on Hornoya, we then examined the importance of parental capacity during various stages of brood rearing, by increasing brood size from 2 to 3 chicks in 33 nests and selecting 34 comparable control nests. In order to assess whether the parents were particularly stretched at any one stage of chick rearing, these manipulations were performed on nests ranging from those with newly-

hatched chicks up to those with chicks aged 15 days. We used only nests where the initial clutch size was 2 eggs. If one of these eggs or chicks had been lost before the experiment, we replaced this with another chick at the time of manipulation. To ensure that both control and experimental nests contained foreign chicks, we moved the donor chick to the control nest and then moved a control chick to an experimental nest.

Monitoring breeding performance

Many predatory herring gulls *Larus argentatus* nest on Hornoya. Because of high rates of egg and chick losses among the Kittiwakes, we continued checking nests every 2-4 days to follow survival of the offspring. Full details of this method are given in chapter 2 section 4. By measuring breeding success in these terms of daily survival rather than in terms of hatching and fledging success, it was possible to remove potential biases caused by comparing nests which were exposed to predation or damage for differing periods (Mayfield 1961, Johnson 1979). Fledging success would have been a particularly poor measure of breeding performance where the number of chicks was manipulated in broods of differing ages.

Further, by calculating average daily egg survival rates of the control and experimental groups, it was possible to estimate the difference in hatching success which would occur if the manipulation could be performed at the moment of clutch completion, rather than after the period required to confirm egg laying was finished. To make these estimates, we assumed an incubation period of 27 days (Cramp and Simmons 1983), we assumed that daily survival rates of the control and experimental groups were constant, and we multiplied the clutch size (after manipulation) by the daily egg survival rate raised to the power 27. Because broods manipulated at age 15 days could only then be followed for the remaining half of the full chick rearing period, and because the daily chick survival rates are unlikely to be constant and equal to the value measured in the 15-20 days following manipulation, we did not attempt to use this

method to extrapolate fledging success from survival rates of chicks following brood manipulations.

In order to distinguish between different types of losses, we calculated the daily survival rates in three different ways for each breeding attempt. We measured vulnerability of the nests to any type of loss using 'Intact clutch/brood' survival, which considered survival of the breeding attempt until at least one egg or chick was lost. This was distinct from 'Full clutch/brood' survival which followed the breeding attempt until all eggs or chicks were lost. In order to integrate all different types of losses into a single measure, we also calculated 'egg/chick survival' for each nest which considered the survival of individual eggs or chicks. Such measures will be referred to as 'breeding survival variables'.

The calculated values of these breeding survival variables for each individual nest were then analysed using generalised linear models assuming binomially distributed errors and the conventional logit link function (GENSTAT5 1987). This technique is similar to logistic regression, but can include categorical independent variables such as experimental treatment. These analytical models will be referred to here as 'binomial models'. Significant effects of laying date on daily survival rate were controlled before adding and testing the effects of experimental treatment (Lane et al. 1987, Digby et al. 1989). The significance of individual effects is presented here using a 't' statistic indicating whether the independent variables have a significant effect on the breeding survival variables. In the case of interaction terms, we have provided the change in mean deviance when these are added to or dropped from the model. (These mean deviances follow a chi-square distribution with one degree of freedom, where the 'dispersion parameter' equals one - i.e the variance in the frequencies of observations equals the mean. Further explanation of these analytical techniques are given in GENSTAT5 1987).

Chick growth rates

By weighing chicks at roughly 5 day intervals it was possible to follow the growth of chicks and to examine whether chicks from large broods were in poor condition for their age. Using all measurements of all chicks, a single standard sigmoid logistic non-linear regression model was then fitted by non-linear regression to describe the average pattern of body weight in relation to chick age (details of the logistic curve and the full procedure of fitting non-linear regression curves is outlined in GENSTAT5 1987 and Digby et al. 1989). As a first measure of chick condition, the residuals from this curve were taken for each measurement of each chick. Variance in weight around the function did however increase with chick age ($F_{1,171}=47.26$, $p<0.001$. see also Fig 1.), and this had to be taken into account when measuring condition. Each residual was therefore divided by the predicted absolute residual for that age to produce a standardised value, and then a single average standardised residual was calculated for each nest. The effects of experimental treatment on these average standardised residuals were then analysed by ANOVA.

Adult condition

After manipulating clutch size in 1992, adults were captured on the nest and a central tail feather was plucked in order to measure the rate of feather regrowth (Grubb 1989, 1991). Adults were then recaptured as the season progressed. Feather growth also was well described by a non-linear sigmoid function (in this case the Gompertz curve - also outlined in GENSTAT5 1987 and Digby et al. 1989), though a number of outliers were apparent (Fig. 2). Regrowth rates were analysed following the same protocol as for the chick growth rates, but the residuals from the Gompertz curve were cube-root transformed to normalise the distribution.

When birds were captured, their body mass was measured using a pesola spring balance and average daily weight changes calculated during incubation and chick rearing. These were then analysed separately using generalised linear modelling (Lane et al. 1987, Digby et al. 1989) with normally distributed errors akin to multiple linear

regression with multiple groups. Significant effects of laying date, recapture period, and sex, were built into these models before testing the effect of experimental treatment.

Results

Birds incubating enlarged clutches were significantly more likely to lose the entire clutch, though effects on the other measures of breeding survival were not significant (Table 1.). The greater losses of clutches did not however outweigh the larger clutch sizes of experimental birds and so nests with enlarged clutches did not on average hatch fewer chicks (Table 2.). After hatching, there were no detectable differences in the chick survival rates between control nests and nests with enlarged clutches (Average values are shown in Table 3.).

Similarly, there was no detectable difference in the chick growth rates between the groups manipulated at the start of incubation ($F_{1,35} = 2.16$, n.s). This may be expected since the brood sizes of control and experimental nests were similar by the time of hatching. Had experimental nests still had consistently larger broods at hatching, chick growth might have been lower - between nests differing in brood size at hatching (rather than between nests differing in experimental treatment), chick growth rates were lower where hatching brood size was large ($F_{2,34} = 5.12$, $P < 0.05$, and see Fig 1).

Where brood size was manipulated after hatching, the rate at which partial losses were suffered was significantly higher among nests with enlarged broods (i.e Intact brood survival was significantly lower: $t_{44} = 3.01$, $p < 0.01$, Table 4.). There was however no evidence that losses were more severe when the manipulation was performed with older broods (Intact brood survival: mean deviance=0.6803, dispersion parameter=1, $df=1$, ns; Full brood survival: mean deviance=1.3412, dispersion param=1, $df=1$, ns; Chick survival: mean deviance=0.4859, dispersion param=1, $df=1$, ns.).

There was no evidence that the number of eggs given to the birds during incubation affected the rates of feather regrowth ($F_{1,43} = 0.00$, ns. Fig. 2). Nor was there

any evidence that the experimental treatment affected the rates of mass change during incubation ($F_{1,22}=0.08$, ns, Fig. 3) or chick rearing ($F_{1,11}=1.58$, ns, Fig. 3), indeed there was no evidence of any regular or consistent pattern of weight change through the season at all ($F_{1,71}=0.24$, ns, Fig. 3).

Discussion

These results indicate that the demands of reproduction can impinge on clutch size at several stages of the breeding season. Enlarged clutches lead to greater losses of eggs, enlarged broods lead to greater losses of chicks regardless of the brood's age at the time of the enlargement. Rather than there being any one bottleneck on reproduction, there may be important demands at several stages through the season. Clutch size in these Kittiwakes would appear not to be an adaptation simply to the number of large chicks the birds can rear, but rather to parents' capacities for rearing and defending their offspring at many stages.

In this colony, the elevated demands of incubation and chick rearing were quickly translated into losses. The ability of the parents to buffer any demands would seem short-lived or ineffective. Rather than the birds enduring any loss of body condition or reduction in feather growth rates, offspring were lost, and with these offspring, the source of the elevated demands was lost too. Similarly, when brood size at hatching was large, chick survival and chick growth rates were depressed, but these same variables were not detectably affected by manipulations of clutch size because the enlargement had largely been nullified by the time of hatching. It is possible instead that both changes in body condition (Bryant 1988, Freed 1981) and in feather regrowth rates (Murphy and King 1991) may be poor indicators of reproductive demands. The lack of any effects of enlarged clutches on body condition and feather regrowth rates may simply arise because body condition and feather regrowth rates do not measure reproductive demands. However, since there is a negative feedback loop whereby more offspring lead to higher losses of offspring, there is no reason to expect elevated reproductive demands to be measurable over any protracted period of time.

Acknowledgements - This work was funded by the Carnegie Trust for the Universities of Scotland. Fieldwork would have been more difficult without the help and support of Rob Barrett (Tromso Museum), Geir Gabrielsen (NINA), John Calladine (SNH), Mike Harris and Sarah Wanless (ITE). Staff at GUCS provided advice with computing and statistics.

References

- Bolton, M., Houston, D. C. and Monaghan, P. 1992. Nutritional constraints on egg formation in the lesser black backed gull: an experimental study.
- J. Anim. Ecol. 61: 521-532.
- Bryant, D. M. 1988. Energy expenditure and body mass changes as measures of reproductive costs in birds. - Functional Ecology 2: 23-34.
- Cramp, S. and Simmons, K.E.L. (eds) 1983. Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Volume III. Waders to Gulls. Oxford University Press, Oxford.
- Digby, P., Galwey, N., and Lane, P. 1989. Genstat5. A Second Course. - Oxford University Press.
- Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. and Zijlstra, M. 1990. Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and adult survival. - J. Anim. Ecol. 59: 269-285.

- Freed, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation?
- Ecology 62: 1179-1186.
- GENSTAT5. 1987. Genstat 5 Reference Manual. Oxford Science Publications, Clarendon Press, Oxford.
- Godfray, H. C. J., Partridge, L., and Harvey, P. H. 1991. Clutch size.
- Ann. Rev. Ecol. Syst. 22: 409-429.
- Grubb, T. C. Jr. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. - The Auk 106: 314-320.
- Grubb, T. C. Jr. 1991. A deficient diet narrows growth bars on induced feathers. - The Auk 108: 725-727.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. The Auk 96(4):651-661.
- Lack, D. 1947. The significance of clutch size. - Ibis 89: 302-352.
- Lane, P., Galwey, N. and Alvey, N. 1987. Genstat 5. An Introduction. - Oxford University Press.
- Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73(3):255-261.
- Moreno, J., Gustafsson, L., Carlson, A. and Part, T. 1991. The cost of incubation in relation to clutch-size in the Collared Flycatcher *Ficedula albicollis*. - Ibis 133: 186-193.

- Moreno, J. and Sanz, J. J. 1994. The relationship between the energy expenditure during incubation and clutch size in the Pied Flycatcher *Ficedula hypoleuca*. - J. Avian Biol. 25: 125-130.
- Murphy, M. E. and King, J. R. 1991. Ptilochronology: a critical evaluation of assumptions and utility. - The Auk 108: 695-704.
- Partridge, L. 1989. Lifetime Reproductive Success and Life-history Evolution. - In Newton, I. (ed.). Lifetime Reproduction in Birds. Academic Press, London.
- Partridge, L. 1992. Measuring reproductive costs. - Trends in Ecology and Evolution 7: 99.
- Van der Werf, E. 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. - Ecology 73: 1699-1705.
- Weathers, W. W. and Sullivan, K. A. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. - Ecol. Monog. 59: 223-246.
- Williams, J. B. 1991. On the importance of energy considerations to small birds with gynelateral intermittent incubation. - Acta XX Congr. Int. Orn. 1964-1975.

	Control (2 eggs) n=80	Experimental (2+1 eggs) n=32	Significance
Intact Clutch Survival	0.967	0.944	P<0.1, N.S.
Clutch survival	0.973	0.967	P<0.05.*
Egg survival	0.970	0.960	P<0.1, N.S.

Table 1. Mean daily survival rates of eggs following manipulation. Significance was tested using a binomial model, after controlling for significant effects of laying date.

	Control (2 eggs). n=80	Experimental (2+1 eggs). n=32
Average brood size at hatching.	0.90	0.99
Average hatching success.	44.8%	32.9%

Table 2a. Projected brood sizes at hatching, assuming control and experimental birds are exposed for a full 27 day incubation period, with constant average egg survival rates shown in Table 1.

	Control (2 eggs). n=80	Experimental (2+1 eggs). n=32
Average brood size at hatching.	0.89	1.12
Average hatching success.	44.3%	37.5%

Table 2b. Observed mean brood sizes at hatching, and hatching successes of control and experimental nests. These differ from results shown in Table 2a because nests were manipulated after clutch completion was confirmed and so nests were not exposed for the full 27 day incubation period.

	Control (2 eggs)	Experimental (2+1 eggs)	Significance
Intact Brood Survival	0.991	0.981	N.S.
Brood survival	0.959	0.936	N.S.
Chick survival	0.978	0.971	N.S.

Table 3. Daily chick survival rates after hatching, following manipulations of clutch size.

	Control (2 chicks)	Experimental (2+1 chicks).
Manipulated <9days.	0.929	0.839
Manipulated ≥9days.	0.982	0.792

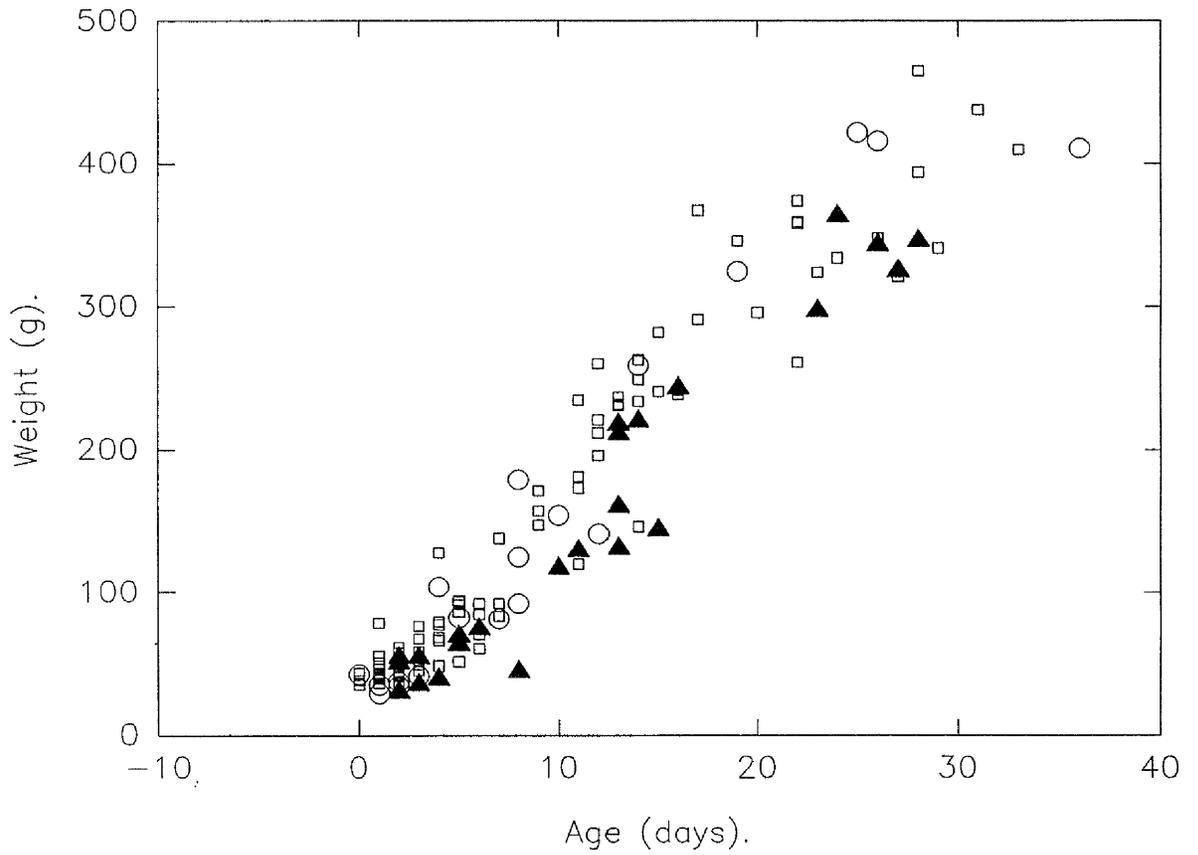
Table 4. Survival rates of intact broods manipulated before or after 9 days of age. Using manipulations of all ages, no interaction between manipulation age and experimental treatment can be detected.

Captions to Figures:

Figure 1. Body masses of chicks hatching in broods of 1, 2, or 3 chicks, through the growing period

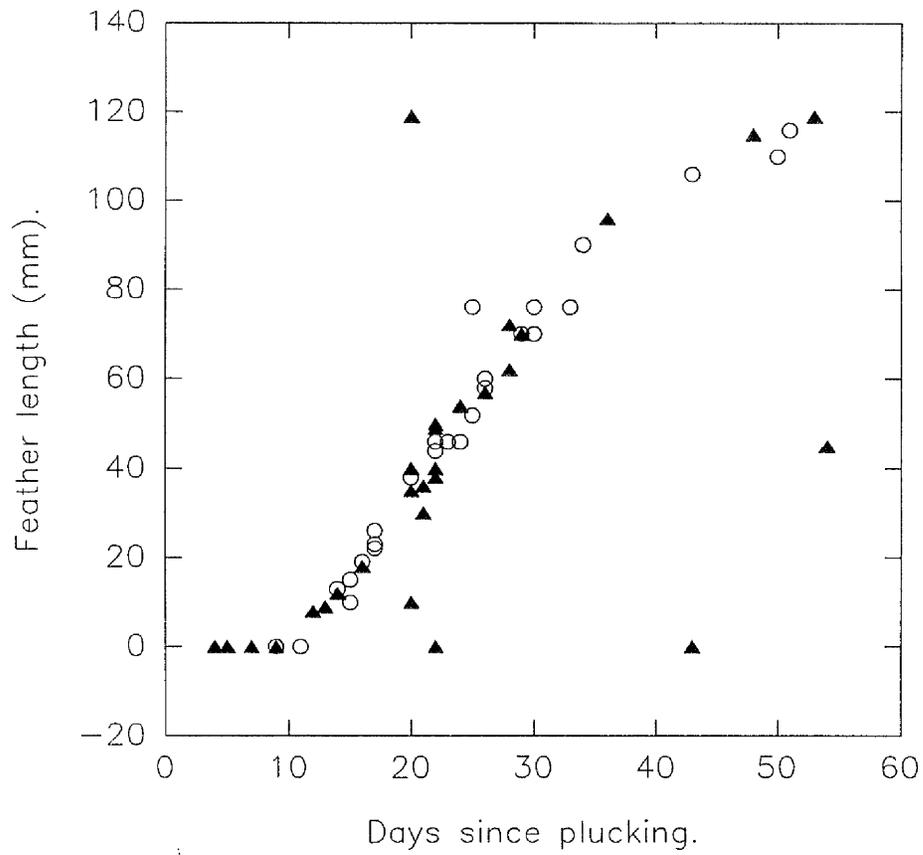
Figure 2. Lengths of growing tail feathers for birds with control (2 eggs) or experimental (2+1 eggs) clutches, against time since plucking

Figure 3. Body masses of adults with control (2 eggs) or experimental (2+1 eggs) clutches, through the breeding season



Circles - 1 chick at hatching.
 Squares - 2 chicks at hatching.
 Triangles - 3 chicks at hatching.

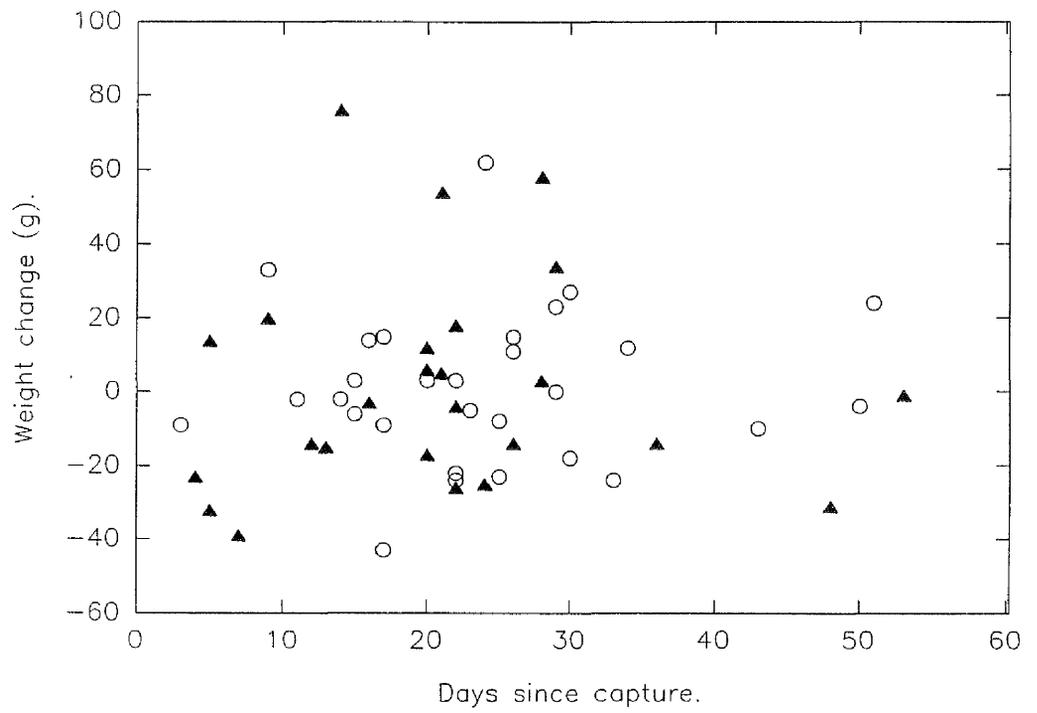
Figure 1.



Triangles - experimental birds (2+1 eggs).

Circles - control birds (2 eggs).

Figure 2



Circles - control nests (2 eggs).

Triangles - experimental nests (2+1 eggs).

Figure 3.

Chapter 6

FIELD METABOLIC RATES OF BLACK-LEGGED KITTIWAKES
RISSA TRIDACTYLA DURING INCUBATION AND CHICK REARING:
A STUDY WITH DOUBLY LABELLED WATER

DAVID L. THOMSON, ROBERT W. FURNESS AND PAT MONAGHAN

*Applied Ornithology Unit, Division of Environmental and Evolutionary Biology, IBLS,
Glasgow University G12 8QQ*

Field metabolic rates of breeding Kittiwakes

*Key words: Field metabolic rate, incubation, Rissa tridactyla, reproductive demands,
doubly-labelled water*

Metabolic rates have been used widely to assess avian reproductive demands (Bryant 1989), but few data are available on the metabolic rates of large birds during the incubation phase (Tatner and Bryant 1993). It is widely recognised that rearing chicks places substantial demands on birds (Lack 1947, references in Van der Werf 1992), and small birds (12-85g) have often been found to have higher metabolic rates when rearing chicks than when incubating eggs (Tatner and Bryant 1993). However, Tatner and Bryant (1993) also proposed that demands of incubation might limit the number of offspring which could be reared, and they found that metabolic rates during incubation were on average only c.20% below those during chick rearing.

We measured field metabolic rates of a relatively large bird - the Black-legged Kittiwake *Rissa tridactyla* (average body mass for birds studied = 404.2g, s.e.=7.1, n=17. Table 1.)- during incubation and compared these with comparable published results from the chick-rearing phase (Gabrielsen et al. 1987).

On the island of Hornøya in north-east Norway, thirteen adult Black-legged Kittiwakes were caught on their nests during the early incubation phase, and injected with doubly labelled water. Seven of these birds were incubating natural clutches of two eggs, while the remaining six had been given an additional egg and so had enlarged clutches of three eggs. A further four birds were caught and injected during the late chick rearing phase; these had laid two eggs and still had these two offspring. Birds were recaptured after roughly 24 or 48 hours and blood samples were taken. These were sealed in glass capillaries and the levels of deuterium and ^{18}O xygen were later determined using isotope ratio mass spectrometry. Two birds were recaptured twice, permitting repeated measurements of their energy expenditure. The full protocol for the doubly labelled water technique is outlined in Tatner and Bryant (1989). Birds of both sexes were caught. Breeding success of kittiwakes in the study colony was low; birds hatched on average only 37% (s.e.=3.5) of the eggs they laid.

The results are presented in Table 1. Measurements of energy expenditure for birds tending two eggs averaged 863 KJday^{-1} (n=8, range 344-1515). Those for birds

rearing two chicks also averaged 863 KJday^{-1} ($n=4$, range 420-1177) and clearly there is no evidence of a difference between these groups ($U_{8,4}=15.0$, ns). Assuming a resting metabolic rate of 314 KJday^{-1} (Gabrielsen et al. 1987), these expenditures represent $2.75 \times \text{RMR}$ (range 1.10-4.82) and $2.75 \times \text{RMR}$ (range 1.34-3.75) respectively. The overall average expenditure of all birds during incubation was 953 KJday^{-1} ($n=15$, range 344-1733). Birds tending three eggs had an average energy expenditure of 1055 KJday^{-1} ($n=7$, range 451-1733). This represents an average of $3.36 \times \text{RMR}$ (range 1.44-5.52). Though this is 22% higher than for birds tending two eggs, there is no evidence that birds with enlarged or normal clutches differed in their energy expenditures (Mann-Whitney $U_{8,7}=22.0$, ns).

Though energy expenditure may vary with many other factors such as weather, location, food abundance and conditions for breeding, these metabolic rates are similar to, or only slightly above, those found by Gabrielsen et al. (1987). They calculated an average energy expenditure of 992 KJday^{-1} for actively foraging birds and 596 KJday^{-1} for birds tending chicks at the nest. They proposed that a typical bird would expend on average 794 KJday^{-1} during the chick-rearing phase.

Our estimate of metabolic rate during incubation for birds tending natural clutches is also slightly above but similar to predictions from the allometric models derived from small birds (Tatner and Bryant 1993). Extrapolation from geometric mean regression and iterative non-linear regression models yields estimates of 799 KJday^{-1} and 763 KJday^{-1} respectively for a bird of 404.2g.

These data, for a larger species, are consistent with Tatner and Bryant's (1993) suggestion that incubation may also be an energetically demanding phase of the breeding season since the metabolic rates of kittiwakes were comparable during the stages of incubation and chick-rearing.

This work was funded by the Carnegie Trust for the Universities of Scotland. Fieldwork would have been very much more difficult without the help of Rob Barrett and Geir Gabrielsen. Steve Newton, Jim Weir and others at SURRC assisted with the isotopic analysis of doubly labelled water samples.

LITERATURE CITED

- BRYANT, D. M. 1989. Determination of respiration rates of free-living animals by the double-labelling technique, p. 85-109. *In* P. J. Grubb and J. G. Whittaker[eds.], *Toward a More Exact Ecology*. 30th BES Symposium. Blackwell Scientific Publications, Oxford.
- GABRIELSEN, G. W., MEHLUM, F., AND NAGY, K. 1987. Daily energy expenditure and energy utilization of free-ranging Black-legged Kittiwakes. *Condor* 89:126-132.
- LACK, D. 1947. The significance of clutch size. *Ibis* 89: 302-352.
- TATNER, P. AND BRYANT, D. M. 1989. The doubly labelled water technique for measuring energy expenditure, p. 77-112. *In* C. R. Bridges and P. J. Butler [eds.], *Techniques in Comparative Respiratory Physiology*. Cambridge University Press, Cambridge.
- TATNER, P. AND BRYANT, D. M. 1993. Interspecific variation in daily energy expenditure during avian incubation. *J. Zool.* 231:215-232.
- VAN DER WERF, E. 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. *Ecology* 73:1699-1705.

TABLE 1. Energy expenditures of birds during incubation and chick rearing.

	Ring no.	Mass (g)	KJday ⁻¹	KJg ⁻¹ day ⁻¹	Sex
Incubation - 2 eggs	MA22722	349	398	1.14	F
	MA22750	382	629	1.65	F
	MA22750	390	344	0.88	F
	MA22969	451	925	2.05	M
	MA21114	403	1515	3.76	M
	MA22959	407	925	2.27	M
	MA21124	397	806	2.03	F
	MA23059	438	1363	3.11	F
Incubation - 2+1 eggs	MA21138	380	451	1.19	F
	MA22728	368	774	2.10	F
	MA22977	403	1339	3.32	F
	673954	450	982	2.18	F
	MA21125	435	1733	3.98	M
	MA22989	443	789	1.78	F
	MA22989	429	1319	3.07	F
Chick rearing - 2 chicks	MA21140	402	420	1.05	F
	MA23081	383	1072	2.80	F
	MA23079	395	1177	2.98	M
	MA23082	388	782	2.02	F

Chapter 7

**A study of breeding performance, colony structure, and nest site quality in
Kittiwakes *Rissa tridactyla***

David L. Thomson, Robert W. Furness, and Pat Monaghan.

Applied Ornithology Unit, Graham Kerr Building, Glasgow University, G12 8QQ.

Abstract

In a two year study of kittiwakes at a colony in north-east Norway, we looked at whether groups of birds showed consistencies in breeding performance, and whether patterns of breeding performance might be related to nest site characteristics. Within the colony, groups of birds nesting close together had similar breeding successes, clutch sizes, and laying dates, but these patterns changed between years. Like breeding success, groups of nest sites also showed similarities with respect not only to height and aspect but also with respect to the presence/ absence of adjacent rock ledges or abutting nest space, levels of fleas, or the frequency of physical damage. Again like breeding success, these attributes other than aspect and height were not fixed between years. However, there was little evidence of important connections between any nest site characteristics and breeding performance, except in one year when birds at sites with abutting nests laid earlier and birds nesting at different heights on the cliffs laid different clutch sizes. Flea levels and breeding performance were correlated with each other - fleas were more abundant early in the season, but birds nesting earlier sustained lower parasite activity at any single snapshot in time. There was no evidence that high flea levels depressed performance. The frequency of nests suffering physical damage was related to the height of the site, and to whether it had an adjacent rock ledge, or abutting nest space, but because many of these nests were not used by breeding birds, physical damage had no detectable influence on breeding success. Nests in the main study plots shared similar aspect, but in a steep sided gulley, nests with southerly rather than northerly aspect were used more frequently and had earlier laying dates. Small differences in both daily minimum and daily maximum air temperatures were found between parts of the colony and were most marked between sites in the gulley which differed in aspect.

The spatial groupings of breeding performance and nest site characteristics were not fixed between years, and no evidence could be found for consistent differences in the quality of individuals at particular sites. Returning birds showed high fidelity to the previous site, but appreciable turnover could still occur. If clutch size or

hatching success at a particular site was low in the first year, then the site was less likely to be used in the second year. Turnover, rejection of poor sites, and pressure on good sites may all then serve to disrupt clusters of good or bad performance and may account for the lack of consistent differences in nest site quality and breeding performance.

Introduction

Regular differences in breeding performance between sections of bird populations may arise either through consistent differences in the quality of individual birds, through differences in the resources held by individuals, or through stochastic processes (Coulson 1968, 1971, Hogstedt 1980, Potts *et al.* 1980, Goodburn 1990, Newton 1989). In kittiwakes *Rissa tridactyla*, breeding performance can be correlated with differences in nest site characteristics (Olsthoorn and Nelson 1990). Competition between kittiwakes for sites where breeding is both early and successful would suggest that nest sites offer valuable resources (Monnat *et al.* 1990, Danchin *et al.* 1991). We know of no studies which have looked explicitly at whether nest site characteristics and nest site quality are grouped in space and whether this grouping could give rise to grouping of birds with similar performance. In typical colonies, such clustering of nest site features might complement the regular spatial patterns of breeding performance caused by the clustering of high quality individuals (Coulson 1968, Coulson and Thomas 1985).

Here we examine whether kittiwakes in particular parts of a typical colony show similar breeding performances and whether these patterns persist between years. We investigate whether areas of the colony are characterised by similarities in nest site characteristics, whether these characteristics are fixed between years, and whether they affect breeding performance, and examine the turnover of birds and sites and consider which features influence the likelihood that a site will be used.

Methods

Nest site characteristics

In order to investigate the spatial patterns and inter-relationships of breeding performance and nest site characteristics, we visited a large kittiwake colony on the island of Høfnøya, north-east Norway, between 8th May and 20th July 1992, and between 15th June and 28th July 1993. The main study plots contained 279 nests in 1992 and 350 nests in 1993. It was possible to record the following nest site characteristics:

- whether nest sites suffered physical damage from storms etc.
- the presence or absence of adjacent rock ledges
- the presence or absence of abutting nests
- height
- parasite activity
- temperature
- aspect

Visits were also made to a further 192 nests in 1993, but these nests were not then followed intensively.

Physical damage to nest sites

As well as measuring breeding success, we noted whether the nest at any particular site was damaged during the course of the season. Because we included damage to nests which were not being used for breeding at the time (e.g. 16 of 46 losses in 1993 were at sites where no birds bred), this is not a measure of breeding success *per se*. Instead, as for the other nest site characteristics, we looked at whether the breeding performance was significantly influenced by whether or not a nest was lost.

Ledges and space next to the nest

Nest sites might be of higher quality if they were situated on secure ledges, or had space outwith the nestcup upon which growing chicks could perch. Two types of such space adjacent to the nests were recognised: rock ledges and abutting nests. A nest was categorised as having a rock ledge if there was a flat rock surface onto which a chick from that nest could move. The nests of neighbouring kittiwakes commonly accumulate nest material and fuse together; and if this nest material offered a surface onto which a chick could move, the nest was categorised as having abutting nest space.

Height

Nests differing in height may differ in their vulnerability to predators or physical damage. We scored sites on a scale of 1-5 according to their height from the base of the cliff.

Parasite activity

Fleas (*Ceratophyllus vagabundus insularis*, identified by Hancock and George *pers. comm.*) were abundant in the colony, and an index of their activity could be obtained for nests with eggs. Blood ingested by the parasites is partly digested, but the red pigmentation persists in the faeces and is voided onto the surface of the birds' eggs during incubation (Feare and Constantine 1980). An ordinal scoring of these red spots was used as a rough measure of flea activity in the nest.

It might seem that this measure would be so crude as to be of little use, but despite the noise inherent in the measurements, significant relationships with other variables were detected. Further, it might be thought that since blood is deposited on the eggs, then it would accumulate through time. Instead, there were significant

declines in the egg blood scores through time (ordinal logistic regression, $z=2.05$, $df=162$, $p<0.05$. Figure 1a.). This effect persisted after controlling for clutch size and laying date, and corresponds with declines in the number of flea-bites suffered by an observer visiting nests consistently through the season (linear regression, square-root transformed counts, $t_{37}=2.76$, $p<0.01$. Figure 1b.). These patterns indicate that the turnover of the red spots was sufficiently rapid to provide a measure of flea activity over a short time scale rather than being an artefact of accumulated activity through the season.

In 1992, scores were recorded over a protracted period of time at various stages through incubation. In 1993, scores were recorded over a shorter period in a single bout of visits to nests containing eggs. Because of seasonal changes in blood scores, an index of parasite activity was obtained by taking residual blood score from a regression of blood score against time.

Aspect

Nests in the main study plots shared similar aspect, but a steep sided rocky gulley on Hornøya made it possible to study the effects of aspect on breeding performance, free from many other potentially confounding differences. On one side of the gulley, birds faced in an essentially northerly direction, while on the other side they had a more southerly aspect. Although Hornøya lies above the Arctic circle and thus experiences continuous daylight for much of the breeding season, the elevation of the sun leads to longer exposure and deeper penetration of sunlight on the south-facing side. Apart from the difference in aspect, the birds on either side were in otherwise similar situations, and birds at extreme ends of the study plots on each side of the gulley were further from each other than from birds directly across the gulley.

It was difficult to visit nests regularly on the northern side of the gulley, so breeding success could not be measured satisfactorily, but occupancy, breeding stage, clutch size, and brood size could be recorded during spot checks. In 1992, only a

single spot check was made and only breeding stage was determined. This was achieved by scoring nests as having offspring at one of five stages - eggs, small downy chicks, large downy chicks, small feathered chicks, or large feathered chicks. In 1993, breeding was more synchronous, and the first three of these categories, as well as the last two were amalgamated. In 1993, we looked at whether birds on the north-facing side nested higher up by comparing heights between 60 pairs of nests, each at similar distances from the mouth of the gully.

Temperature

In 1993, we mounted 5 min-max thermometers in different parts of the colony in order to gain an indication of whether temperature varied within the colony. The thermometers were mounted on wooden planks, facing the rock so as to shelter them from the direct effects of solar radiation. The thermometers were calibrated against each other for consistency. Each day, we noted the minimum and maximum temperatures for the preceding 24 hrs. It was not possible to measure temperatures in more numerous areas or at individual nest sites and so it was not possible to look at how temperature affected breeding performance - only at whether there were gross differences in temperatures between different parts of the colony.

Breeding performance

By visiting nests every 2-3 days it was possible to determine laying dates, clutch completion dates, clutch sizes and breeding success. In 1993, some nests already had full clutches at the time of arrival, and so the clutch completion dates were estimated from egg density (Furness and Furness 1981, Barrett unpubl.). Nests observed with eggs or chicks were categorised as 'occupied', while the remainder were considered 'unoccupied'. It was not possible to follow all nests from laying to fledging, so we calculated daily survival rates of eggs and chicks instead of recording hatching and fledging success. Because many breeding attempts were lost when nests were

physically damaged by waves, weather, predators or competitors, we distinguished such losses of nests from losses of individual eggs or chicks. To do this, we calculated two different types of breeding survival variables - 'nest survival' which recognised failure as occurring when all the offspring were lost through damage to the nest, and 'egg/chick survival' which calculated the average daily survival of the offspring in the nest and specifically excluded losses due to nest-damage. We calculated these two types of breeding survival variables separately for the incubation and chick-rearing periods to produce four breeding survival variables in total.

The statistical analysis of spatial patterns

If there exist good and bad areas for breeding, then neighbouring nests will share high breeding performance in good areas and poor breeding performance in bad areas. This will lead to correlations between the performances of birds at neighbouring nests. We looked for such effects using the broad framework of generalised linear modelling (McCullagh and Nelder 1983) - depending on the distribution of residual variance, we used multiple linear, binomial or ordinal logistic regression models to test whether the breeding performance at a particular nest was influenced by that at the neighbouring nest (McCullagh 1980, Lane *et al.* 1987, Digby *et al.* 1989, Cole and Lane 1989). Thus, in the case of laying date, we assumed normally distributed errors because the residual variance followed a continuous normal distribution, while in the case of the breeding survival variables, which lay between zero and one, we assumed binomially distributed errors. For clutch size which is an ordinal categorical variable we used ordinal logistic regression. Where normally distributed errors were assumed, we presented the F statistic associated with the change in explained variance when the variable of interest was added to or dropped from the model. In the other models, we have presented the t or z statistic which indicates whether each variable has a significant effect.

We similarly looked for relationships between the physical characteristics of adjacent nests using log-linear models. These are akin to chi-square analyses but can accommodate more variables and offer greater flexibility. Here, the dependent variable is the frequency of observations and the independent variables are the categorical variables describing the characteristics of a nest and its neighbour respectively. If nest site characteristics occur in groups within the colony, then this will be revealed by a significant positive interaction between the variables describing the characteristics of each nest and the neighbouring nest. The significance of these interactions has been presented using the change in mean deviance when this interaction term is added to or dropped from the model. We have assumed Poisson distributed errors where the mean equals the variance (- the 'dispersion parameter' equals one). Abutting nest space must inevitably be shared between neighbours, so for this variable we looked instead for relationships between sites separated by two nests.

Parasite levels were measured using the ordinal variable of blood score, and so spatial patterns in this were tested using ordinal logistic regression. Where 'residual blood score' was used to correct for the time when blood scores were taken, the values no longer followed an ordinal distribution and so normally distributed errors were used in a generalised linear model.

Testing whether nest site characteristics affect breeding performance

Using the same generalised linear modelling approach, we looked at whether breeding performance was affected by nest site characteristics. If both breeding performance and nest site characteristics are arranged in clusters within the colony, then spurious relationships between site characteristics and performance could arise. If a cluster of high breeding performance happens to overlap with a cluster of say rock ledges, then a significant but spurious association between these variables could arise. To avoid this problem, we determined whether breeding performance was relatively good or relatively poor for its cluster. Hence, in the models of breeding performance in

relation to nest site characteristics, breeding performance of the neighbouring nest was entered as an independent variable before adding the variable to be tested.

Identifying nests and birds between years

By using photographs and by mapping out the distribution of nests, it was possible to determine if nests persisted between years and to look at which sites were re-used. We then checked whether breeding performance and nest site characteristics of particular sites were consistent between years, or whether they changed. To do this we used generalised linear modelling techniques similar to those used for examining spatial patterns. Using binomially distributed errors, we looked at whether the breeding survival variables recorded in the second year were significantly influenced by those at the same site in the preceding year. We used ordinal logistic regression and multiple linear regression to look for similar consistencies in clutch size and laying date respectively. We constructed log-linear models to look at whether the space provided by attached abutting nests and unobstructed rock ledges might not be fixed between years. Similar log-linear models were constructed to look at whether sites where the nest was physically damaged might be more prone to such damage in the second year. Ordinal logistic regression models and multiple linear regression models were used to test whether blood scores and residual blood scores at particular nests were consistent between years.

By attaching metal rings to 163 adult Kittiwakes in 1992, we established the identity of 35 of these birds occupying nests in 1993. It was not possible to determine whether birds dispersed out of the study area, but of those which returned, it was possible to examine whether they were loyal to their site.

Results

Are there spatial patterns of breeding performance?

There was grouping of birds with similar performance. In 1993, but not in 1992, there were clusters of birds suffering similar losses of eggs. There was no detectable clustering of birds suffering similar losses of nests or of chicks (Table 1.). In 1992, but not 1993, adjacent birds had similar laying dates (1992: $F_{1,99}=12.70$, $p<0.001$; 1993 $F_{1,293}=2.42$, ns.). In 1993, but not 1992, adjacent birds laid similar numbers of eggs (1992: mean residual deviance=0.4550, $df=4$, ns; 1993: 4.047, $df=1$, $p<0.05$.). As might be expected from these inter-annually changing spatial patterns of breeding performance, there was no evidence that sites were consistently good or bad between years. Few nests survived as far as chick rearing in both years ($n=8$), but during incubation, there was no evidence that the breeding survival variables of particular nests were correlated between years (Table 2). There was similarly no evidence of consistencies in clutch size (ordinal logistic regression: $z=0.94$, $df=92$, ns. Table 3), nor laying dates ($F_{1,58}=0.54$, ns) at particular sites between years.

Thus, if the spatial patterns of breeding performance are due principally to nest site characteristics, three criteria must be fulfilled : groups of adjacent nests must have similar characteristics; the nest site characteristics must not be fixed between years; and the nest site characteristics must correlate with breeding performance.

Physical damage to nests

It might be thought that differences in the likelihood of physical damage could account for spatial patterns of breeding success. Indeed for both years, there were significant spatial associations of nests which suffered physical damage (log-linear mean residual deviance:- 1992: 45.03, $df=1$, $p<0.001$; 1993: 45.63, $df=1$, $p<0.001$. See Table 4).

Nest sites damaged in the first year were not necessarily damaged in the next, but they were significantly more likely to be damaged (log-linear residual mean deviance =23.22, df=1, $p < 0.001$. Table 5.). This contrasts with the lack of consistency in daily nest survival during incubation at sites used for breeding (Table 2).

Indeed, surprisingly, whether or not the site was damaged at some point in the season had no detectable significant relationship with the daily nest survival rates of nests used for breeding (1992: incubation, binomial model, $z = 1.14$, df=137, ns; chick rearing, binomial $z = 0.86$, df=67, ns. 1993: incubation, binomial model, $z = 1.24$, df=199, ns; chick rearing - no nests lost). Similarly, although nests suffering physical damage are grouped in space, the daily nest survival rates of breeding birds are not (Table 1.). There was also no detectable relationship between clutch size and whether a site was physically damaged (1992: log-linear residual mean deviance =0.273, df=2, dispersion=1, ns. 1993: log-linear residual mean deviance =0.001, df=1, dispersion=1, ns.). There was no evidence that laying dates differed between nests suffering or not suffering physical damage (1992: $F_{1,194} = 2.99$, ns, 1993: $F_{1,201} = 2.76$, ns.).

Consistent physical damage to particular groups of nests sites would thus seem of little consequence for breeding birds, and it does not account for the patterns of breeding success observed within the colony.

Rock ledges and abutting nest space

Nest sites with adjacent rock ledges also were aggregated in space in both years (log-linear mean residual deviance:- 1992: 42.07, df=1, $p < 0.001$; 1993: 28.84, df=1, $p < 0.001$. See Table 6.).

Nest sites with abutting nest space were similarly aggregated in space (log-linear mean residual deviance:- 1992: 8.101, df=1, $p < 0.01$; 1993: 15.81, df=1, $p < 0.001$. See Table 7).

Surprisingly, there was evidence that physical nest site characteristics were not fixed between years (Tables 8a and 8b) and although there was evidence that the

presence of abutting nest space at particular sites was consistent between years (log-linear residual mean deviance: 4.615, $df=1$, dispersion=1, $p<0.05$), there was no evidence of similar consistency in the presence of rock ledges (log-linear residual mean deviances: rock ledges - 3.719, $df=1$, dispersion=1, ns). In 1992, there was a significant association between the presence of rock ledges and the presence of adjacent nest space (log-linear mean residual deviance=23.36, $df=2$, $p<0.002$) but in 1993 there was a significant dissociation of these two attributes (log linear mean residual deviance = 4.406, $df=1$, $P<0.05$). Abutting nests could be lost through physical damage, and rock ledges could become blocked by nest material, vegetation or debris.

Although, like breeding performance, these characteristics were grouped in space, there was no indication that daily losses of offspring were influenced by the presence of either rock ledges or adjacent nest space (Table 9). In neither year was there any evidence that clutch size was influenced by the presence of rock ledges (1992: ordinal logistic regression, $z=0.55$, $df=129$, ns; 1993: $z=1.03$, $df=309$, ns.) nor by the presence of abutting nests (1992: ordinal logistic regression, $z=0.78$, $df=129$, ns; 1993: $z=0.42$, $df=309$, ns.). There was no evidence that laying date was influenced by the presence of rock ledges (1992: $F_{1,64}=0.01$, ns; 1993: $F_{1,294}=1.72$, ns). In the second year, laying date was on average 2.9 days earlier in nests with abutting space (1992: $F_{1,64}=0.22$, ns; 1993: $F_{1,294}=24.18$, $p<0.001$).

Although not strongly linked with breeding performance, the presence of adjacent ledges and abutting nests were related to the frequency of physical damage. For all nests, whether occupied and in use or otherwise, the chance of suffering physical damage at some point in the season is positively related to the presence of rock ledges (log-linear mean residual deviance:- 1992: 3.978, $df=1$, $p<0.05$; 1993: 6.720, $df=1$, $p<0.01$) and negatively related to the presence of abutting space (log-linear mean residual deviance:- 1992: 11.70, $df=1$, $p<0.001$; 1993: 11.97, $df=1$, $p<0.001$). These effects persist even after controlling for all other associations and dissociations of ledges, adjacent nests and physical losses.

Height

Obviously, adjacent nests sites were of similar height (ordinal logistic regression: 1992 - $z=8.13$, $df=133$, $p<0.001$; 1993 - $z=11.76$, $df=231$, $p<0.001$), and the height of a nest site was of course consistent between years (ordinal logistic regression: $z=7.10$, $df=121$, $p<0.001$). There was no evidence that daily losses of offspring were influenced by the height of the nest site (Table 10). There was no evidence that laying date was influenced by the height of the nest site (Multiple linear regression: 1992 - $F_{1,86}=0.48$, ns; 1993 - $F_{1,110}=0.33$, ns). In 1993, but not 1992, there was evidence that clutch size was influenced by the height of the nest site, and the linear relationship between these two variables was significantly improved by introduction of a quadratic component - clutch size increased towards both the lowest and highest sites, though the biggest difference in average clutch size between zones of particular height was only 0.165 eggs (ordinal logistic regression: 1992 - $z=1.32$, $df=135$, ns; 1993 - $z=2.75$, $df=233$, $p<0.01$ [linear component] and $z=2.30$, $df=233$, $p<0.05$ [quadratic component]).

Although not related to the rate at which breeding birds lost their offspring, nests at higher sites were significantly less likely to be damaged in 1993 (Generalised linear model with binomially distributed errors: 1992 - $z=0.04$, $df=136$, ns; 1993 - $z=3.48$, $df=234$, $p<0.001$).

Parasite levels

In 1993 but not 1992, parasite scores of adjacent nests were more similar than would be expected by chance (ordinal logistic regression:- 1992: $z=1.66$, $df=135$, ns;

1993: $z=6.07$, $df=284$, $p<0.001$). Even when residual blood score was used to contend with the temporal biases, there was still no evidence that sites with similar parasite levels were grouped in space in 1992 ($F_{1,101}=0.17$, ns).

There was no evidence that the blood scores or residual blood scores of particular nests were correlated between years (ordinal logistic regression: $z=0.29$, $df=90$, ns; $F_{1,54}=0.26$, ns).

There was no evidence that parasite levels affected breeding success, even after controlling for the confounding influences of laying date and the spatial clustering (Table 11.).

There were however correlations between breeding performance and parasite levels. When recording period was protracted in 1992, declining parasite levels (ordinal logistic regression $z=2.05$, $df=162$, $p<0.05$, Figure 1) produced a negative correlation between laying date and parasite levels (1992: ordinal logistic regression, $z=3.00$, $df=192$, $p<0.01$). There was however no evidence of a similar negative relationship when parasite scores were collected over a shorter bout in time in 1993 (ordinal logistic regression, $z=0.84$, $df=475$, ns.), nor after controlling for observation date in 1992 (ordinal logistic regression, $z=0.88$, $df=163$, ns.).

Further, in 1993, after controlling for observation date, birds with earlier laying dates actually had lower blood scores (ordinal logistic regression, $z=2.75$, $df=297$, $p<0.01$), despite commencing nesting when parasite levels were higher (linear regression, square-root transformed counts of bites, $t_{37}=2.76$, $p<0.01$). Early nesting birds tended to have larger clutches (1992: ordinal logistic regression $z=3.52$, $df=118$, $p<0.001$; 1993: binomial model $z=3.57$, $df=294$, $p<0.001$). Yet despite nesting at times when the parasite levels were higher, birds with larger clutches did not have significantly higher blood scores in 1992 (ordinal logistic regression, $z=1.32$, $df=192$, ns), and in 1993 they actually had significantly lower blood scores (ordinal logistic regression, $z=2.69$, $df=475$, $p<0.01$).

Laying date thus correlates with parasite activity in two ways. Firstly birds nesting early have higher parasite levels because parasite levels are higher at this time.

Secondly, at any snapshot in time, the birds which laid earlier contend better with the current parasite levels. Parasite levels would seem not to affect breeding performance, but breeding performance is correlated with parasite levels.

Aspect

In both years, breeding stage was significantly later among the birds on the north-facing side of the gulley (log-linear residual mean deviance, 1992: 3.961, $df=4$, $p<0.05$; 1993: 6.046, $df=1$, $p<0.05$. Figure 2). In 1993, north-facing sites were significantly less likely to be occupied (log-linear residual mean deviance =10.70, $df=1$, $p<0.005$. Table 12.) and birds on the north-facing side nested higher up (binomial test, $z=7.746$, $df=59$, $p<0.001$). There was however no evidence that aspect affected clutch or brood size (log-linear residual mean deviance=0.1364, $df=1$, ns); south-facing sites used for breeding had an average 1.35 offspring while north-facing sites had 1.38.

Temperature

In 1993, both minimum and maximum daily temperatures showed significant differences between sites within the colony (Table 13). The biggest difference in average minimum temperature between sites was 0.8°C. The biggest difference in average maximum temperature was 2.4°C and this was recorded between two sites at the gulley which differed in aspect.

Past breeding performance and the choice of nest sites

Changing patterns of breeding performance could arise if breeding birds used the site's track record of previous breeding success as a cue when deciding whether to use sites in subsequent years. Among the nests which were physically intact during the 1993 season, a site was more likely to be used by breeding birds if daily egg survival rates at that site had been high 1992 (Table 14). All nests which survived as far as the chick stage in 1992 were used by breeding birds in 1993. There was no detectable

effect of laying date on subsequent re-use (binomial: $z=0.80$, $df=102$, ns), but a site was more likely to be used for breeding in 1993 if clutch size had been large in 1992 (binomial model: $z=5.50$, $df=180$, $p<0.001$).

There was however no evidence that these patterns of site usage were due to established birds changing sites between years. Of the 35 ringed birds identified in 1993, 31 used the same site as in 1992 and the remaining four occupied neighbouring sites. Of the birds which definitely remained in the study area, all were loyal to the area, and most were loyal to the site.

Despite this, there was still considerable turnover of birds at sites. Of 106 nests used for breeding in 1992 and identifiable in 1993, 26 (=24.5%, s.e.=4.2%) were not used in the second year. Of 18 nests which were not used in 1992 and which were identifiable in 1993, 13 (=72.2%, s.e.=11%) were used for breeding. Further, of 43 nests where it was possible to determine whether both birds were the same in both years, or whether at least one bird was different, at least one bird was different in 12 cases (28%).

Discussion

Breeding performance and spatial structure.

Within the colony, there is a spatial structure to breeding performance, but it is not fixed between years. Breeding success, laying date and clutch size all show spatial patterns, but these patterns are not consistent between years. If the regular spatial patterns of breeding performance are caused by the quality of individuals, then either 'quality' is a transient phenomenon which changes between years, or there is considerable turnover of birds at sites between years.

One study (Coulson and Wooller 1976) has found that established kittiwakes do not move between breeding areas, while others have found that movements do occur (Danchin *et al.* 1992, Hatch *et al.* 1993, Harris *pers comm.*). Within our study area,

except for extremely local movements, there was no evidence that the birds which returned to the plot moved between nest sites, though it remains possible that birds moved outwith the plot.

There was however a substantial fraction of nests with new birds the following year. A substantial fraction of nests used one year were not used the second year, and nests not used in the first year were used in the second. Even if birds are faithful to sites, and even if adult survival is high e.g. 80-85% (c.f. Aebischer and Coulson 1990) then 27-36% of nest sites would lose a bird each year, and the potential for turnover at particular sites is still considerable. High site fidelity among established breeders does not preclude appreciably dynamic patterns of site exchange.

This natural turnover would disrupt spatial patterns yet further if recruitment occurred only at sites where performance had been good. The positive relationship between breeding success and subsequent occupancy is consistent with this, though similar patterns could also be produced if breeding failure caused adults to disperse out of the colony.

If however there is no consistency in the quality of nest sites, it must be asked why recruits would try to assess site quality from breeding performance. The processes involved may however be difficult to disentangle. Without any monitoring of site quality by prospective breeders, catastrophic sites would continue to be occupied, and regular patterns of breeding success would persist between years. Instead, the exposure of nest sites to physical damage was consistent between years, but by avoiding the risky sites, the population may have evaded any effects of this on breeding success. A population in which recruits continually select sites on the basis of past performance will be a population which uses only the better sites and in which there may come to be little variance in site quality. If this process becomes established, recruits come to select sites on the basis of performance even though this performance is no longer related to site quality.

If this were true, then physical site characteristics must also be poor indicators of site quality among nests used for breeding. Indeed, though height, rock ledges and abutting nest space do correlate with exposure to physical damage, they have no detectable effects on the breeding success at nests used for breeding, and because damage often occurs at sites which are not used for breeding, there is no detectable relationship between physical damage to nest sites and breeding success. The regular spatial groupings of nest sites with similar characteristics - height, rock ledges, abutting nest space - can not account for the spatial patterns of breeding performance nor for the changing patterns of breeding performance between years.

Fleas

Again, there is spatial structure to ecto-parasite levels but neither this nor their lack of consistency between years account for the shifting patterns of breeding performance. Although many studies have found fleas to be important for breeding performance (e.g. Richner *et al.* 1993, Oppliger *et al.* 1994, Eeva *et al.* 1994), there was no such evidence in this study and there was more evidence that breeding competence affected flea activity than vice versa. The activity of fleas declines seasonally but although early nesting birds, which tend to have larger clutches and higher breeding performance, are thus exposed to higher levels, they sustain relatively lower flea activity in their nests.

Aspect and temperature

Barring exceptional circumstances, the aspect of nest sites is obviously both spatially structured and consistent between years. All nests within the main study plot did however share the same aspect, and so the spatial structures in breeding performance discussed here did not arise through gross differences in aspect. More generally however, it is clear that laying date, occupancy, and the height of the nest site, are connected with aspect, though there is no evidence for similar effects on clutch size.

The mechanism by which aspect affects breeding performance is presumably thermal. In arctic areas, this may also include the indirect practical considerations of snow-lie though differences in laying date between the two sides of the gulley were apparent in 1992 even though there was no snow covering the nest sites around the time of laying. (Comparable observations were not made in 1993).

Temperature does indeed vary between different parts of the colony, and the differences in daily maxima are potentially important. The South-facing site was significantly warmer than the North facing site. If temperature is related to permanent physical features such as aspect, it would seem reasonable to assume that there is some consistency between years, and thus that aspect and temperature are fixed features. The birds did however avoid nesting lower on the North-facing side, and such compensatory selection of sites may explain why clutch and brood size were not affected by aspect, even though laying date was.

The picture of the seabird colony which emerges is indeed one of considerable structure and heterogeneity. Nest sites do differ in their physical and biotic characteristics, and these characteristics are aggregated in space rather than being randomly distributed. There are areas where breeding performance is good and areas where breeding performance is poor. There is however relatively little evidence that any of the nest site features affect breeding performance, and further, some of the nest site characteristics and the spatial distributions of breeding success show changes between years. A nest which is successful one year may well be unsuccessful another year, and while it may be in an area of abundant parasites one year or abut onto a neighbouring nest, the same site may have few parasites the following year and the adjoining nest may have disappeared. With the results of a purely observational study, it is difficult to establish causation from correlation. What is clear from these results is that the marked spatial structures of breeding performance, parasite levels, and even physical nest site characteristics, observed in this particular Kittiwake colony were largely transient between years. We therefore propose that while seabird colonies may

be highly structured assemblages, this need not always reflect either consistent nest site quality or consistent adult quality. There is considerable turnover of birds at sites, and there are processes by which poor quality sites can fall into disuse, leaving a population which uses only the better sites.

When all these processes serve to disrupt spatial patterns of breeding success, it might be asked why spatial patterns occur at all. It is not possible to identify and record all facets of nest site quality and some transient but important features could easily be overlooked. However, as well as these, if local groups of birds copy each others' behaviour, then there could arise, by chance, groups of birds with behaviour appropriate for the conditions of that year. Even if birds consistently and repeatedly copy their neighbours' in say laying date, this does not imply that groups will continue to select the laying date most appropriate for the annual conditions. Clustering of good and poor performance could thus arise from a combination of stochastic factors and a lack of independence. It need not reflect regular differences in the quality of sites or of individuals.

Acknowledgements

The Carnegie Trust supported the work financially. Fieldwork on Høfnøya would have been difficult without the help of Rob Barrett (Tromsø Museum) and Geir Gabrielsen (N.I.N.A.). Jeff Hancock (Kelvingrove Museum) and Bob George identified the fleas. Glasgow University Computing Service provided assistance with computing, and in particular, James Currall gave advice regarding statistics.

References

- Aebischer, N.J. and Coulson, J.C. 1990. Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *J. Anim. Ecol.* 59: 1063-1071.
- Cole, T.J. and Lane, P.W. 1989. Procedure ORDINALLOGISTIC. in Payne, R.W. and Arnold, G.M. (eds.). *Genstat 5. Procedure Library Manual*. Lawes Agricultural Trust, Rothamsted Experimental Station, NAG, Oxford.
- Coulson, J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature* 217:478-479
- Coulson, J.C. 1971. Competition for breeding sites causing segregation and reduced young production in colonial animals. In 'Dynamics of populations' Eds. den Boer, P.J. and Gradwell, G.R. pp257-268. Centre for Agricultural Publishing, Wageningen.
- Coulson, J.C. and Thomas, C. 1985. Differences in the breeding performance of individual kittiwake gulls *Rissa tridactyla* (L.). in *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Sibly, R.M. and Smith, R.H. (eds). pp489-503. Blackwell Scientific, Oxford.
- Danchin, E., Cadiou, B., Monnat, J.-Y., and Estrella, R.R. 1991. Recruitment in long lived birds: conceptual framework and behavioural mechanisms. *Acta XX Congressus Internationalis Ornithologici* 1641-1656.

- Danchin, E. and Monnat, J-Y. 1992. Population dynamics of two neighbouring Kittiwake *Rissa tridactyla* colonies. *Ardea* 80: 171-180.
- Digby, P., Galwey, N., and Lane, P. 1989. *Genstat5. A Second Course*. Oxford University Press.
- Eeva, T., Lehikoinen, E., and Nurmi, J. 1994. Effects of ectoparasites on breeding success of great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) in an air pollution gradient. *Can. J. Zool.* 72:624-635.
- Feare, C.J. and Constantine, D.A.T. 1980. Starling eggs with spots. *Bird Study* 27:119-120.
- Furness, R.W. and Furness, B.L. 1981. A technique for estimating the hatching date of eggs of unknown laying date. *Ibis* 123:98-102.
- Goodburn, S.F. 1990. Territory quality or bird quality? Factors determining breeding success in the Magpie *Pica pica*. *Ibis* 133:85-90.
- Hatch, S.A., Roberts, B.D. and Fadely, B.S. 1993. Adult survival of Black-legged Kittiwakes *Rissa tridactyla* in a Pacific colony. *Ibis* 135:247-254.
- Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territorial quality. *Science* 210:1148-1150.
- Lane, P., Galwey, N. and Alvey, N. 1987. *Genstat5. An Introduction*. Oxford University Press.

- McCullagh, P. and Nelder, J. A. 1983. Generalized linear models. Chapman and Hall, London.
- McCullagh, P. 1980. Regression Models for Ordinal Data. J.R. Statist. Soc. B. 42:109-142.
- Monnat, J.-Y., Danchin, E., and Estrella, R.R. 1990. Evaluation de la qualite du milieu dans le cadre de la prospection et du recrutement: le squatterisme chez la Mouette tridactyle. C.R. Acad. Sci. Paris, t. 311, serie III:391-396
- Newton, I. (ed.) 1989. Lifetime reproduction in birds. Academic Press, London.
- Olsthoorn, J.C.M. and Nelson, J.B. (1990). The availability of breeding sites for some British seabirds. Bird Study 37:145-164.
- Oppliger, A., Richner, H. and Christe, P. 1994. Effect of an ectoparasite on lay date, nest site choice and desertion, and hatching success in the great tit (*Parus major*). Behavioural Ecology 5:130-134.
- Potts, G.R., Coulson, J.C. and Deans, I.R. 1980. Population dynamics and breeding success of the Shag, *Phalacrocorax aristotellus* on the Farne Islands, Northumberland. J. Anim. Ecol. 49:465-484.
- Richner, H., Oppliger, A. and Christe, P. 1993. Effect of an ectoparasite on reproduction in great tits. J. Anim. Ecol. 62:703-710.
- Thomson, D.L., Monaghan, P., and Furness, R.W. *submitted a*. Calculating nesting success: some refinements on the Mayfield method

Thomson, D.L., Furness, R.W. and Monaghan, P. *submitted b*. The technique of ordinal logistic regression for analysing ecological data.

Captions to Figures:

Figure 1a. Declining parasite levels in 1992 measured by scoring the amount of blood on eggs throughout the season.

Figure 1b. Declining parasite levels in 1993 measured by counting the bites on an observer exposed to parasites for constant periods throughout the season. (In 1993, blood scores on eggs were collected in a single short bout of visits to the nests, rather than over a protracted period, and so blood scores could not be used to examine seasonal changes in parasite activity).

Figure 2. Frequency of nests at stages indicated by the presence of 1.eggs, 2.small downy chicks, 3.large downy chicks, 4.small feathered chicks, 5.large feathered chicks. These are separated to show the differences in laying date between birds nesting on south-facing and north-facing sides of the gulley in 1992 and 1993.

Table 1. Relationships between daily breeding success of adjacent nests.

Type of losses	Spatial aggregations
1992 Nest(eggs)	$z=0.08$, $df=102$, ns
1992 egg	$z=0.46$, $df=98$, ns
1992 nest(chicks)	$t_{55}=0.41$, ns
1992 chick	$t_{52}=0.06$, ns
1993 nest(eggs)	$z=0.11$, $df=192$, ns
1993 egg	$z=2.33$, $df=192$, $P<0.05$
1993 nest(chicks)	$t_{51}=0.00$, ns
1993 chick	$t_{51}=0.15$, ns

Table 2. Relationship between breeding success observed at particular nest sites in the 2 years. (Tested using the 1992 breeding success as the independent variable in a binomial model of breeding success in 1993).

Measure of breeding success.	Binomial model of breeding success between years
Nest losses (incubation)	$t_{44}=0.15$, ns.
Egg losses	$t_{43}=0.27$, ns

Table 3. Frequencies of clutch sizes at particular sites between years.

		Clutch Size		
		1992		
		1	2	3
1993 Clutch	1	8	16	4
	2	10	36	6

Table 4. Frequencies where nests and nearest neighbours were lost or not lost.

	Nearest neighbour nest physically damaged	Nearest neighbour nest not physically damaged
Nest physically damaged - 1992	129	40
Nest not physically damaged - 1992	40	70
Nest physically damaged - 1993	281	23
Nest not physically damaged - 1993	23	23

Table 5. Frequencies of nests at particular sites which were physically damaged or not physically damaged during each of the years 1992 and 1993.

	Nest not lost in 1993	Nest lost in 1993
Nest not lost in 1992	85	7
Nest lost in 1992	18	16

Table 6. Spatial aggregations of nests with or without adjacent rock ledges.

	Adjacent nest with rock ledges	Adjacent nest without rock ledges
Nest with adjacent rock ledges - 1992	72	15
Nest without adjacent rock ledges - 1992	17	40
Nest with adjacent rock ledges - 1993	157	64
Nest without adjacent rock ledges - 1993	64	65

Table 7. Spatial aggregations of nests with or without adjacent nest space.

	Third nearest neighbour with abutting nest space	Third nearest neighbour without abutting nest space
Nest with abutting nest space - 1992	57	28
Nest without abutting nest space - 1992	21	29
Nest with abutting nest space - 1993	212	51
Nest without abutting nest space - 1993	51	36

Table 8a Frequencies of nest sites with or without unobstructed rock ledges in 1992 and 1993.

	Rock ledges in 1992	No rock ledges in 1992
Rock ledges in 1993	38	29
No rock ledges in 1993	30	10

Table 8b Frequencies of nest sites with or without abutting nest space in 1992 and 1993.

	Nest space in 1992	No nest space in 1992
Nest space in 1993	51	35
No nest space in 1993	7	14

Table 9. Effects of rock ledges and abutting nest space on breeding success.

Measure of breeding success (daily survival)	Effect of rock ledges	Effect of abutting nest space
Nest losses (incubation), 1992.	$z=0.88$, $df=95$, ns	$z=1.20$, $df=95$, ns
Egg losses, 1992	$z=0.21$, $df=92$, ns	$z=0.39$, $df=92$, ns
Nest losses(chick stage), 1992	$t_{40}=0.25$, ns	$t_{40}=0.60$, ns
Chick losses, 1992	$t_{38}=0.53$, ns	$t_{38}=0.52$, ns
Nest losses (incubation), 1993.	$z=0.17$, $df=198$, ns	$z=0.68$, $df=198$, ns
Egg losses, 1993	$z=0.06$, $df=196$, ns	$z=0.46$, $df=196$, ns
Nest(chick rearing), 1993	$t_{51}=0.00$, ns	$t_{51}=0.00$, ns
Chick losses, 1993	$t_{51}=0.94$, ns	$t_{51}=0.88$, ns

Table 10. Effect of nest site height on the daily rates of offspring losses. Height was treated as a five point scored ordinal variable in models of daily survival with binomially distributed errors.

Type of losses	Year	Significance of height effect
Nest survival (incubation)	1992	$t_{57}=1.07$, ns
Egg survival	1992	$t_{55}=1.67$, ns
Nest survival (chick rearing)	1992	$t_{16}=0.69$, ns
Chick survival	1992	$t_{15}=0.46$, ns
Nest survival (incubation)	1993	$z=0.74$, $df=109$, ns
Egg survival	1993	$z=1.39$, $df=109$, ns
Nest survival (chick rearing)	1993	no nests lost
Chick survival	1993	$t_{33}=0.27$, ns

Table 11. Effect of parasite levels on daily losses of offspring.

Breeding survival measure	Year	Effect of blood score (full model)
Nest losses (incubation)	1992	$z=1.07$, $df=119$, ns
Losses of eggs	1992	$z=0.21$, $df=115$, ns
Nest losses (chick stage)	1992	$t_{59}=0.18$, ns
Losses of chicks	1992	$t_{57}=0.04$, ns
Nest losses (incubation)	1993	$z=0.02$, $df=199$, ns
Losses of eggs	1993	$z=1.29$, $df=175$, ns
Nest losses (chick stage)	1993	No nests lost.
Losses of chicks	1993	$t_{51}=0.45$, ns

Table 12. Frequencies of occupied and unoccupied nests on the 2 sides of the gulley.

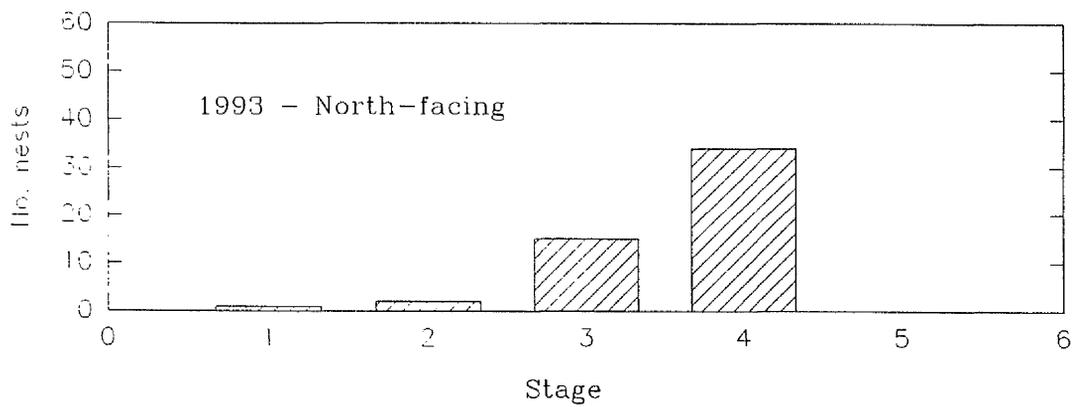
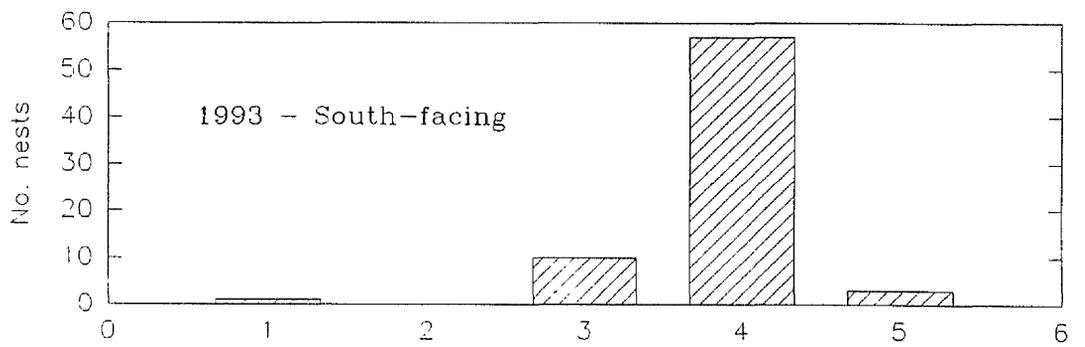
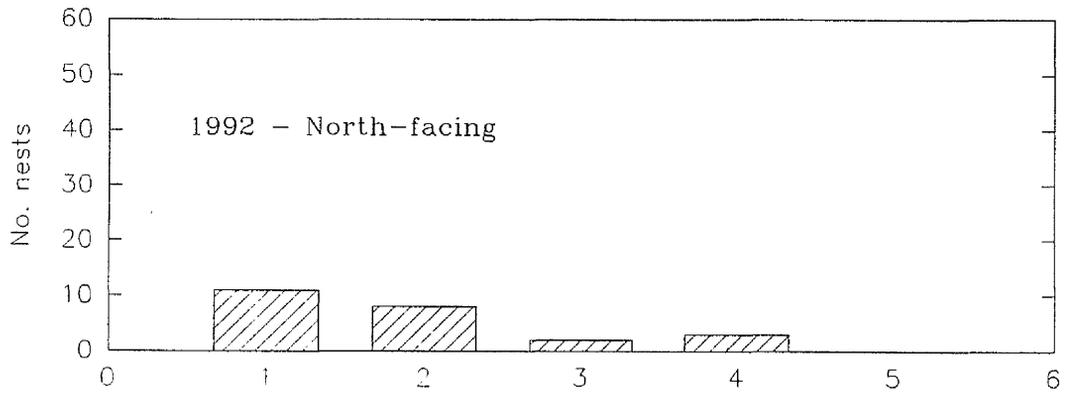
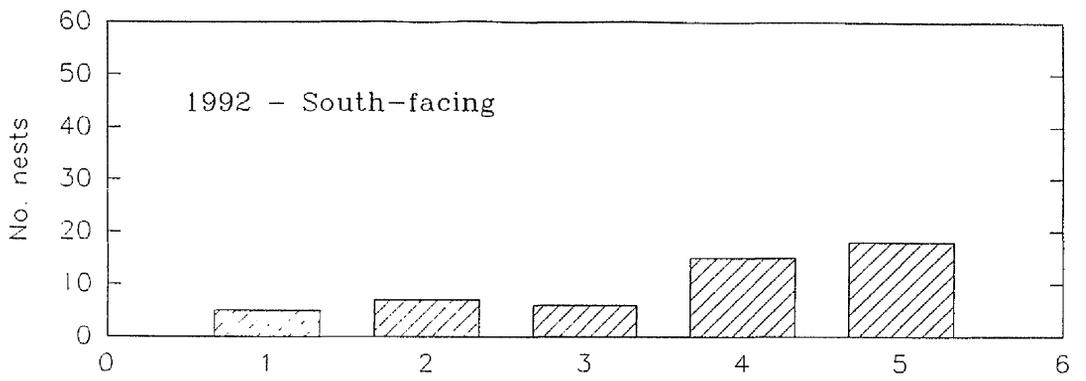
	Number of unoccupied nests	Number of occupied nests
South-facing	30	71
North-facing	56	52

Table 13. Temperature differences between 5 parts of the colonies.

	Min. daily temperature (°C)	Max. daily temperature (°C)
Effect of site on temperature	$F_{4,194}=2.60, p<0.05$	$F_{4,194}=4.34, p<0.01$
Site	Mean min daily temperature (°C)	Mean max daily temperature (°C)
1	5.9	9.9
2	6.7	12.1
3	6.6	9.8
4	6.3	12.2
5	6.6	10.3

Table 14. Effects of breeding success in 1992 on the likelihood that a site will be used for breeding in 1993.

Breeding survival variable	Statistics(binomial models).
Nest survival (incubation)	$z=0.64$, $df=95$, ns.
Egg survival	$z=2.72$, $df=93$, $p<0.01$
Nest survival (chick rearing)	$z=0.00$, $df=44$, ns
Chick survival	$z=0.00$, $df=43$, ns



Chapter 8

Does adult quality or chance account for the uneven division of lifetime reproductive success among individual swifts *Apus apus*?

David L. Thomson, Robert W. Furness, Pat Monaghan and Henry Douglas-Home.

Applied Ornithology Unit, Zoology Department, Glasgow University, G12 8QQ.

Abstract

If breeding adults differ in their quality - their ability to survive or reproduce - then this could give rise to an uneven division of lifetime reproductive success between members of a population. Individuals are however also subject to more random influences outwith their control and these could also affect the distribution of lifetime reproductive success within the population. We examined the importance of both adult quality and chance in the determination of annual breeding success, inter-annual survival, and lifetime reproductive success using models derived from a long term study of Swifts breeding in a fluctuating environment. Adult quality had a significant effect on annual breeding success - some good quality birds bred consistently well - but this accounted for only 10-15% of the variance. Further the survival of good breeders was no higher than that of poor breeders. Even in models which assumed that all individuals were of the same intrinsic quality, the most productive 20% of the birds could produce roughly half of all the offspring. When adult quality was then incorporated into the models, this result was virtually unaltered. Although adult quality was apparent in this population, it had almost no influence the distribution of lifetime reproductive success. For these Swifts breeding in fluctuating conditions, it is proposed that stochastic and environmental processes outwith the control of the birds have an important bearing on lifetime reproductive success. We further suggest that uneven divisions of lifetime reproductive success can not be assumed to reflect adult quality, and that significant adult quality effects may be overshadowed by stochastic effects and need not translate into marked differences in lifetime reproductive success.

Introduction

Studies of lifetime reproductive success in bird populations have generally revealed an uneven division of productivity, with a small number of successful birds in each generation producing a substantial fraction of all the offspring (Newton 1989). The annual reproductive success of individuals in the population is also far from uniform (Hogstedt 1980, 1981, Newton 1985), and in some species certain high quality individuals show not only consistently good annual success but combine this with high inter-annual survival (Smith 1981, Coulson and Thomas 1985). Lifetime reproductive success ('LRS') provides a reasonable measure of fitness (Gustafsson 1986, Newton 1989) and where the uneven divisions of success are linked to competitive dominance and the attainment of valuable resources such as territories or nest sites (Hogstedt 1980, Potts et al 1980), the concept of adult quality can be seen as a mechanism whereby intraspecific competition could mediate natural selection. If quality translates directly into fitness differences, then although it will generally not itself be a heritable trait (Fisher 1930), it can serve to integrate the selective benefits of adaptive genotypes, and thus provide an effective means by which good genes can spread through the population. However, the survival and reproductive success of birds is also influenced by factors outwith the control of either high or low quality individuals, and these random factors could have an important bearing on the distribution of LRS (Newton 1988, Fitzpatrick and Woolfenden 1989). To date, although both adult quality and stochastic factors have been shown to influence annual performance, and although LRS has been shown to be both unfairly divided yet consistent with a random distribution, the actual implications of both adult quality and stochastic factors for the distribution of LRS have not themselves been explored.

From the results of a long term study of marked Swifts *Apus apus*, Thomson et al. (*in press*) were able to construct regression models of both breeding success and adult survival which incorporated the multiple effects of weather, long term trends and breeding experience. By combining these models in a simulation, they explored the

potential implications of climatic variability for lifetime reproductive success. This same long term study also offers here the opportunity to examine whether individuals differ in quality. Further, by predicting the distribution of LRS between individuals using the regression models, it would be possible to predict the division of LRS caused by stochastic effects in the absence of quality effects. This distribution could then be compared with a more direct assessment of LRS which would include the effects of adult quality.

This study therefore aims to quantify the importance of adult quality for annual reproductive success and inter-annual survival in Swifts, to examine the division of lifetime reproductive success amongst members of the population, and then to consider whether it is the differences in adult quality which are translated into these differences in lifetime reproductive success. In so doing, the study aims to elucidate whether the most productive members of the population are also the highest quality members of the population or whether the lifetime productivities are governed more by stochastic processes.

Methods

A small population of individually ringed Swifts in 15 nest boxes has been visited annually since 1954 in order to follow breeding success and adult survival. Full details regarding the study site, methods of data collection, the construction of regression models and the execution of simulations are contained in Thomson et al. (*in press*). We aim not to replicate details of either methods or results here, but rather to apply the same data and analytical techniques to these distinct questions concerning the importance of adult quality.

Using ordinal logistic regression (McCullagh 1980, Cole and Lane 1989), a model of breeding success in relation to age, time, and weather, was constructed by Thomson et al. (*in press*). Ordinal logistic can estimate the probabilities of producing 0,1,2 or 3 chicks under any specified set of conditions. In thus recognising the

discontinuous nature of breeding success, it is highly suitable for predicting the distribution of breeding success between individuals. Comparable models of adult survival were generated using SURGE4 - the theory behind this technique is outlined in Clobert *et al.* (1987), numerous biological applications are outlined in Lebreton *et al.* (1992), and Pradel (1989) is a manual for executing the analyses.

Determining the effects of adult quality on annual breeding success and survival.

We examined whether certain individuals performed consistently well or consistently badly, and therefore whether adult quality was important in determining reproductive success. For each breeding attempt, we calculated residual breeding success from the mean predicted for a bird of the specified age breeding under the specified conditions using the models of Thomson *et al.* (*in press*). For adults which were captured more than once, we then analysed breeding success and residual breeding success for repeatability (Lessells and Boag 1989). Since adult quality can only be determined by repeated measures of performance, it is not readily incorporated into conventional regression models of this performance.

We examined whether birds with high breeding success also had high survival. We used SURGE4 to examine whether there were differences in survival between those producing more or fewer young than expected.

Simulations to explore the implications of the models for lifetime reproductive success.

After constructing the regression models of annual breeding success and inter-annual survival, their implications for the distribution of LRS among individuals was examined using a simulation following the techniques of Thomson *et al.* (*in press*). These models included no term for adult quality and so could be used to examine the predicted distribution of LRS generated from other factors. Full details of the methodology used in this simulation are given in Thomson *et al.* (*in press*).

The results were then compared with the empirical data which naturally includes any adult quality effects. For all adults captured at least once, the average annual

breeding performance was calculated, and lifetime reproductive success was estimated by projecting this over the period from first to last capture inclusive.

Results

Does adult quality influence annual breeding success?

For birds that were recorded breeding in more than one year, 'individual' had a significant effect on reproductive success ($F_{87,226}=1.662$, $p<0.01$) explaining 15.5% of the variance and constituting a repeatability of 0.155 ($N_0=3.626$. [N_0 is a parameter which describes the distribution of repeated observations between individuals - see Lessels and Boag (1989)]). However, part of this 'individual' effect may be an 'environment' effect because birds were breeding over narrow time spans ($\bar{x}=4.47$ years) in an environment showing long term changes (Thomson and Douglas-Home 1993) over the full 40 year study period. When residual reproductive success was used to control for this, 'individual' had a smaller, but still significant effect ($F_{87,226}=1.479$, $p<0.05$). The repeatability of residual breeding success is 0.117 - individuals explain 11.7% of the variance in residual annual breeding success.

Does adult quality influence annual survival?

No evidence could be found that birds producing greater than the predicted number of offspring had a survival rate which differed from those which produced fewer than predicted (Table 1.).

Is lifetime reproductive success distributed unevenly among individuals?

Figure 1a gives a frequency distribution of lifetime reproductive success, generated from the simulation which excludes effects of adult quality. The most

productive 20% of the population produce 53.0% of the offspring. The most productive 10% of the population produce 32.1%.

Does adult quality make the division of success more uneven?

When the empirical results are used (Figure 1b), and thus the effects of adult quality are included, the 20% with the highest lifetime success contribute 54%, and the top 10% produce 34.2% of the total offspring.

Discussion

Do individual swifts differ in quality?

There are indeed individuals which perform consistently well or consistently badly; not all Swifts are of equal quality. Even though Swifts can not defend territories or monopolise nutritional resources, differences in the performance of individuals are still an important determinant of annual breeding success and account for roughly 10-15% of the variance in breeding success. This does however leave 85-90% of the variance under stochastic influences, and further there is no evidence that these higher quality breeders are any better at surviving.

Birds which are competent breeders need not always have high LRS, especially if these good birds are not better at surviving. As in many other studies (Newton 1989), Thomson et al. (*in press*) found that breeding lifespan had a much greater influence on LRS than did mean annual breeding success. Breeding lifespan could account uniquely for 81.5% of the variance in LRS while mean annual breeding success could explain uniquely only 11.4%. Thus when individuals account for just over 10% of the variance in annual breeding success, and when mean annual breeding success then accounts for a similarly small fraction of the variance in LRS, then the product of these effects becomes negligible and adult quality has little impact on the variance in LRS.

Just as consistent differences in breeding success need not create marked differences in LRS, marked differences in LRS can arise without marked consistency in individual performance. Even in the simulation which excludes effects of adult quality, there are marked differences in the LRS of individuals. Though more egalitarian than some species (Newton 1989), the performance of individual birds is not uniform; some do very much better than others, and a small fraction of one generation contributes a large fraction of the next. These differences are apparent but are not due to adult quality - they are derived from a simulation which specifically excludes adult quality.

Lifetime reproductive success *is* thus unevenly divided, but incorporating the effects of adult quality does little to alter the patterns generated by the more stochastic environmental influences. The most productive section of the population is composed neither exclusively nor even largely of the highest quality individuals. In Swift populations, some poor birds 'strike it lucky' while many good birds are ruined by factors outwith their control. On average, good birds may do substantially better, but there are so many other factors influencing lifetime performance that simply being good is a very poor guarantee of success. Thomson et al. (*in press*) found that June temperatures affected breeding performance and that the form of this relationship had changed through time. They found additional long term trends in breeding success, mirrored by trends in adult survival, and they found adult survival was further influenced by July temperatures. With several stochastic and environmental factors impinging on LRS, small differences in individual breeding performance become swamped.

Is adult quality unimportant?

It remains possible that aspects of quality influence adult survival without influencing annual breeding success. These would be extremely difficult to measure - while consistently good breeding can be recognised as an indicator of quality, birds can only die once so consistently good survival can not easily be distinguished from chance.

These results demonstrate that adult quality accounts for a small fraction of the *variance* in LRS, but it remains possible that the *average* LRS performance of high quality birds could be substantially greater.

These results do not demonstrate that adult quality *does not* influence LRS - simply that stochastic processes do and that stochastic processes are important. For these swifts in a fluctuating environment, the results do not show that intraspecific competition and adult quality are unimportant. They show firstly that uneven divisions of LRS *can* arise by chance. Secondly, uneven divisions of LRS should not be assumed to reflect adult quality and intraspecific competition. Thirdly, even when adult quality effects are apparent and clear, they will not necessarily have an over-riding influence in the determination of lifetime reproductive success.

Acknowledgements

Carnegie Trust for the Universities of Scotland funded this analysis. We acknowledge Lady Caroline Douglas-Home, W.Murray, A.MacMillan, S. da Prato, A.Kerr, C.Badenoch, and the late R.J. Robertson for access to the birds and data collection. J.Currall, J.Buchanan, M.Partridge provided help and advice with statistics and computing, and R.Sibly, D.C.Houston and J.Currall kindly read drafts. Having begun the study in 1954, Henry Douglas-Home sadly died many years before the results of his work could be seen

References

- Clobert, J., Lebreton, J-D., and Allaine, D. 1987. A general approach to survival rate estimation by recaptures or resightings of marked birds. *Ardea* 75(1): 133-142.
- Cole, T.J. and Lane, P.W. 1989. Procedure ORDINALLOGISTIC. in Payne, R.W. and Arnold, G.M. (eds.). *Genstat5. Procedure Library Manual*. Lawes Agricultural Trust, Rothamsted Experimental Station, NAG, Oxford.
- Coulson, J.C. and Thomas, C. 1985. Differences in the breeding performance of individual kittiwake gulls *Rissa tridactyla* (L.). in *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Sibly, R.M. and Smith, R.H. (eds). pp489-503. Blackwell Scientific, Oxford.
- Digby, P., Galwey, N., and Lane, P. 1989. *Genstat5. A Second Course*. Oxford University Press.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Fitzpatrick, J.W. and Woolfenden, G.E. (1989). Florida Scrub Jay. In Newton, I. (ed.). 'Lifetime Reproduction in Birds.' Academic Press, London.
- Gustafsson, L. 1986. Lifetime reproductive success and heritability: Empirical support for Fisher's fundamental theorem. *Am. Nat.* 128: 761-764.
- Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territorial quality. *Science* 210:1148-1150.

- Hogstedt, G. 1981. Should there be a positive or a negative correlation between survival of adults in a bird population and their clutch size?
Am. Nat. 118: 568-571.
- Lack, D and Lack, E. 1951. The Breeding Biology of the Swift *Apus apus*.
Ibis 93(4): 501-546.
- Lane, P., Galwey, N. and Alvey, N. 1987. Genstat5. An Introduction. Oxford University Press.
- Lebreton, J-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62(1):67-118.
- Lessells, C.M. and Boag, P. T. 1989. Unrepeatable repeatabilities: a common mistake. The Auk 104:116-121.
- McCullagh, P. 1980. Regression Models for Ordinal Data. J.R. Statist. Soc. B. 42:109-142.
- Newton, I. 1985. Lifetime reproductive output of female sparrowhawks.
J. Anim. Ecol. 54:241-253.
- Newton, I. 1988. Individual performance in Sparrowhawks: the ecology of two sexes. Proc. Int. Orn. Congr. 19: 125-154.
- Newton, I. (ed). 1989. Lifetime reproduction in birds. Academic Press, London.

- Potts, G.R., Coulson, J.C. and Deans, I.R. 1980. Population dynamics and breeding success of the shag, *Phalacrocorax aristotellus* on the Farne Islands, Northumberland. *J. Anim. Ecol.* 49: 465-484.
- Pradel, R. 1989. User's Manual for Program SURGE4. Version 4.0.
C.E.P.E./C.N.R.S. BP5051 34033 MONTPELLIER-Cedex, France.
- Smith, J.N.M. 1981. Does high fecundity reduce survival in song sparrows. *Evolution* 35:1142-1148.
- Thomson, D.L. and Douglas-Home, H. 1994. Long term changes in weather and in the breeding schedule of Common Swifts *Apus apus*. in Malacarne, G. Collins, C.T. and Cucco, M.(eds) 'Recent Advances in the study of the Apodidae.' pp199-202. Avocetta 17, Turin.
- Thomson, D.L., Douglas-Home, H., Furness, R.W. and Monaghan, P. (*in press*). Breeding success and survival in the common swift *Apus apus*: a long term study on the effects of weather. *Journal of Zoology*, (London).

Table 1. Survival rates of Swifts producing more or fewer offspring than predicted.

	Survival from first to second year.	Survival beyond second year.
Birds producing fewer offspring than predicted.	70.75%. 95% C.I.=54.66-82.91	78.49%. 95% C.I.=71.75-83.99
Birds producing more offspring than predicted.	67.94%. 95% C.I.=52.75-80.09	77.49%. 95% C.I.=70.57-83.17

Captions to Figures.

- Figure 1. a. Frequency distribution of lifetime reproductive success generated from a simulation excluding the effects of adult quality.
b. Frequency distribution of lifetime reproductive success estimated from the average annual performance of individuals, and thus including the effects of adult quality.

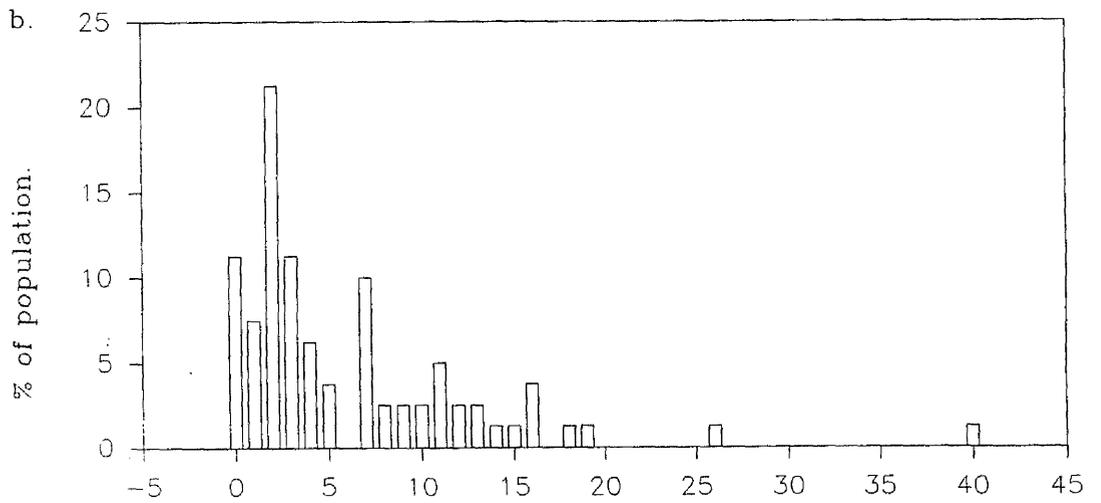
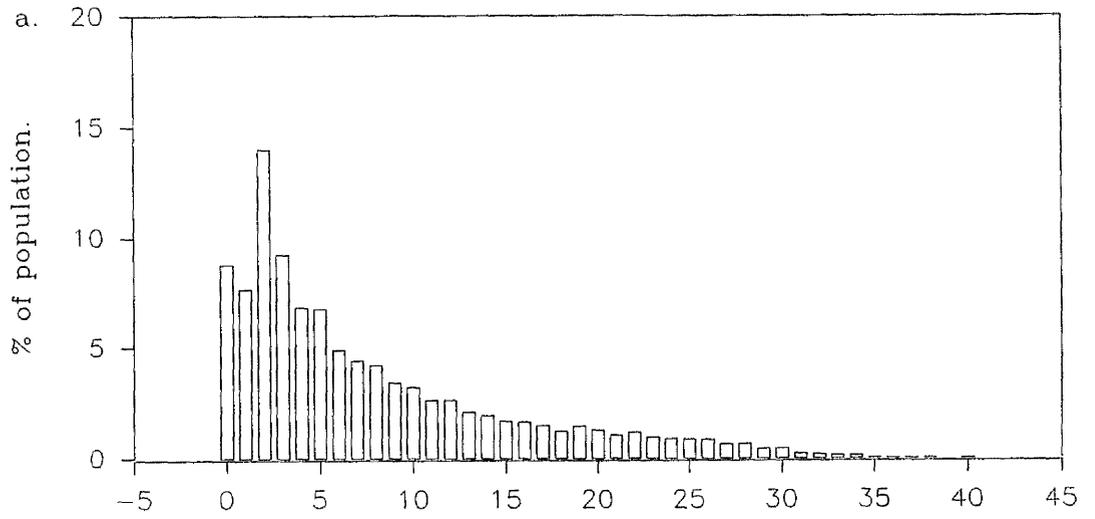


Figure 1.

Chapter 9

Does the life history strategy of the common swift *Apus apus* provide insurance in a fluctuating environment?

David L. Thomson, Henry Douglas-Home, Robert W. Furness, and Pat Monaghan

Applied Ornithology Unit, Division of Environmental and Evolutionary Biology,
Institute of Biomedical and Life Sciences, Glasgow University, G12 8QQ.

Abstract

Using the results of a long term study, the implications of fluctuating environmental conditions for the lifetime reproductive success of swifts were modelled. We examined whether the high survival and low reproductive output could reduce variance in lifetime reproductive success and thus insure the birds against environmental perturbations. Such buffering was found but it applied only in the narrow context of short term fluctuations in the breeding conditions afforded by temperatures during the early chick rearing stage. The birds were poorly protected from longer term fluctuations of temperatures at this stage and from short and long term changes in the conditions for adult survival afforded by the temperatures at the end of the breeding season. Although adult survival was high, it varied with July temperatures at the end of the season and this had major implications for variance in lifetime reproductive success. The environment also showed fluctuations which were of longer duration than could be insured against. Because the insurance was not effective, cohorts showed markedly different lifetime reproductive successes, and 8.8% of birds which attempted breeding showed complete lifetime reproductive failure. It is proposed that the life history strategy of the swift does not generally serve to reduce variance in reproductive performance.

Introduction

Although the *average* breeding success is of immense importance in determining fitness, organisms which can reduce the *variance* of their breeding success may protect themselves from catastrophes and thereby enhance their fitness (Stearns 1976, Bulmer 1985, 1992, Boyce 1988, Orzack and Tuljapurkar 1989). In fluctuating environments, it may be worth sacrificing average reproductive output for a safer bet-hedging strategy. Just as financial investors will accept lower profits in return for lower risks, so birds may adopt those life history strategies which reduce the risks of failure rather than those which simply maximise the average success.

Although the subject of much theoretical discussion, there have been few empirical tests of whether avian life history strategies offer appreciable bet-hedging. Results are equivocal and the empirical relevance of bet-hedging has been the subject of debate (Boyce and Perrins 1987, Liou *et al.* 1993).

The breeding biology of swifts *Apus apus* is heavily influenced by weather which varies from year to year (Lack and Lack 1951, Thomson *et al.* accepted). They might thus be expected to conform to the models of life history evolution within fluctuating environments, and to show patterns which reflect selection for reduced variance in performance. Swifts have a high adult survival rate of around 80% (Perrins 1971, Baillie and Green 1987, Lebreton *et al.* 1992), a single brood per year, and clutch sizes rarely greater than 3 eggs (Lack and Lack 1951). Swifts may deploy reproductive restraint to attain high survival, and they may use this high survival to maximise the chances of breeding in at least some good years. If adult survival is high and constant, while breeding success is low and temporally variable, then reproductive restraint could allow the birds to hedge their bets.

However, in analysing results from a long term study on swifts, Thomson *et al.* (accepted) found that adult survival itself was also affected by weather. If such effects on survival were sufficiently large, the high survival could cease to buffer the birds

against fluctuations in breeding success and could even increase variance in lifetime reproductive success. The potential of swifts to hedge their bets thus begs closer examination and swifts would seem to offer a good empirical test case on the existence of bet-hedging within avian life histories.

Using the regression models of annual breeding success, inter-annual survival, and lifetime reproductive success presented in Thomson et al. (*in press*), this study aims to determine whether the life history strategy of the swift allows the birds to absorb shocks of environmental fluctuations and thus reduces variance in lifetime performance. In examining the role of life histories in buffering LRS against environmental fluctuations we consider:

- whether cohorts differ in their lifetime reproductive success, in their mean annual breeding success, and in their mean breeding lifespan, or whether buffering smoothes out such potential differences.

- whether the differences in lifetimes reproductive success of cohorts increase with the time gap separating the cohorts, and thus whether the LRS is less well buffered against longer term fluctuations of periods longer than the birds' lifespans.

- whether many birds show complete lifetime failure or whether bet-hedging renders this much less frequent than failure in any one year.

Methods

Details of the study site, data collection, and weather records are given in Thomson et al. (*in press*), as are the techniques for modelling annual breeding success and inter-annual survival. Long term trends in weather are presented in Thomson and Douglas-Home (1993). We aim not to duplicate presentation of these methods or results. Rather we aim to exploit the same study and to employ similar modelling techniques for examining the separate question of whether the high survival of swifts can hedge bets in a fluctuating environment.

An individually marked population of swifts in 15 nest boxes has been followed annually since 1954, allowing the monitoring of breeding success and inter-annual survival in relation to age, time, and weather conditions. Thomson *et al.* (*in press*) constructed models of annual breeding success using ordinal logistic regression (McCullagh 1980, Cole and Lane 1989). They found that breeding success was positively correlated with June temperatures, that this relationship changed significantly through time, that there were further long term non-linear trends, and that breeding success increased then decreased with breeding age. They also constructed survival models using SURGE4 (Clobert *et al.* 1987, Pradel 1989, Lebreton *et al.* 1992), and found a positive relationship between survival and July temperatures. They found non-linear long term trends in survival which were comparable with those of breeding success. They then used simulations to consider the implications of these models for lifetime reproductive success.

Because the final regression models were built from variables whose significance had already been tested, it would be meaningless to test again the significance of effects on LRS with data yielded by the simulation. The simulation sought instead to explore and quantify the implications for LRS of the established significant effects on breeding success and survival. An indirect simulation, rather than direct observation of LRS was necessary because birds were only captured in 50% of breeding years.

We looked firstly at whether LRS varied between cohorts by examining whether 'cohort' explained any of the variance in LRS using a generalised linear model with normally distributed errors (see GENSTAT5 1987 for details of this technique). We then fitted a sine model by non-linear regression to look at how much of the variance in mean cohort LRS could be accounted for by a long term trend (the full protocol for non-linear regression is explained in GENSTAT5 1987 and Digby *et al.* 1989).

In order to identify whether fluctuations in LRS could be caused by fluctuations in breeding success, we used the same simulation to calculate the mean annual breeding success of the cohort as a whole. Using the weather variables which affected annual breeding success, we then looked at whether the weather in the year a cohort

commenced breeding explained any of the variance in the cohorts' overall mean annual breeding success (generalised linear model with normally distributed errors).

We repeated this procedure to look at whether fluctuations in LRS could be caused instead by fluctuations in adult survival. From the simulation, we calculated the mean breeding lifespan of individuals in the cohorts, and using the same generalised linear modelling approach with the weather variables which affected adult survival, we looked at whether weather conditions in the first year of breeding explained any of the variance in the mean breeding lifespan of the cohorts.

We examined also how the absolute magnitude of any differences between cohorts in mean LRS, mean annual breeding success, and mean breeding lifespan were affected by the time period separating them, and thus considered whether buffering might apply only to short term environmental fluctuations. To do this, we calculated the mean LRS, mean annual breeding success and mean breeding lifespan for each cohort from the simulation, and we then calculated, averaged, and plotted the absolute differences between all combinations of cohorts separated by 1,2,3... years.

Lastly, we examined whether high survival and repeated breeding made swifts less prone to complete catastrophic failure than birds which could breed only once in the fluctuating environment. Among those birds which attempted breeding, we calculated the frequency of cases where simulated LRS equalled zero and compared this with the frequency of failure among annual breeding attempts.

Results

Is LRS buffered against the fluctuating environment?

14.2% of the variance in LRS could be accounted for by cohort effects. In contrast to the overall mean of 7.65 young calculated from the simulation, birds in the most productive cohort produced on average 11.58 young per lifetime while those in the least productive cohort averaged only 3.04. Through time, a sine model (mean

cohort LRS = $6.03545 - \{2.45675 \times [\sin((\text{cohort number} + 0.35) / (24.21 / 2\pi))]\}$

accounted for 52% of the variance in mean cohort LRS, indicating that long term trends in environmental conditions caused long term trends in LRS (Figure 1.).

Lifetime reproductive success was thus not comprehensively insured against environmental fluctuations, and this begs the question of whether fluctuations in LRS are brought about by fluctuations in annual breeding success or by fluctuations in adult survival.

Is cohort mean annual breeding success buffered against fluctuations in annual breeding conditions?

Although Thomson et al. (*in press*) found that mean daily maximum June temperatures had a significant effect on the breeding success of birds in any one year, we found here that the June temperature in a cohort's first year of breeding explained none of the variance in the mean annual reproductive success experienced over the lives of individuals in that cohort ($F_{1,22} = 0.0167$. [That this is less than unity indicates that there can be no effect and that none of the variance is explained]). Thus while a cohort might get off to a bad start by breeding first in a poor year, survival is high enough to ensure that many of the individuals go on to breed in a mixture of good and bad years. The overall average annual breeding success of a cohort commencing breeding in a bad year can thus be similar to a cohort which happens to start breeding in a good year. The fluctuations in LRS would seem not to be due to these fluctuations in conditions for breeding.

Is cohort mean breeding lifespan buffered against fluctuations in annual conditions for survival?

Thomson et al. (*in press*) found that mean daily maximum July temperatures had a significant effect on the survival of birds to the next year, and here we found that July

temperatures in the first year of breeding could also account for 16.1% of the variance in mean cohort longevity. The performance of a cohort is reduced if breeding happens to commence in a year which is poor for survival.

Buffering and the duration of fluctuations

There was evidence that even short term fluctuations affected cohort LRS, and that the impact of fluctuations became even more marked when cohorts separated by increasing time spans were considered. Figure 2 shows how the average differences in mean LRS for cohorts changes with increasing time gaps between these cohorts. Adjacent cohorts show average absolute LRS differences of 1.52 young, while those separated by 15 years differ on average by 3.78 young. These differences between cohorts are appreciable since overall, the simulation calculates average lifetime productivities of 7.65 young.

The long term trend in mean cohort LRS described by the sine model accounted for 52% of the variance, but this left 48% of the variance unexplained - the importance of even short term environmental noise is still appreciable. The differences in mean LRS between cohorts separated by short time intervals are not due to effects of fluctuating breeding conditions because the high survival does ensure that overall average breeding success is averaged over several years and that breeding conditions in the first year of breeding have little impact. Adjacent cohorts differ in their mean annual reproductive success by only 0.06 young, which, all else being equal, translates into an LRS difference of only 0.27 young. By contrast, these neighbouring cohorts differ by 0.9 years in their mean longevity and all else being equal, this would translate into a 1.6 offspring difference in LRS. Short term fluctuations in annual conditions do translate into LRS differences, but the effect is mediated through fluctuating survival not through fluctuating annual reproductive success.

In contrast to cohorts separated by short time intervals, cohorts separated by 15 years differed in their mean annual reproductive success by 0.49 young, and all else

being equal, this translates into a 2.2 offspring difference in LRS. Thus although high survival may buffer birds from the effects of short term environmental fluctuations on breeding success, it provides no protection from long term perturbations. The difference in longevity of cohorts separated by 15 years amounts to 1.46 years or a 2.6 young difference in LRS. If they affect annual survival at all, environmental fluctuations of any duration can have an important effect on the lifetime performance of the cohort. Further, with an average breeding lifespan of 4.47 years, the life history strategy of the swift does not buffer either annual or lifetime breeding success against the longer term fluctuations which are characteristic of its aerial environment.

Do many birds show complete lifetime reproductive failure?

From the simulation, 8.8% of the birds which attempted breeding showed complete lifetime reproductive failure. This is indeed less than the 20.8% of annual breeding attempts which failed, but the reduction in the frequency of lifetime failure as compared with annual failure is far from impressive. High survival and an average breeding lifespan of 4.47 years does little better than halving the chances of producing no offspring at all.

Discussion

Do cohorts differ in lifetime reproductive success?

Marked differences in cohort LRS were detectable. Even cohorts commencing breeding in adjacent years differed in their lifetime performances. It would appear that the bet-hedging of swifts is very poor.

Adjacent cohorts did not differ substantially in the mean annual breeding success, measured over the lives of all individuals in the cohort. The birds would seem to be buffered from the short term fluctuations in breeding success, but the differences

in cohort LRS arise instead through effects on survival. The mean longevity of individuals differs substantially even between adjacent cohorts. Adult survival is exposed to fluctuations, and unlike breeding success, there is no way of protecting birds from this - a bird which fails to breed one year may survive to breed the next, but a bird which dies gets no such second chance.

Do longer term fluctuations have a greater impact?

As well as short fluctuations, Thomson and Douglas-Home (1993) found that long term trends in weather variables over the 40 year study period had occurred. Since these birds have an average breeding lifespan of 4.47 years, it is not surprising that longer term fluctuations have substantial effects. Even though the swifts are well buffered against short inter-annual fluctuations in June temperatures, they are not well buffered against the longer term changes which have occurred in their aerial environment.

Is the frequency of lifetime failure reduced by the life history strategy?

By breeding in more than one year, swifts can reduce the frequency of lifetime failure from 20.8% to 8.8% of breeding birds. Although some insurance is thus provided by the high survival, there still remains an appreciable number of birds which failed entirely.

The idea that swifts hedge their bets effectively in a fluctuating environment is not well borne out. Not only is the lifespan too short to contend with the typical longer term fluctuations, adult survival itself is strongly affected by variability in environmental conditions. Birds breeding in different cohorts did not show similar lifetime reproductive success, and repeated breeding only halved the frequency of complete failure compared with birds that could breed in only one year. Although the effects of short term fluctuations in breeding success are damped out by high survival, the life history strategy of these swifts is not one of effective bet-hedging.

Acknowledgements

The analysis of these data was funded by the Carnegie Trust for the Universities of Scotland. The nest boxes were erected and monitored initially by H D-H, but numerous others have helped check boxes and ring birds over the years. In particular we acknowledge W. Murray, A. MacMillan, S. da Prato, A. Kerr, C. Badenoch, and the late R.J. Robertson. C.O. Badenoch has also provided help with archiving and collating records, and with attempts to obtain research grants. Lady Caroline Douglas Home has kindly allowed us access to the birds each year. Drs. P. Monaghan and R. W. Furness have supervised DLT while analysing the data. Prof. R. Sibly, Dr. D.C. Houston, and Dr. J. Currall kindly read and commented on earlier drafts. J. Buchanan, J. Currall, and M. Partridge provided help with statistics and computing. Staff at the Meteorological Office provided help with the provision of data and discussed long term trends. Prof. C.M. Perrins suggested using SURGE4 to analyse the survival data, and Dr. R. McLeery helped in obtaining this software. Having begun the study in 1954, Henry Douglas-Home sadly died many years before the results of his work could be seen.

References

- Baillie, S.R. and Green, R.E. 1987. The importance of variation in recovery rates when estimating survival rates from ringing recoveries. In: North, P.M. (ed.). Ringing Recovery Analytical Methods. Acta Orn. 23:41-60.
- Boyce, M.S. and Perrins, C.M. 1987. Optimizing Great Tit clutch size in a fluctuating environment. Ecology 68:142-153.

- Boyce, M.S. 1988. Bet Hedging in Avian Life Histories. Proc. XIX Int. Orn. Congr. :2131-2139.
- Bulmer, M.G. 1985. Selection for iteroparity in a variable environment. Am. Nat. 126:63-71.
- Clobert, J., Lebreton, J-D., Allaine, D. 1987. A general approach to survival rate estimation by recaptures or resightings of marked birds. Ardea 75(1):133-142.
- Cole, T.J. and Lane, P.W. 1989. Procedure ORDINALLOGISTIC. in Payne, R.W. and Arnold, G.M. (eds.). GENSTAT5. Procedure Library Manual. Lawes Agricultural Trust, Rothamsted Experimental Station, NAG, Oxford.
- Digby, P., Galwey, N., and Lane, P. 1989. Genstat5. A Second Course. Oxford University Press.
- Lack, D. and Lack, E. 1951. The Breeding Biology of the Swift *Apus apus*. Ibis 93(4):501-546.
- Lane, P., Galwey, N. and Alvey, N. 1987. Genstat5. An Introduction. Oxford University Press.
- Lebreton, J-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62(1):67-118.
- Liou, L.W., Price, T., Boyce, M.S. and Perrins, C.M. 1993. Fluctuating environments and clutch size evolution in Great Tits. Am. Nat. 141(3):507-516.

- McCullagh,P. 1980. Regression Models for Ordinal Data.
J.R.Statist. Soc. B. 42:109-142.
- Orzack,S.H. and Tuljapurkar, S. 1989. Population dynamics in variable environments. VII. The demography and evolution of iteroparity.
Am.Nat. 133:901-923.
- Perrins,C. 1971. Age of First Breeding and Adult Survival Rates in the Swift.
Bird Study 18:61-70.
- Pradel,R. 1989. User's Manual for Program SURGE4. Version 4.0.
C.E.P.E./C.N.R.S. BP 5051 34033. MONTPELLIER-Cedex, France.
- Stearns, S.C. 1976. Life history tactics: a review of ideas. Q.Rev.Biol.51:3-47.
- Stearns,S.C. 1992. The Evolution of Life Histories. Oxford University Press,
Oxford. (Oxford Series in Ecology and Evolution).
- Thomson,D.L. and Douglas-Home,H. 1993. Long term changes in weather and in the breeding schedule of Common Swifts *Apus apus*. in Malacarne, G. Collins,C.T. and Cucco,M.(eds). Recent Advances in the Study of the Apodidae. pp199-202. Avocetta 17, Turin.
- Thomson, D.L., Douglas-Home, H., Furness, R.W. and Monaghan, P. (accepted).
Breeding success and survival in the common swift *Apus apus*: a long term study on the effects of weather. Journal of Zoology, (London).

Captions to Figures:

Figure 1. Long term trends in mean cohort lifetime reproductive success, described by a sine model.

Figure 2. Calculated average absolute differences in the mean lifetime reproductive success of cohorts separated by increasing time spans, as yielded by the simulation. Comparable values are shown for longevity, mean annual breeding success, and weather variables.

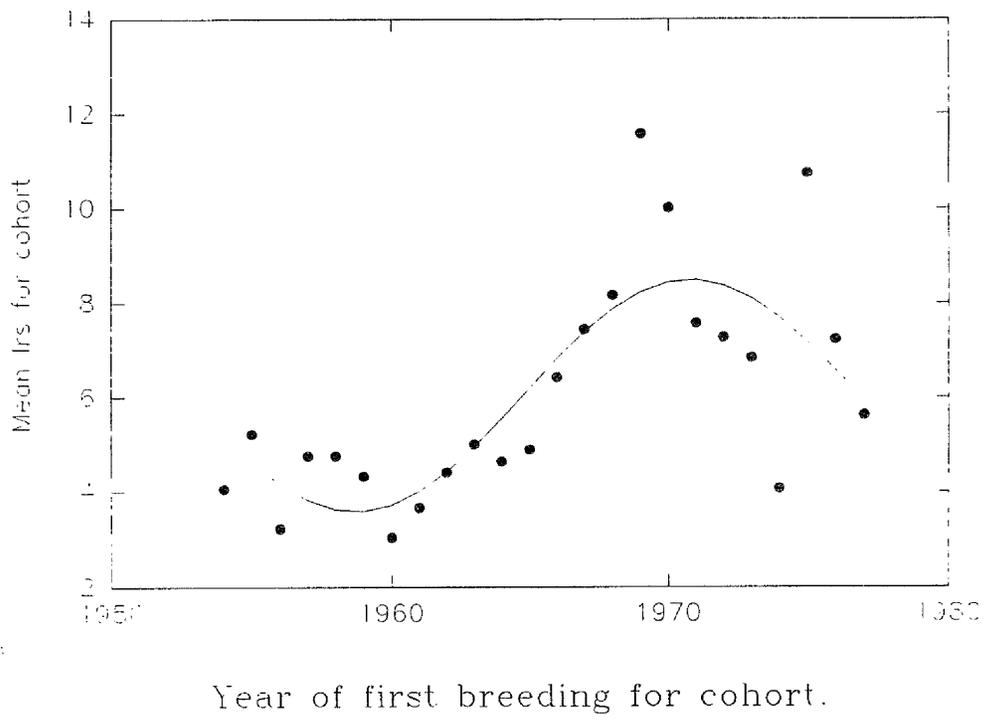


Figure 1

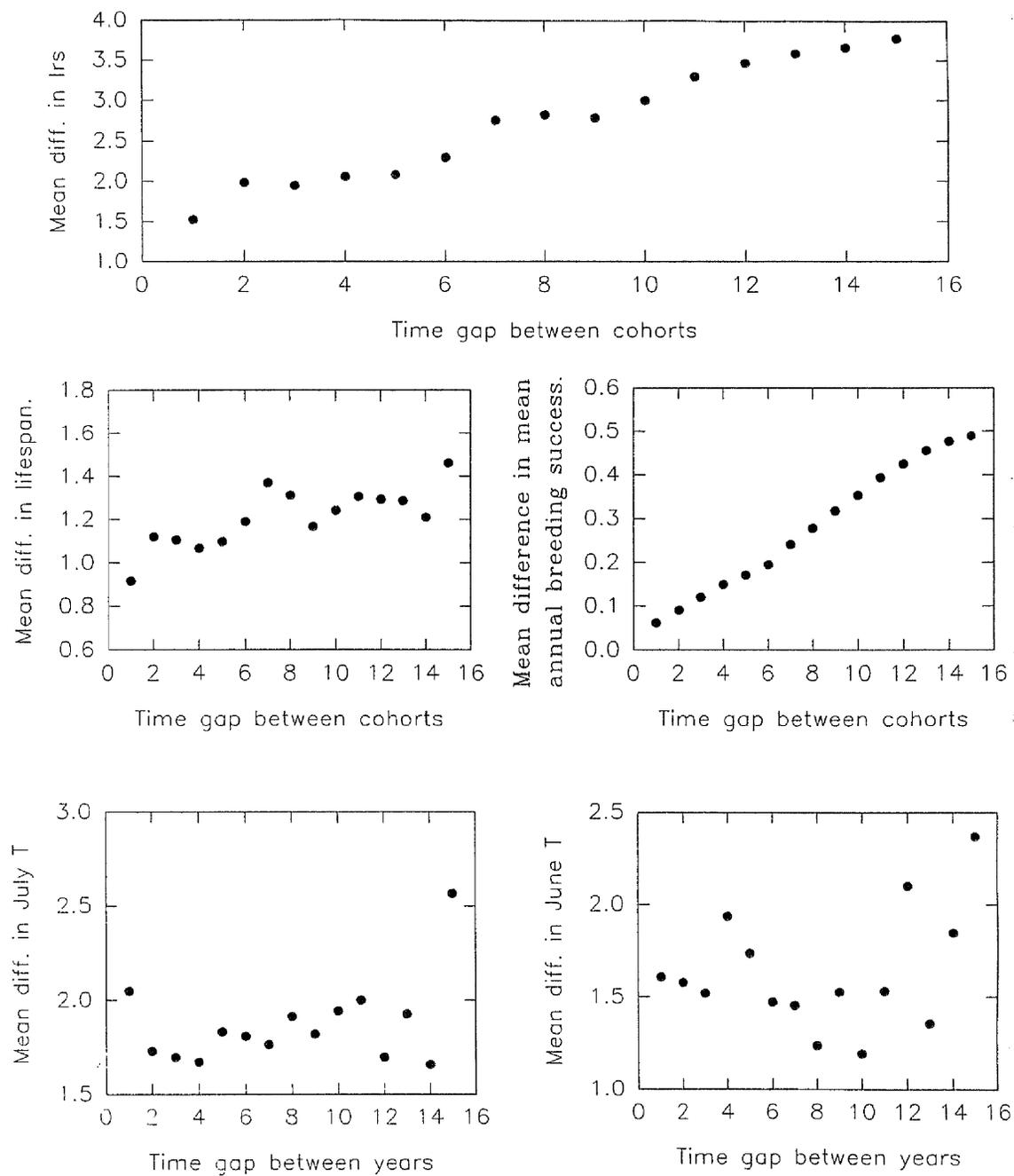


Figure 1.

Chapter 10

Do spatial constraints influence clutch size in a cliff nesting seabird?

David L. Thomson, Robert W. Furness, Pat Monaghan

Applied Ornithology Unit,
Zoology Department,
Glasgow University G12 8QQ.

Abstract

We examined whether differences in clutch size of cliff nesting kittiwakes could be due to differences in space available at the nest site for raising the offspring. Conventionally, clutch size is thought to be more influenced by the food available to meet the demands of breeding, but in cliff nesting birds, the amount of space available for the chicks, could conceivably influence the optimal clutch size. Using cliff-nesting Kittiwakes, and by comparing these with ground-nesting Herring Gulls, we looked at whether larger clutches were found in more spacious nests. We looked also at whether Kittiwakes with more spacious nest sites could sustain higher chick survival chick survival after brood size was enlarged. Nest size was very slightly larger where clutch size was larger, but the differences were too small to be important. This effect was apparent in Herring Gulls as well as Kittiwakes and was due to small physical effects of clutch size on nest diameter rather than biological effects of nest size on clutch size. There was no evidence that Kittiwake clutch sizes were larger when the nests had either adjacent rock ledges or abutting nest space. Where Kittiwake brood sizes were artificially increased to 3 chicks, there was no evidence that chicks survived better in large nests or in nests with either adjacent rock ledges or abutting nest space. It is concluded that spatial constraints did not affect clutch size in this study of cliff-nesting Kittiwakes.

Introduction

In the evolution of clutch size, the ecological factors regarded as being of critical importance have usually been nutritional or energetic (Drent and Daan 1980, Martin 1987, Bryant and Tatner 1988, Godfray *et al.* 1991). The capacity of birds to meet the energetic demands of chick-rearing (Lack 1947, Nur 1984), egg formation (Bolton *et al.* 1992), or incubation (Williams 1991, Moreno *et al.* 1991) are considered important in determining the optimal clutch size. Some other factors such as predation (Slagsvold 1982a, 1984, Lima 1987, Nur 1988) and parasitism (Moller 1992, Richner *et al.* 1993), which may arise from or aggravate nutritional stress, have received some attention, but the regulation of clutch size through spatial constraints (Slagsvold 1989a, 1989b) is more anomalous and has rarely been examined. Spatial constraints have been found not only in the special case of hole nesting species (Van Balen 1984, Slagsvold and Amundsen 1991), but also in open-nesters (Slagsvold 1982b), and so their wider applicability is quite possible. It is conceivable that evolutionary pressures might sometimes select for the clutch size which maximises breeding success given the space available for the chicks, rather than maximising breeding success given the overall nutritional resources. Further, just as birds with better territories and more abundant food can afford to lay larger clutches (Hogstedt 1980), so it is possible that birds which can build larger nests or defend more spacious sites could also afford to lay larger clutches.

Several cliff nesting seabird species select narrow ledges, and feed their chicks at these sites until they are fully grown (Olsthoorn and Nelson 1990). Spatial constraints are thus readily conceivable, but they have not previously been examined in this group of birds. Black-legged Kittiwakes *Rissa tridactyla* construct small nests on steep rock faces, and in contrast to many other cliff-nesters which produce only 1 egg, they can produce up to 3 eggs. They do however still commonly lay smaller clutches than comparable ground-nesters such as the Herring Gull *Larus argentatus*, and while the chicks of ground nesting gulls can wander freely near the nest, Kittiwakes can use

only the nest and the space provided by adjacent rock ledges or abutting nests. Given that breeding sites differ firstly in nest size, secondly in the presence or absence of adjacent rock ledges, and thirdly in the presence or absence of abutting nests, it would seem reasonable that the amount of space available to the chicks might account for differences in clutch size between Kittiwakes.

In this study, we aim to test the importance of space as a determinant of natural clutch size variance in Kittiwakes. We formulate and test the following predictions:

1. There may be an association between large nests and large clutches in cliff-nesting nidicolous Kittiwakes, but not in ground-nesting nidifugous Herring gulls.
2. Kittiwakes with adjacent rock ledges or abutting nest space may have larger clutches.
3. If brood size is increased experimentally, Kittiwakes with bigger nests, adjacent rock ledges or abutting nest space may be more successful in rearing these chicks.

Methods

In order to measure nest cup diameter and clutch size, 542 Kittiwake nests and 131 Herring Gull nests were visited during the incubation period, on the island of Hornoya, Norway, in 1993. Because of high measurement error, nest cup diameter was measured twice to the nearest millimetre and the average of the two measurements taken. The presence or absence of adjacent rock ledges and the presence or absence of abutting nest space was recorded for the Kittiwake nests, and the date of clutch completion was estimated from egg density (Furness and Furness 1981). Kittiwakes laid only clutches of one or two eggs, while Herring Gulls laid one, two or three.

In examining the association between measured nest diameter and clutch size it was necessary to control for the effects of laying date and the time since clutch completion. Measurements of Kittiwake nest cup diameter increased significantly with number of days since egg laying (Linear regression: $F_{1,287}=11.531$, $P<0.001$). Early clutches tended to be larger (Generalised linear model of clutch size [1 or 2 eggs] with binomially distributed errors: 'z' statistic of laying date effect =3.57, $df=294$, $P<0.001$. ['t' distributions converge towards 'z' distributions as the degrees of freedom exceed 60]) and thus larger clutches were measured later into their incubation period. The statistical significance of the effects of clutch size on nest diameter was therefore tested by adding clutch size as a categorical variable into a multiple linear regression model which already contained, and thus controlled for, the potentially confounding effects of time since laying and laying date.

In 1992, in order to check whether possible associations between nest size and clutch size might stem spuriously from simultaneous independent effects of adult body size on both variables, 80 female and 66 male adults were also trapped, and standard biometrics were taken. Lengths of sternum, head and bill, and bill *per se* were measured to the nearest 0.01mm using dial reading callipers. Tarsus and toe, and wing length were measured to the nearest millimeter using a ruler. Body weight was measured to the nearest gram using a pesola balance. A composite measure of body size was attained using principal components analysis (Rising and Somers 1989, Freeman and Jackson 1990). Clutch size and nest diameter were also determined for these birds. Using ANOVA, there was no evidence that any of these biometrics of either parent varied according to clutch size (all $p>0.1$) and similarly, using linear regression, there was no evidence that nest diameter was related to any measure of body size of either adult. This potentially confounding effect was therefore disregarded.

To look at whether spatial considerations might affect the number of chicks which could be reared, brood sizes of 3 chicks were created by adding chicks to 34 nests which originally had 2 eggs. After manipulating brood size, nests were then

visited every 2-3 days and breeding success was measured as daily survival rates of chicks, and analysed using generalised linear models with binomially distributed errors (chapter 2, section 4). In order to resolve the details of losses, three survival variables were used, and these were based on: (1.) Whether or not any chicks remained in the nest ('brood survival'); (2.) Whether or not any losses had occurred ('intact brood survival'); (3.) The average survival rates of the chicks in the nest ('chick survival'). Full details of this method are outlined in (chapter 2, section 4).

Results

Nest cup diameter and clutch size

Highly significant increases in nest diameter with clutch size could be detected in both Kittiwakes ($z=3.14$, $df=285$, $p<0.002$) and Herring Gulls ($F_{2,106}=9.61$, $p<0.001$), but these were too small to be of biological importance - in Kittiwakes an increase in clutch size from 1 to 2 eggs was matched by an average increase in nest diameter of only 2.91mm and Herring Gull nest diameter increased only 7.58mm with each extra egg. As is clear from figure 1, nest diameter increases through the incubation period, and it increases more where clutch size is larger.

Is clutch size affected by the presence of adjacent rock ledges or abutting nest space?

There was no evidence that clutch size was affected by adjacent rock ledges (ordinal logistic regression, $z=1.03$, $d.f.=309$, ns) nor by abutting nest space (ordinal logistic, $z=0.42$, $d.f.=309$, ns). [see McCullagh 1980, Cole and Lane 1989, and chapter 2, section 4 for details of ordinal logistic regression]. This conclusion was not altered if nest cup diameter was controlled in the analysis.

Nest cup diameter and breeding success.

Because nest diameter increases both with increasing time since laying, and with increasing clutch size, a measure of relative initial diameter was attained by using the residual diameter after controlling for the effects of clutch size and time since laying. Residual nest diameter had no detectable effects on any of the breeding survival variables after increasing brood size to 3 chicks (all $p > 0.1$, except 'intact brood survival' which showed an effect $0.1 > p > 0.05$ but this non-significant result was of the sign opposite to that predicted).

Adjacent rock ledges, abutting nest space, and breeding success.

There is no evidence that the presence of adjacent rock ledges affected any of the breeding survival parameters after increasing brood size (all $p > 0.1$), and nor was there any evidence that the presence of adjacent nest space had any influence on these parameters either (all $p > 0.1$).

Discussion

1. In Kittiwakes, there was a highly significant association between large nests and large clutches in 1993, but the magnitude of the differences in nest diameter were particularly small (less than 3mm per egg), and the effect was apparent in ground-nesting nidifugous Herring Gulls as well. In Kittiwakes, the mean nest diameter of 2 egg clutches was only 2.9mm larger than that of 1 egg clutches. A 100% increase in clutch size was matched by only a 1.84% increase in nest diameter. Nest diameter increased with time since egg-laying, and the nests of early breeding birds with larger clutches were measured later into incubation. It would seem that nest diameter is pushed out very slightly as incubation proceeds and that this effect is very slightly greater where clutch size is larger (Figure 1). It would seem less plausible that early breeding birds command sites where they can construct large nests and thus

accommodate large clutches. Clutch size causes small differences in nest size; it is not that small differences in nest size permit differences in clutch size.

2. Although it might be thought that nests with extra space available outwith the nest could accommodate more offspring, there was no evidence that the presence of either adjacent rock ledges nor abutting nest space were associated with larger clutches.

3. When brood size was enlarged experimentally from two to three chicks, there was no evidence that chicks survived better in nests which were larger, or which had either adjacent rock ledges or abutting nest space.

In these cliff nesting Kittiwakes, the hypothesis that clutch size is influenced ultimately by the amount of space available for the offspring was not supported. Some of the results were superficially consistent with the predictions outlined, but not in a way which was biologically meaningful. We propose that the results which appear consistent with the predictions are due to mundane physical processes rather than real biological phenomena.

This study indicates that in this species at this site during these years, the choice between the observed natural clutch size strategies was not influenced by spatial resources. This is not to say that space might not be of greater importance under different circumstances.

Acknowledgements

This research was supported by the Carnegie Trust for the Universities of Scotland. The fieldwork would have been very much more difficult without the help and cooperation of Rob Barrett (Tromso Museum), and Geir Gabrielsen (N.I.N.A). Staff at Glasgow University Computing Service helped with computing facilities, and in particular James Currall provided statistical advice. Neil Metcalfe gave useful comments on an earlier draft of this manuscript.

References

- Andersson, M. (1976). Clutch size in the Long-tailed Skua *Stercorarius longicaudus*: some field experiments. *Ibis* 118:586-588.
- Balen, J.H. van (1984). The relationship between nest-box size, occupation and breeding parameters of the great tit *Parus major* and some other hole-nesting birds. *Ardea* 72:163-175.
- Bolton, M, Houston,D. and Monaghan,P.(1992). Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. *J. Anim. Ecol.* 61:521-532.
- Bryant,D.M. and Tatner,P.(1988). The costs of brood provisioning: effects of brood-size and food supply. *Acta XIX Congressus Internationalis Ornithologicii*: 364-379.
- Bryant, D.M. (1988). Energy expenditure and body mass changes as measures of reproductive costs in birds. *Functional Ecology* 2:23-34.
- Cole,T.J. and Lane,P.W.(1989). Procedure ORDINALLOGISTIC. in Payne,R.W. and Arnold, G.M.(eds.). GENSTAT5. Procedure Library Manual. Lawes Agricultural Trust, Rothamsted Experimental Station, NAG, Oxford.
- Digby, P., Galwey,N., and Lane,P.(1989). *Genstat5. A Second Course*. Oxford University Press.
- Drent,R.H. and Daan,S (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225-252.

- Freeman, S. and Jackson, W.M. 1990. Univariate metrics are not adequate to measure avian body size. *Auk* 107:69-74.
- Furness, R.W. and Furness, B.L. 1981. A technique for estimating the hatching date of eggs of unknown laying date. *Ibis* 123:98-102.
- Godfray, H.C.J., Partridge, L. and Harvey, P.H. (1991). Clutch size. *Ann. Rev. Ecol. Syst.* 22:409-429.
- Hogstedt, G. (1980). Evolution of clutch size in birds: adaptive variation in relation to territorial quality. *Science* 210:1148-1150.
- Lack, D. (1947). The significance of clutch size. *Ibis* 89:302-352.
- Lima, S.L. (1987). Clutch size in birds: a predation perspective. *Ecology* 68:1062-1070.
- Lane, P., Galwey, N. and Alvey, N. (1987). *Genstat5. An Introduction*. Oxford University Press.
- Martin, T.E. (1987). Food as a limit on breeding birds: a life history perspective. *Ann. Rev. Ecol. Syst.* 18:453-487.
- McCullagh, P. (1980). Regression Models for Ordinal Data. *J.R. Statist. Soc. B* 42:109-142.

- Moreno, J., Gustafsson, L., Carlson, A. and Part, T. (1991). The cost of incubation in relation to clutch size in the Collared Flycatcher *Ficedula albicollis*. *Ibis* 133:186-193.
- Moller, A.P. (1993). Ectoparasites increase the cost of reproduction in their hosts. *J. Anim. Ecol.* 62:309-322.
- Nur, N. (1984). The consequences of Brood size for Breeding Blue Tits II. Nestling weight, offspring survival and optimal brood size. *J. Anim. Ecol.* 53:497-517.
- Nur, N. (1988). The cost of reproduction in birds: An examination of the evidence. *Ardea* 76.
- Olsthoorn, J.C.M. and Nelson, J.B. (1990). The availability of breeding sites for some British seabirds. *Bird Study* 37:145-164.
- Richner, H., Oppliger, A. and Christe, P. 1993. Effect of an ectoparasite on reproduction in great tits. *J. Anim. Ecol.* 62(4):703-710.
- Rising, J.D. and Somers, K.M. 1989. The measurement of overall body size in birds. *Auk* 106:666-674.
- Slagsvold, T. (1982a). Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54:159-169.
- Slagsvold, T. (1982b). Clutch size, nest size, and hatching asynchrony in birds: experiments with the Fieldfare (*Turdus pilaris*). *Ecology* 63:1389-1399.

Slagsvold, T. (1984). Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *J. Anim. Ecol.* 53:945-953.

Slagsvold, T. (1989a) On the evolution of clutch size and nest size in passerine birds. *Oecologia* 79:300-305.

Slagsvold, T. (1989b). Experiments on clutch size and nest size in passerine birds. *Oecologia* 80:297-302.

Slagsvold, T. and Amundsen, T. (1992). Do great tits adjust hatching spread, egg size and offspring sex ratio to changes in clutch size? *J. Anim. Ecol.* 61:249-258.

Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford University Press, Oxford. (Oxford Series in Ecology and Evolution).

Williams, J. B. (1991). On the importance of energy considerations to small birds with gynelateral intermittent incubation. *Acta XX Congressus Internationalis Ornithologici*: 1964-1975.

Captions to figures:

Figure 1. Relationship between nest diameter and time since the onset of incubation, separating nests differing in clutch size. There were no nests with clutches of 3 eggs.

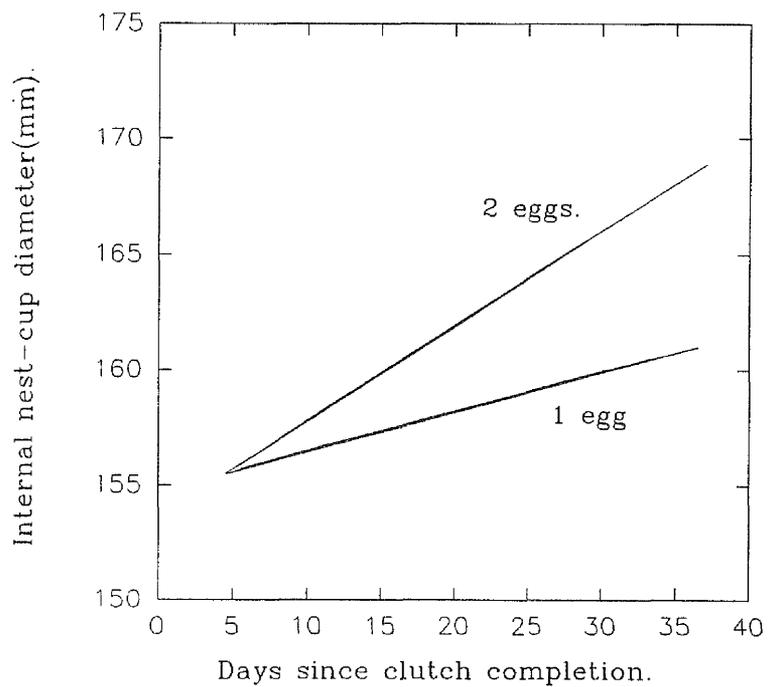


Figure 1.

Chapter 11

This manuscript has been provisionally accepted by 'Ecological Research'.

**Age-specific life history tactics in organisms with determinate growth:
optimal models for non-optimal behaviour?**

David L. Thomson.

Applied Ornithology Unit, Division of Environmental and Evolutionary
Biology, Institute of Biomedical and Life Sciences, Glasgow University
G12 8QQ.

Telephone 041 339 8855 ext 8033

Fax 041 330 5971

E-mail gbzv57@udcf.gla.ac.uk

Age-specific reproductive tactics

Abstract

Optimization models predict that reproductive effort should increase as individuals approach old age, but the assumptions are invalid since the senescence which generates the selective pressure may not itself be optimal. Population genetics models were developed to examine whether, in organisms with determinate growth, genes for age-specific changes in reproductive effort could invade the population when senescence was held in the population by 'mutation-accumulation'. In asexually reproducing organisms it was found that effort strategists could not invade unless their fitness exceeded the fitness of non-senescent individuals less the probability of suffering at least one mutation. In sexually reproducing organisms, genes for age-specific changes in effort could spread in the population under most circumstances.

Key words: age, reproductive effort, life history evolution, senescence, evolutionary model.

Introduction

Among organisms with determinate growth, reproductive effort is predicted to increase with age (Newton 1989, Clutton-Brock 1991, Roff 1992). However, conventional optimization techniques may be inappropriate here since reproductive effort is modelled as a response to senescence which may itself be non-optimal and maladaptive (Rose 1991).

Williams (1966b) proposed that the optimal behaviour of any individual is influenced by a balance between the immediate benefits it stands to gain from any current activity versus the concomitant future losses it stands to suffer. During breeding, this trade-off between current reproductive success and residual reproductive value is mediated by the costs of reproduction (Williams 1966a, Bell & Koufopanou 1986, Nur 1988, Roff 1992). Because individuals senesce as they grow old (Newton 1989, Saether 1990), residual reproductive value declines, the balance thus shifts, and the optimal response is to increase reproductive effort (Gadgil & Bossert 1970, Pianka & Parker 1975, Charlesworth & Leon 1976). If an individual is approaching senescence, it has little to lose in the future, so it makes sense to work hard and to take risks for the sake of its current offspring.

These predictions of optimality models may be satisfactory if senescence is pleiotropically adaptive (Williams 1957, Gustafsson & Part 1990) or if it is otherwise fixed in the population, but senescence may be a purely maladaptive character, maintained at equilibrium frequencies by a balance between mutation and selection (Medawar 1952, Rose 1991). If this 'mutation-accumulation hypothesis' applies, and if senescence is itself a maladaptive character under selection, then it would seem counter-intuitive that such senescence could provide the rigid basis upon which changing reproductive effort could be selected into the population. A senescing individual which adjusts its reproductive effort may be fitter than one which does not, but an individual which avoids senescence altogether would be fitter still.

When optimization techniques are inappropriate tools for studying either senescence or characters which respond to it, it would be valuable to use an alternative

approach. Life history models fall into two broad categories: optimality and population genetics (Roff 1992). Given that the assumptions of the former may be inappropriate, and given also that the relevant empirical evidence is both scant (Pugesek 1981, Clutton-Brock 1984, Gustafsson 1990, Hamer & Furness 1991) and equivocal (Nur 1984, Newton 1989), it would seem worth pursuing the latter. Population genetic models are used here to study whether an optimal strategy of age-related reproductive tactics can spread through a large population where senescence is maladaptive, non-pleiotropic and is held at equilibrium levels by a balance between mutation and selection.

Methods

The Modelling Approach

Population genetics models were constructed to examine the relative performances of the different possible age-related-effort and senescence strategies, taking into account their fitnesses and the mutation rates involved (Crow 1986, Hartl & Clark 1989). We identified the conditions under which a strategy of increasing reproductive effort could invade the population. Separate models of asexually and sexually reproducing individuals were constructed.

Although both traits are undoubtedly controlled by multiple genes, the complexity of the models quickly becomes impracticable if numerous genes are included (Hartl & Clark 1989). In order to maintain mathematical tractability, it was assumed initially that only two loci were involved - one for age-related-effort and one for senescence. Senescence was thus modelled as a trait caused by a very high mutation rate at a single locus rather than a low mutation rate at very many loci. Additional loci were then incorporated and I examined whether the conclusions were affected or whether the model was robust.

Also in order to preserve tractability and to avoid excessive complexity, I assumed that generations were non-overlapping, and that there was linkage equilibrium.

The Strategies

In the models, four phenotypic strategies were considered: 'constant', 'senescent', 'effort', and 'effort-plus-senescence'. The 'effort-plus-senescence' strategy was defined to show both senescence and the optimal age-related patterns of reproductive effort which correspond with this. Although the 'effort' strategy was defined as showing these same patterns of reproductive effort, it differed from 'effort-plus-senescence' because it did not actually suffer senescence. Thus 'effort' and 'effort-plus-senescence' both showed the same patterns of reproductive effort, but 'effort-plus-senescence' showed senescence, while 'effort' did not. The 'constant' strategy did not suffer senescence and was defined to maximise fitness in the absence of senescence - it did not adjust reproductive effort in the way that 'effort-plus-senescence' did. The 'senescent' strategy was defined to suffer senescence and declining residual reproductive value at older ages, but similarly it did not adjust its reproductive effort in response to this.

It is well established that the optimal response to inevitable senescence involves increasing effort with age (Gadgil & Bossert 1970, Pianka & Parker 1975, Charlesworth & Leon 1976). This derivation will not be presented again, nor will genetic models be employed to study circumstances where senescence is inevitable. This study aims to examine instead whether this optimal strategy can be selected into the population when senescence is not fixed.

Asexual Reproduction

In the models of asexual reproduction, each individual could possess only one of the four strategies and, except where mutations occurred, could conceive only

offspring with this strategy. Changes in the relative frequencies of the four strategies could occur by replication and mutation. The performance of pairs of strategies in relation to each other were studied in turn. Having established conclusions from this model, the number of loci at which senescence could occur was increased and the robustness of the conclusions was studied.

Sexual Reproduction

In models of diploid sexually reproducing organisms, selection was studied at 2 loci; one for 'senescence' and one for 'effort', each with a dominant and a recessive allele. Separate models were constructed to look at senescence as a dominant and as a recessive trait, but genes for increased effort were assumed to be dominant over the 'constant' counterparts. The genes were termed 'senescent', 'nosen', 'effort', and 'coneff'.

The frequency changes of the phenotypic strategies depend on gene assortment and recombination as well as mutation and replication. Random mating, linkage equilibrium and no overdominance were assumed (see e.g. Hartl & Clark 1989).

At first equilibria between senescent and non-senescent strategies in the absence of any age-related increases in reproductive effort were studied. Having identified these equilibria, the ability of strategies of increasing reproductive effort to invade was examined.

Terms and symbols.

The following terms were used in the equations:

Gene frequencies:

These are the frequencies in the current generation; p' and q' etc. are used to represent frequencies in the next generation, and p^{\wedge} and q^{\wedge} denote equilibrium frequencies.

p_{coneff} - The frequency of the 'coneff' gene in the population.

p_{nosen} - The frequency of the 'nosen' gene in the population.

q_{effort} - The frequency of the 'effort' gene in the population.

$q_{\text{senescent}}$ - The frequency of the 'senescent' gene in the population.

Gene fitnesses:

\bar{w} - Average fitness of all genes in the population.

ω_{coneff} - The average fitness of the 'coneff' gene in the population.

ω_{nosen} - The average fitness of the 'nosen' gene in the population.

ω_{effort} - The average fitness of the 'effort' gene in the population.

ω_{senesent} - The average fitness of the 'senescent' gene in the population.

These average fitnesses vary depending on the frequencies of the phenotypes of which they are part. Formulae for calculating these average gene fitnesses are given in Appendix I.

Phenotype frequencies:

These are frequencies in the current generation; F' etc. is used to indicate frequencies in the next generation. Non-overlapping generations are assumed.

F_{constant} - Frequency of the 'constant' phenotype in the population of sexually reproducing individuals.

F_{effort} - Frequency of the 'effort' phenotype.

$F_{\text{senescent}}$ - Frequency of the 'senescent' phenotype.

F_{effsen} - Frequency of the 'effort-plus-senescent' phenotype.

Strategy-dependent fitnesses:

These are the fitnesses of genes in particular phenotypes. In asexual reproducers, these are the per capita growth rates of individuals. In sexual reproducers, these are the per gene-copy rates of replication of genes in individuals with the 'constant' phenotype. In all cases, these are the fitnesses in the absence of mutation.

W_{constant} - Average fitness of 'constant'.

W_{effort} - Average fitness of 'effort'.

$W_{\text{senescent}}$ - Average fitness of 'senescent'.

W_{effsen} - Average fitness of 'effort-plus-senescent'.

\bar{W} - Average fitness of strategies in population.

Mutation rates:

$\mu_{\text{senescence}}$ - mutation rate for senescence. The probability that an asexual 'constant' or 'effort' individual will mutate at conception to 'senescent' or 'effort-plus-senescence' respectively

μ_{nosen} - mutation rate of 'nosen' genes to 'senescent' genes in sexually reproducing organisms.

The rate of back-mutation from senescence may be similar to the rate of mutation producing age-related strategies of reproductive effort, and both are here assumed to be negligible. It is assumed that all mutations occur at conception of the offspring.

The ranking of strategies according to fitness

By definition, $W_{\text{effort}} < W_{\text{constant}}$. Further, because 'effort-plus-senescence' by definition shows the age-specific pattern of reproductive effort which maximises fitness in the presence of inevitable senescence, it follows that $W_{\text{senescent}} < W_{\text{effsen}}$, i.e. an individual which makes the optimal adjustment of reproductive effort in the face of senescence is fitter than an individual which fails to adjust its reproductive effort, but works instead at the level appropriate in the the absence of senescence. Also, if senescence persists by mutation-accumulation, then $W_{\text{senescent}} < W_{\text{effsen}} < W_{\text{constant}}$. Generally also, $W_{\text{senescent}} < W_{\text{effsen}} < W_{\text{effort}} < W_{\text{constant}}$. Because 'constant' is the fittest strategy, $W_{\text{constant}} = 1$.

Results and discussion

A. Asexually reproducing organisms.

a.) Equilibrium between 'senescent' and 'constant'.

The frequency of 'senescent' strategists changes between generations according to:

$$F'_{\text{senescent}} = \{ [F_{\text{senescent}} \times W_{\text{senescent}}] + [F_{\text{constant}} \times W_{\text{constant}} \times \mu_{\text{senescence}}] \} \bar{W}$$

The frequency of 'constant' strategists changes between generations according to:

$$F'_{\text{constant}} = [F_{\text{constant}} \times W_{\text{constant}} \times (1 - \mu_{\text{senescence}})] / \bar{W}$$

If stability of gene frequencies is attainable, then at equilibrium $F'_{\text{senescent}}/F'_{\text{constant}}$ is constant, $k_2 = F_{\text{senescent}}/F_{\text{constant}}$. If such a point can be reached, then the relative frequencies must clearly then be stable because relative gene frequencies in one generation always equal those in the next. Although it is not so easy to determine whether frequencies will always converge towards this point, by identifying a point which fulfills these conditions, it is possible to determine whether there is a stable point or whether such an equilibrium is unattainable.

$$F'_{\text{senescent}}/F'_{\text{constant}} = \frac{([F_{\text{senescent}} \times W_{\text{senescent}}] + [F_{\text{constant}} \times W_{\text{constant}} \times \mu_{\text{senescence}}]) / \bar{W}}{([F_{\text{constant}} \times (W_{\text{constant}} \times (1 - \mu_{\text{senescence}}))] / \bar{W})}$$

$$\Rightarrow k_2 = \frac{([F_{\text{senescent}} \times W_{\text{senescent}}] + [F_{\text{constant}} \times \mu_{\text{senescence}}])}{([F_{\text{constant}} \times (1 - \mu_{\text{senescence}})])}$$

$$= [k_2 \times W_{\text{senescent}} / (1 - \mu_{\text{senescence}})] + [\mu_{\text{senescence}} / (1 - \mu_{\text{senescence}})]$$

$$\Rightarrow k_2 \times \{1 - (W_{\text{senescent}}) / (1 - \mu_{\text{senescence}})\} = [\mu_{\text{senescence}} / (1 - \mu_{\text{senescence}})]$$

$$\Rightarrow k_2 = [\mu_{\text{senescence}} / \{1 - \mu_{\text{senescence}} - W_{\text{senescent}}\}]$$

A balance between 'constant' and 'senescent' can occur provided $\mu_{\text{senescence}} > 0$, and $W_{\text{senescent}} < 1 - \mu_{\text{senescence}}$. In other words, senescence must be perpetually produced by mutations and 'senescent' strategists must be less fit than 'constant' strategists less the mutation rate. These requirements are fulfilled here, and this implies that there do indeed exist some conditions under which senescence can persist as a maladaptive character without becoming fixed in the population. This does not however necessarily imply that the equilibrium will always be attained. The issue of attainability need not be tackled until the stability of the the other strategies relative to these *potentially* stable strategies has been considered.

b.)Relative performance of 'effort' and 'constant' strategies.

The frequency of the effort strategists changes according to:

$$F'_{\text{effort}} = [F_{\text{effort}} \times (W_{\text{effort}} \times (1 - \mu_{\text{senescence}}))] / \bar{W}$$

Stability in the frequencies of the 'effort' and 'constant' strategies relative to each other implies that $F'_{\text{effort}}/F'_{\text{constant}}$ is constant $=k_1 = F_{\text{effort}}/F_{\text{constant}}$. So

$$F'_{\text{effort}}/F'_{\text{constant}} = \frac{\{[F_{\text{effort}} \times (W_{\text{effort}} \times (1 - \mu_{\text{senescence}}))] / \bar{W}\}}{\{[F_{\text{constant}} \times (W_{\text{constant}} \times (1 - \mu_{\text{senescence}}))] / \bar{W}\}}$$

$$\Rightarrow k_1 = \frac{\{[F_{\text{effort}} \times (W_{\text{effort}} \times (1 - \mu_{\text{senescence}}))]\}}{\{[F_{\text{constant}} \times (W_{\text{constant}} \times (1 - \mu_{\text{senescence}}))]\}}$$

$$\Rightarrow k_1 = k_1 \times \{(W_{\text{effort}} \times (1 - \mu_{\text{senescence}})) / (W_{\text{constant}} \times (1 - \mu_{\text{senescence}}))\}$$

$$\Rightarrow W_{\text{effort}} \times (1 - \mu_{\text{senescence}}) = W_{\text{constant}} \times (1 - \mu_{\text{senescence}})$$

$$\Rightarrow W_{\text{effort}} = W_{\text{constant}}$$

These 2 strategies can only co-exist relative to each other if they share identical fitnesses. However $W_{\text{effort}} < W_{\text{constant}}$ and $W_{\text{constant}} = 1$, so 'effort' can not persist relative to 'constant' and this clearly implies also that it can not persist in the population. In other words, the only stable points are degenerate e.g. when $k_1 = 0$, which would occur if $F_{\text{effort}} = 0$. Under these circumstances, because:

$$F'_{\text{effort}} = [F_{\text{effort}} \times (W_{\text{effort}} \times (1 - \mu_{\text{senescence}}))] / \bar{W}$$

then

$$F'_{\text{effort}} = [0 \times (W_{\text{effort}} \times (1 - \mu_{\text{senescence}}))] / \bar{W} = 0$$

and also because

$$F'_{\text{effort}}/F'_{\text{constant}} = \frac{\{[F_{\text{effort}} \times (W_{\text{effort}} \times (1 - \mu_{\text{senescence}}))] / \bar{W}\}}{\{[F_{\text{constant}} \times (W_{\text{constant}} \times (1 - \mu_{\text{senescence}}))] / \bar{W}\}}$$

then

$$0/F'_{\text{constant}} = \frac{\{[0 \times (W_{\text{effort}} \times (1 - \mu_{\text{senescence}}))] / \bar{W}\}}{\{[F_{\text{constant}} \times (W_{\text{constant}} \times (1 - \mu_{\text{senescence}}))] / \bar{W}\}} = 0 = k_1$$

and thus the system is stable once 'effort' has gone to extinction.

c.) Relative performance of 'effort' and 'senescent' strategies.

It follows that if an equilibrium is reached between 'constant' and 'senescent', and if 'effort' can not persist relative to 'constant', then 'effort' also can not persist relative to 'senescent' either, unless $W_{\text{constant}} = W_{\text{effort}}$.

d.) Relative performance of 'constant' and 'effort-plus-senescence'.

The 'effort-plus-senescence' strategy changes frequency between generations according to the equation:

$$F'_{\text{effsen}} = \{ [F_{\text{effsen}} \times W_{\text{effsen}}] + [F_{\text{effort}} \times \mu_{\text{senescence}}] \} / \bar{W}$$

Equilibrium between 'constant' and 'effort-plus-senescence' implies that $F'_{\text{effsen}} / F'_{\text{constant}}$ is constant, $= k_3 = F_{\text{effsen}} / F_{\text{constant}}$. Thus:

$$\begin{aligned} k_3 &= \left(\frac{[F_{\text{effsen}} \times W_{\text{effsen}}] + [F_{\text{effort}} \times \mu_{\text{senescence}}]}{[F_{\text{constant}} \times (W_{\text{constant}} \times (1 - \mu_{\text{senescence}}))]} \right) / \bar{W} \\ &= \frac{[F_{\text{effsen}} \times W_{\text{effsen}}] + [F_{\text{effort}} \times \mu_{\text{senescence}}]}{[F_{\text{constant}} \times (W_{\text{constant}} \times (1 - \mu_{\text{senescence}}))]} \\ &= \left\{ k_3 \times \frac{W_{\text{effsen}}}{(1 - \mu_{\text{senescence}})} \right\} + \\ &\quad \left\{ [F_{\text{effort}} / F_{\text{constant}}] \times (1 - \mu_{\text{senescence}}) \right\} \end{aligned}$$

However, $F_{\text{effort}} / F_{\text{constant}}$ tends towards zero (see b.) so this simplifies to:

$$\begin{aligned} k_3 &= \left\{ k_3 \times \frac{W_{\text{effsen}}}{(1 - \mu_{\text{senescence}})} \right\} \\ \Rightarrow \quad \frac{W_{\text{effsen}}}{(1 - \mu_{\text{senescence}})} &= 1 \\ \Rightarrow \quad W_{\text{effsen}} &= 1 - \mu_{\text{senescence}} \end{aligned}$$

The conditions for stability are so narrowly defined that equilibrium is again unlikely. If $W_{\text{effsen}} < W_{\text{constant}}$, and if this fitness difference exceeds the mutation rate, then 'effort-plus-senescence' will go towards extinction - where F_{effort} tends to zero, the rate at which 'effsen' spreads equals ' W_{effsen} ', while 'constant' spreads at a rate of ' $W_{\text{constant}} \times (1$

- $\mu_{\text{senescence}}$)' or $(1 - \mu_{\text{senescence}})$ '. The strategy which spreads less fast is 'effsen' so, relative to 'constant', it must follow a path of diminishing importance within the population. In the less likely event that $W_{\text{effsen}} > W_{\text{constant}} - \mu_{\text{senescence}}$, 'effsen' will invade because it will spread faster.

Thus, if senescence is a maladaptive trait held at equilibrium frequencies by a balance between mutation and selection, then a strategy of increased reproductive effort with age can not invade the population unless its fitness exceeds the fitness minus the mutation rates of non-senescent individuals which do not display this strategy. This is unlikely, and so even if an equilibrium between senescent and non-senescent individuals can be attained, a strategy of increasing reproductive effort can not invade.

Although 'senescent' individuals are less fit than 'constant' ones, they can potentially persist because new stocks are perpetually produced by mutation. 'Effsen' individuals are also less fit than 'constant' strategists, but unlike 'senescent' individuals, they are not produced by mutation. In asexual reproducers, 'senescent' individuals can not acquire the 'effort' strategy to become 'effsen' by recombination. Thus, although it might be thought that the ability of 'effsen' strategists to spread in the population would depend directly on the equilibrium abundance of 'senescent' individuals and on the fitness of 'effsen' relative to 'senescence', this model indicates that the ability of 'effsen' to spread in the population depends more directly on its fitness relative to the fitness of 'constant' less the mutation rate. Overall, even if senescence is an abundant trait and even if increasing reproductive effort would enhance the fitness of these senescent individuals, any trait which spreads less rapidly than 'constant' individuals and which can not be propped up by recurrent mutation must inevitably be selected out of the population. 'Effsen' may be selected out of the population less quickly than 'senescent', but it is indeed still selected out and unlike 'senescent' it is not perpetually reintroduced by mutation.

Do these conclusions change if senescence occurs at more than one locus?

In reality, senescence occurs at more than one locus. The model would be more realistic if the same mutations were spread over a greater number of loci.

With more loci, there are many more strategies in the population, but the arguments are similar. Partial and complete senescence can potentially persist in equilibrium with 'constant' provided the mutation rate is greater than zero, and provided the senescent strategies are less fit than 'constant'. If each can persist in equilibrium with 'constant', then it follows that they must also be able to reach equilibrium with each other.

With 2 potentially senescent loci, 'effort plus partial senescence' can invade only if $W_{\text{effsen1}} - \mu_{\text{sen}} > W_{\text{constant}} - [(2x\mu_{\text{sen}}) - \mu_{\text{sen}}^2]$. If this is not possible, then 'effort plus complete senescence' can invade only if $W_{\text{effsen2}} > W_{\text{constant}} - [(2x\mu_{\text{sen}}) - \mu_{\text{sen}}^2]$.

' W_{senj} ' is the fitness of individuals with senescence at 'j' loci. μ_{sen} is the per-locus mutation rate producing senescence. The term $[(2x\mu_{\text{sen}}) - \mu_{\text{sen}}^2]$ is the probability that a 'constant' individual will suffer at least one mutation in any generation. In expanding the model, it is assumed that the same per-individual mutation rate is spread over a greater number of loci, so in fact the conditions change little even though more loci are involved.

Introducing a third locus, it follows that 'effort plus senescence at one locus' invades only if $W_{\text{effsen1}} - [(2x\mu_{\text{sen}}) - \mu_{\text{sen}}^2] > W_{\text{constant}} - [(3x\mu_{\text{sen}}) - \{(2x\mu_{\text{sen}}^2) - \mu_{\text{sen}}^3\}]$, and if this is not possible, then 'effort plus senescence at two loci' can invade only if $W_{\text{effsen2}} - \mu_{\text{sen}} > W_{\text{constant}} - [(3x\mu_{\text{sen}}) - \{(2x\mu_{\text{sen}}^2) - \mu_{\text{sen}}^3\}]$. If this is not possible, then 'effort plus senescence at all loci' can invade only if $W_{\text{effsen3}} > W_{\text{constant}} - [(3x\mu_{\text{sen}}) - \{(2x\mu_{\text{sen}}^2) - \mu_{\text{sen}}^3\}]$. Here, the term $[(3x\mu_{\text{sen}}) - \{(2x\mu_{\text{sen}}^2) - \mu_{\text{sen}}^3\}]$ is the probability that a 'constant' individual will suffer at least one mutation in any generation, and so again the conditions show little change.

With a fourth locus, if 'effort plus partial senescence' can not invade, then again 'effort plus senescence at all loci' invades only if $W_{\text{effsen4}} > W_{\text{constant}} - [(4 \times \mu_{\text{sen}}) - \{(3 \times \mu_{\text{sen}}^2) - (2 \times \mu_{\text{sen}}^3 - \mu_{\text{sen}}^4)\}]$. But once more $[(4 \times \mu_{\text{sen}}) - \{(3 \times \mu_{\text{sen}}^2) - (2 \times \mu_{\text{sen}}^3 - \mu_{\text{sen}}^4)\}]$ is the probability that a 'constant' individual will suffer at least one mutation in any generation, and so the conditions continue to show little change.

Essentially, unless the effort-plus-senescence strategy is fitter than the non-senescent strategy less the probability of at least one mutation, then the increased effort strategy will not invade. By distributing the same mutation rate over numerous loci, the conditions are not markedly affected and the predictions show little change.

In asexually reproducing organisms, the model indicates that a strategy of increasing reproductive effort will not normally invade a population where senescence is a maladaptive character held in equilibrium by a balance between mutation and selection. Although the model is derived initially for senescence at a single locus, the conclusions are robust to the addition of further loci.

B. Sexually reproducing organisms.

a) Equilibrium between 'senescent' and 'nosen' genes.

In the absence of 'effort', the frequency of 'nosen' genes changes between generations according to:

$$p'_{\text{nosen}} = (p_{\text{nosen}} \times [\omega_{11} + q_{\text{senescent}} \times \omega_{12}]) \times (1 - \mu_{\text{nosen}}) / \bar{w}$$

where $\omega_{11} = W_{\text{constant}} = 1$, $s = W_{\text{constant}} - W_{\text{senescent}}$, h is the degree of dominance, and $\omega_{12} = 1 - hs$. If 'senescence' tends towards dominance, then $h=1$ and so $\omega_{12} = W_{\text{senescent}}$. Equilibrium can occur if $p'_{\text{nosen}} = p_{\text{nosen}} = p^{\wedge}_{\text{nosen}}$, and from equation 4.62 in Hartl and Clark 1989:

$$q^{\text{senescent}} = (\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}]) = (\mu_{\text{nosen}} / s)$$

If 'senescence' is instead recessive, then from equation 4.63 in Hartl and Clark 1989:

$$q^{\text{senescent}} = (\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}])^{1/2} = (\mu_{\text{nosen}} / s)^{1/2}$$

(In order to avoid further lengthy derivations, I have assumed that the conditions and assumptions associated with these approximations (Hartl and Clark 1989, 4.62 and 4.63) are fulfilled.)

As before, the fitness difference between 'nosen' and 'senescent' must exceed the mutation rate if equilibrium is to occur. Senescence is more abundant at equilibrium if it is recessive.

b.) Can 'effort' then invade?

'Effort' can invade if it is fitter than 'coneff', and from Appendix I, if senescence is dominant then:

$$\omega_{\text{coneff}} = (W_{\text{constant}} \times p_{\text{nosen}}^2 \times p_{\text{coneff}}) + (W_{\text{effort}} \times q_{\text{effort}} \times p_{\text{nosen}}^2) + (W_{\text{senescent}} \times (1 - p_{\text{nosen}}^2) \times p_{\text{coneff}}) + (W_{\text{effsen}} \times q_{\text{effort}} \times [1 - p_{\text{nosen}}^2]) \dots \dots \dots (A2)$$

$$\omega_{\text{effort}} = (W_{\text{effort}} \times p_{\text{nosen}}^2) + (W_{\text{effsen}} \times [1 - p_{\text{nosen}}^2]) \dots \dots \dots (A4)$$

prior to invasion, $p_{\text{coneff}} = 1$. If the equilibrium at the senescence locus lies towards 'nosen', then ω_{coneff} tends towards W_{constant} and ω_{effort} tends towards W_{effort} . Under these circumstances, effort does not invade because $W_{\text{effort}} < W_{\text{constant}}$. If the equilibrium lies instead towards 'senescent', then ω_{coneff} tends towards $W_{\text{senescent}}$ and ω_{effort} tends towards W_{effsen} . Under these circumstances, 'effort' does invade. There is a critical balance point between these 2 extremes at which $\omega_{\text{coneff}} = \omega_{\text{effort}}$. From equations A2 and A4, this occurs when:

$$(W_{\text{constant}} \times p_{\text{nosen}}^2 \times p_{\text{coneff}}) + (W_{\text{effort}} \times q_{\text{effort}} \times p_{\text{nosen}}^2) + (W_{\text{senescent}} \times (1 - p_{\text{nosen}}^2) \times p_{\text{coneff}}) + (W_{\text{effsen}} \times q_{\text{effort}} \times [1 - p_{\text{nosen}}^2]) = (W_{\text{effort}} \times p_{\text{nosen}}^2) + (W_{\text{effsen}} \times [1 - p_{\text{nosen}}^2])$$

and since $p_{\text{coneff}} = 1$, this means

$$(W_{\text{constant}} \times p_{\text{nosen}}^2) + (W_{\text{senescent}} \times (1 - p_{\text{nosen}}^2)) = (W_{\text{effort}} \times p_{\text{nosen}}^2) + (W_{\text{effsen}} \times [1 - p_{\text{nosen}}^2])$$

$$\Rightarrow p_{\text{nosen}}^2 x (W_{\text{constant}} - W_{\text{senescent}}) + W_{\text{senescent}} = p_{\text{nosen}}^2 x (W_{\text{effort}} - W_{\text{effsen}}) + W_{\text{effsen}}$$

$$\Rightarrow p_{\text{nosen}}^2 x (W_{\text{constant}} + W_{\text{effsen}} - W_{\text{senescent}} - W_{\text{effort}}) = W_{\text{effsen}} - W_{\text{senescent}}$$

$$\Rightarrow p_{\text{nosen}}^2 = (W_{\text{effsen}} - W_{\text{senescent}}) / ([W_{\text{constant}} + W_{\text{effsen}}] - [W_{\text{senescent}} + W_{\text{effort}}])$$

$$\Rightarrow p_{\text{nosen}} = \{(W_{\text{effsen}} - W_{\text{senescent}}) / ([W_{\text{effsen}} - W_{\text{senescent}}] + [W_{\text{constant}} - W_{\text{effort}}])\}^{1/2}$$

If the equilibrium frequency of 'nosen' is greater than this value, then effort can not invade, but if it is less, then it can. In other words, the more abundant senescence is, the more likely it is that a strategy of increased effort will spread. Note that the larger the fitness difference between 'constant' and 'effort', the lower the frequency of 'nosen' has to be before invasion can occur. By contrast, the threshold frequency of 'nosen' increases as the fitness difference between 'effsen' and 'senescent' increases, so a large difference will permit 'effort' to invade even when senescence is not abundant.

It is known from 4.62 (Hartl & Clark 1989) that:

$$q^{\text{senescent}} = (\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}])$$

so

$$p^{\text{nosen}} = 1 - (\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}])$$

and thus the chance that effort will invade is greater if :

$$\{1 - (\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}])\} / \{(W_{\text{effsen}} - W_{\text{senescent}}) / ([W_{\text{effsen}} - W_{\text{senescent}}] + [W_{\text{constant}} - W_{\text{effort}}])\}^{1/2} < 1$$

$$\{[W_{\text{constant}} - W_{\text{senescent}} - \mu_{\text{nosen}}] / [W_{\text{constant}} - W_{\text{senescent}}]\} / \{(W_{\text{effsen}} - W_{\text{senescent}}) / ([W_{\text{effsen}} - W_{\text{senescent}}] + [W_{\text{constant}} - W_{\text{effort}}])\}^{1/2} < 1$$

$$\{[W_{\text{constant}} - W_{\text{senescent}} - \mu_{\text{nosen}}] / [W_{\text{constant}} - W_{\text{senescent}}]\} / \{(W_{\text{effsen}} - W_{\text{senescent}}) / ([W_{\text{constant}} - W_{\text{senescent}}] - [W_{\text{effort}} - W_{\text{effsen}}])\}^{1/2} < 1$$

There are 4 prominent features of this expression:

1. As the fitness advantage of 'effsen' over 'senescent' diminishes, it becomes increasingly difficult for 'effort' to invade.
2. The smaller the fitness difference between 'constant' and 'senescence', the more likely it is that 'effort' will invade.
3. The higher the mutation rate, the more likely it is that 'effort' will invade.

4. Invasion of 'effort' is favoured if there is only a small difference in fitness between 'constant' and 'effort'.

If 'senescent' is recessive, then from equations A2b and A4b

$$\omega_{\text{coneff}} = (W_{\text{constant}} \times (1 - q_{\text{senescent}}^2) \times p_{\text{coneff}}) + (W_{\text{effort}} \times q_{\text{effort}} \times (1 - q_{\text{senescent}}^2)) \\ + (W_{\text{senescent}} \times (q_{\text{senescent}}^2) \times p_{\text{coneff}}) + (W_{\text{effsen}} \times q_{\text{effort}} \times [q_{\text{senescent}}^2]) \dots \dots \dots (\text{A2b})$$

$$\omega_{\text{effort}} = (W_{\text{effort}} \times (1 - q_{\text{senescent}}^2)) + (W_{\text{effsen}} \times q_{\text{senescent}}^2) \dots \dots \dots (\text{A4b})$$

prior to invasion, $p_{\text{coneff}}=1$. If the equilibrium at the senescence locus lies towards 'nosen', then ω_{coneff} tends towards W_{constant} and ω_{effort} tends towards W_{effort} . Under these circumstances, effort again does not invade because $W_{\text{effort}} < W_{\text{constant}}$. If the equilibrium lies instead towards 'senescent', then ω_{coneff} tends towards $W_{\text{senescent}}$ and ω_{effort} tends towards W_{effsen} . Under these circumstances, 'effort' again invades. As before, there is a critical balance point between these 2 extremes at which $\omega_{\text{coneff}} = \omega_{\text{effort}}$. From equations A2b and A4b, this occurs when:

$$(W_{\text{constant}} \times (1 - q_{\text{senescent}}^2) \times p_{\text{coneff}}) + (W_{\text{effort}} \times q_{\text{effort}} \times (1 - q_{\text{senescent}}^2)) \\ + (W_{\text{senescent}} \times (q_{\text{senescent}}^2) \times p_{\text{coneff}}) + (W_{\text{effsen}} \times q_{\text{effort}} \times [q_{\text{senescent}}^2]) \\ = (W_{\text{effort}} \times (1 - q_{\text{senescent}}^2)) + (W_{\text{effsen}} \times q_{\text{senescent}}^2)$$

and since $p_{\text{coneff}}=1$,

$$(W_{\text{constant}} \times (1 - q_{\text{senescent}}^2)) + (W_{\text{senescent}} \times (q_{\text{senescent}}^2)) \\ = (W_{\text{effort}} \times (1 - q_{\text{senescent}}^2)) + (W_{\text{effsen}} \times q_{\text{senescent}}^2)$$

$$q_{\text{senescent}}^2 \times (W_{\text{senescent}} - W_{\text{constant}}) + W_{\text{constant}} \\ = q_{\text{senescent}}^2 \times (W_{\text{effsen}} - W_{\text{effort}}) + W_{\text{effort}}$$

$$q_{\text{senescent}}^2 \times [(W_{\text{senescent}} - W_{\text{constant}}) - (W_{\text{effsen}} - W_{\text{effort}})] \\ = W_{\text{effort}} - W_{\text{constant}}$$

$$q_{\text{senescent}}^2 = [W_{\text{effort}} - W_{\text{constant}}] / [(W_{\text{senescent}} - W_{\text{constant}}) - (W_{\text{effsen}} - W_{\text{effort}})]$$

$$q_{\text{senescent}} = \{ [W_{\text{effort}} - W_{\text{constant}}] / [(W_{\text{senescent}} - W_{\text{constant}}) - (W_{\text{effsen}} - W_{\text{effort}})] \}^{1/2}$$

If 'senescent' is more abundant than this, then effort will spread. From equation 4.63 (Hartl & Clark 1989), it is known that at equilibrium:

$$q^{\wedge} \text{senescent} = (\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}])^{1/2} = (\mu_{\text{nosen}} / S)^{1/2}$$

so if

$$\frac{(\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}])^{1/2}}{\{[W_{\text{effort}} - W_{\text{constant}}] / [(W_{\text{senescent}} - W_{\text{constant}}) - (W_{\text{effsen}} - W_{\text{effort}})]\}^{1/2}} > 1$$

Within the numerator of this expression, both the numerator and the denominator will be negative. This can be more conveniently rearranged by multiplying by -1/-1 i.e. 1:

$$\frac{(\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}])}{([W_{\text{constant}} - W_{\text{effort}}] / [(W_{\text{constant}} - W_{\text{senescent}}) - (W_{\text{effort}} - W_{\text{effsen}})])} > 1$$

and

$$\frac{(\mu_{\text{nosen}} / [W_{\text{constant}} - W_{\text{senescent}}])}{([W_{\text{constant}} - W_{\text{effort}}] / [(W_{\text{effsen}} - W_{\text{senescent}}) + (W_{\text{constant}} - W_{\text{effort}})])} > 1$$

The same 4 features apply:

1. The higher the mutation rate, the more likely the effort strategy is to spread.
2. The smaller the fitness difference between 'constant' and 'senescent' the more likely 'effort' is to spread.
3. The larger the fitness difference between 'effsen' and 'senescent', the more likely 'effort' is to invade.
4. The smaller the fitness difference between 'constant' and 'effort', the more likely 'effort' is to spread.

Senescence involves only minor effects on fitness but a high rate of mutation (c.1 per generation (e.g. Ayala 1982, Ewens 1969)). If senescence is abundant in the population, then the conditions for invasion will generally be satisfied in sexually reproducing organisms, and although the assumptions of optimisation techniques are not strictly valid, their predictions would seem to be robust. It follows that if a strategy of increased effort can invade when senescence is caused by mutation at just a single locus, then it will also invade when mutation occurs at several loci. For sexually reproducing organisms with determinate growth, declining residual reproductive value

caused by senescence will generate conditions where increasing reproductive effort will be favoured, even when senescence is neither adaptive nor fixed.

In sexually reproducing organisms, because of recombination, the overall spread of 'effort' genes depends largely on the relative abundances of 'senescent' and 'nosen' genes. If 'senescent' genes are abundant, then 'effort' genes will on average enhance performance and spread, but if 'nosen' genes are abundant, then they will depress the average performance and will fail to spread. Among asexually reproducing organisms, there is no recombination, so the fate of 'effort-plus-senescence' depends entirely on its performance relative to 'constant' strategists. There would thus seem to be a general dichotomy in the predictions of these models: strategies of increased effort should generally spread in sexually reproducing populations, but this is not true for asexual reproducers.

Acknowledgements

The author was supported by a Postgraduate Scholarship from the Carnegie Trust for the Universities of Scotland. Staff at Glasgow University Computing Service helped with the running of computer simulations. Dr.R.W. Furness and Dr. N.H. Barton kindly read and offered valuable comments on an earlier draft of this paper.

References

- Ayala, F.J. (1982). *Population and Evolutionary Genetics: A Primer*. Benjamin Cummings, California.
- Bell, G. and Koufopanou, V. (1986). The cost of reproduction. *Oxford Surveys in Evolutionary Biology* 3:83-131.

- Brown, D. and Rothery, P. (1993). *Models in Biology: Mathematics, Statistics and Computing*. Wiley, Chichester
- Charlesworth, B. and Leon, J.A. (1976). The relation of reproductive effort to age. *American Naturalist* 110: 449-459.
- Clutton-Brock, T.H. (1991). *The Evolution of Parental Care*. Monographs in Behaviour and Ecology. Princeton University Press, Princeton, N.J.
- Crow, J.F. (1986). *Basic concepts in population, quantitative and evolutionary genetics*. Freeman, New York.
- Ewens, W.J. (1969). *Population Genetics*. Methuen, London.
- Gadgil, M. and Bossert, W.H. (1970). Life historical consequences of natural selection. *American Naturalist* 104:1-24.
- Gustafsson, L. (1990). Life-history trade-offs and optimal clutch size in relation to age in the Collared Flycatcher. In: *Population biology of passerine birds: an integrated approach* (eds J. Blondel, A. Gosler, J-D. Lebreton, and R. McCleery). Springer, Berlin.
- Gustafsson, L. and Part, T. (1990). Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. *Nature* 347:279-281.
- Hamer, K.C. and Furness, R.W. (1991). Age-specific breeding performance and reproductive effort in great skuas *Catharacta skua*. *Journal of Animal Ecology* 60:693-704.

Hartl, D.L. and Clark, A.G. (1989). *Principles of Population Genetics*. 2nd Edition. Sinauer Associates Inc., Sunderland, Massachusetts.

Medawar, P.B. (1952). *An unsolved problem in Biology*. H.K. Lewis, London.

Newton, I. (ed.) (1989). *Lifetime reproduction in birds*. Academic Press, London.

Nur, N. (1988). The cost of reproduction in birds: An examination of the evidence. *Ardea* 76.

Pianka, E.R. and Parker, W.S. (1975). Age specific reproductive tactics. *American Naturalist* 109:453-464.

Pugesek, B.H. (1981). Increased reproductive effort with age in the California Gull (*Larus californicus*). *Science* 212:822-823.

Roff, D.A. (1992). *The Evolution of Life Histories*. Theory and Analysis. Chapman and Hall, New York.

Rose, M. (1991). *Evolutionary biology of aging*. Oxford University Press, Oxford.

Saether, B-E. (1990). Age-specific variation in reproductive performance of birds. *Current Ornithology* 7:251-283.

Stearns, S.C. (1992). *The Evolution of Life Histories*. (Oxford Series in Ecology and Evolution.) Oxford University Press, Oxford.

Williams, G.C. (1957). Pleiotropy, natural selection and the evolution of senescence. *Evolution* 11: 298-411.

Williams, G.C. (1966a). *Adaptation and Natural Selection*. Princeton University Press, Princeton, N. J.

Williams, G.C.(1966b). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*. 100:687-690.

Appendix I.

Calculating phenotype frequencies.

At any time, the frequencies of the phenotypes can be calculated from the frequencies of the genotypes:

a) Senescent genes dominant:

$$F_{\text{constant}} = (p_{\text{coneff}})^2 \times (p_{\text{nosent}})^2$$

and

$$F_{\text{effort}} = [(q_{\text{effort}})^2 + (2 \times q_{\text{effort}} \times p_{\text{coneff}})] \times (p_{\text{nosent}})^2 = (1 - p_{\text{coneff}})^2 \times (p_{\text{nosent}})^2$$

and

$$F_{\text{senescent}} = [(q_{\text{senescent}})^2 + (2 \times q_{\text{senescent}} \times p_{\text{nosent}})] \times (p_{\text{coneff}})^2 \\ = (1 - p_{\text{nosent}})^2 \times (p_{\text{coneff}})^2$$

and

$$F_{\text{effsen}} = [(q_{\text{effort}})^2 + (2 \times q_{\text{effort}} \times p_{\text{coneff}})] \times [(q_{\text{senescent}})^2 + (2 \times q_{\text{senescent}} \times p_{\text{nosent}})] \\ = (1 - p_{\text{coneff}})^2 \times (1 - p_{\text{nosent}})^2$$

b) Senescent genes recessive

$$F_{\text{constant}} = (p_{\text{coneff}})^2 \times (1 - q_{\text{senescent}})^2$$

and

$$F_{\text{effort}} = [(q_{\text{effort}})^2 + (2 \times q_{\text{effort}} \times p_{\text{coneff}})] \times (1 - q_{\text{senescent}})^2 \\ = (1 - p_{\text{coneff}})^2 \times (1 - q_{\text{senescent}})^2$$

and

$$F_{\text{senescent}} = (q_{\text{senescent}})^2 \times (p_{\text{coneff}})^2$$

and

$$F_{\text{effsen}} = [(q_{\text{effort}})^2 + (2 \times q_{\text{effort}} \times p_{\text{coneff}})] \times (q_{\text{senescent}})^2 \\ = (1 - p_{\text{coneff}})^2 \times (q_{\text{senescent}})^2$$

Calculating gene fitness and the distribution of genes among possible phenotypes.

i) Senescent genes dominant.

a) 'coneff' genes.

The fraction of 'coneff' genes existing as say 'constant' phenotypes is calculable from the frequencies of phenotypes as follows:

$$(2 \times F_{\text{constant}}) / [(2 \times F_{\text{constant}}) + ((2 \times q_{\text{effort}} \times p_{\text{coneff}}) \times (p_{\text{nosent}})^2) + (2 \times F_{\text{senescent}}) + \\ ((2 \times q_{\text{effort}} \times p_{\text{coneff}}) \times [(q_{\text{senescent}})^2 + (2 \times q_{\text{senescent}} \times p_{\text{nosent}})])]$$

i.e. in each 'constant' phenotype individual, there are 2 copies of the 'coneff' gene. Dividing this frequency by the frequency of 'coneff' genes in all the phenotypes together gives the fraction of the 'coneff' genes existing as 'constant' phenotypes. The denominator of the above equation has four components - 'coneff' genes existing firstly

as 'constant' phenotypes (2 copies per phenotype), secondly as heterozygous 'effort' phenotypes (1 copy per phenotype), thirdly as 'senescent' phenotypes (2 copies per phenotype), and fourthly as heterozygous 'effort-plus-senescent' phenotypes (1 copy per phenotype). 'coneff' genes can not possibly be contained in homozygous 'effort' or homozygous 'effort-plus-senescent' phenotypes, so this component of F_{effort} and F_{effsen} must be excluded from the calculations. Heterozygous 'effort' or 'effort-plus-senescent' phenotypes contain a single copy of the 'coneff' gene. 'Constant' and 'senescent' phenotypes can only be homozygous with respect to the 'coneff' gene and so contain 2 copies.

Because all components of the numerator and denominator involve multiplication by 2, this expression simplifies to:

$$(F_{\text{constant}})/[(F_{\text{constant}})+((q_{\text{effort}} \times p_{\text{coneff}}) \times (p_{\text{nosen}})^2)+(F_{\text{senescent}})+((q_{\text{effort}} \times p_{\text{coneff}}) \times [(q_{\text{senescent}})^2+(2 \times q_{\text{senescent}} \times p_{\text{nosen}}))]]$$

and this can be rearranged to give:

$$(F_{\text{constant}})/[F_{\text{constant}}+F_{\text{senescent}}+(q_{\text{effort}} \times p_{\text{coneff}} \times [q_{\text{senescent}}^2+(2 \times q_{\text{senescent}} \times p_{\text{nosen}})+p_{\text{nosen}}^2])]$$

but since $[q_{\text{senescent}}^2+(2 \times q_{\text{senescent}} \times p_{\text{nosen}})+p_{\text{nosen}}^2]$ must equal 1, this simplifies to give:

$$F_{\text{constant}}/[F_{\text{constant}}+F_{\text{senescent}}+(q_{\text{effort}} \times p_{\text{coneff}})] \dots \dots \dots (A1)$$

further, since $F_{\text{constant}} = (p_{\text{coneff}})^2 \times (p_{\text{nosen}})^2$ and $F_{\text{senescent}} = [(q_{\text{senescent}})^2+(2 \times q_{\text{senescent}} \times p_{\text{nosen}})] \times (p_{\text{coneff}})^2 = (1-p_{\text{nosen}}^2) \times (p_{\text{coneff}})^2$ then the expression can be presented as:

$$\begin{aligned} & [(p_{\text{coneff}})^2 \times (p_{\text{nosen}})^2] / [(p_{\text{coneff}})^2 \times p_{\text{nosen}}^2 + [(1-p_{\text{nosen}}^2) \times (p_{\text{coneff}})^2] + (q_{\text{effort}} \times p_{\text{coneff}})] \\ & = p_{\text{nosen}}^2 / [p_{\text{nosen}}^2 + [(1-p_{\text{nosen}}^2)] + (q_{\text{effort}}/p_{\text{coneff}})] \\ & = p_{\text{nosen}}^2 / [1 + (q_{\text{effort}}/p_{\text{coneff}})] \\ & = p_{\text{nosen}}^2 / [(p_{\text{coneff}} + q_{\text{effort}})/p_{\text{coneff}}] \end{aligned}$$

and since $p_{\text{coneff}} + q_{\text{effort}} = 1$, this simplifies to give

$$= p_{\text{nosen}}^2 \times p_{\text{coneff}}$$

This means that the fraction of the 'coneff' genes existing as 'constant' phenotypes increases with the square of the frequency of 'nosen' genes, and with the frequency of 'coneff' genes.

It follows from expression (A1) that the fraction of 'coneff' genes existing as 'effort' phenotypes is:

$$[(q_{\text{effort}} \times p_{\text{coneff}}) \times (p_{\text{nosen}})^2] / [F_{\text{constant}} + F_{\text{senescent}} + (q_{\text{effort}} \times p_{\text{coneff}})]$$

and again this can be re-expressed:

$$\begin{aligned} & [(q_{\text{effort}} \times p_{\text{coneff}} \times p_{\text{nosen}}^2) / [(p_{\text{coneff}}^2 \times p_{\text{nosen}}^2) + [(1 - p_{\text{nosen}}^2) \times (p_{\text{coneff}})^2] + (q_{\text{effort}} \times p_{\text{coneff}})]] \\ & = [q_{\text{effort}} \times p_{\text{nosen}}^2] / [(p_{\text{coneff}} \times p_{\text{nosen}}^2) + [(1 - p_{\text{nosen}}^2) \times p_{\text{coneff}}] + (q_{\text{effort}})] \\ & = [q_{\text{effort}} \times p_{\text{nosen}}^2] / [(p_{\text{coneff}} \times p_{\text{nosen}}^2) + (q_{\text{effort}}) + [p_{\text{coneff}} - p_{\text{nosen}}^2 \times p_{\text{coneff}}]] \end{aligned}$$

but since $q_{\text{effort}} + p_{\text{coneff}} = 1$, this simplifies to give:

$$\begin{aligned} & [q_{\text{effort}} \times p_{\text{nosen}}^2] / [(p_{\text{coneff}} \times p_{\text{nosen}}^2) + [1 - p_{\text{nosen}}^2 \times p_{\text{coneff}}]] \\ & = q_{\text{effort}} / [p_{\text{coneff}} + 1/p_{\text{nosen}}^2 - p_{\text{coneff}}] \\ & = q_{\text{effort}} \times p_{\text{nosen}}^2 \end{aligned}$$

So the fraction of 'coneff' genes existing as heterozygous 'effort' phenotypes increases with the frequency of the 'effort' genes and with the square of the frequency of 'nosen' genes.

The fraction of 'coneff' genes existing as senescent phenotypes can be expressed as:

$$(1 - p_{\text{nosen}}^2) \times (p_{\text{coneff}})^2 / [F_{\text{constant}} + F_{\text{senescent}} + (q_{\text{effort}} \times p_{\text{coneff}})]$$

and this can be re-expressed as:

$$\begin{aligned} & (1 - p_{\text{nosen}}^2) \times (p_{\text{coneff}})^2 / [(p_{\text{coneff}}^2 \times p_{\text{nosen}}^2) + [(1 - p_{\text{nosen}}^2) \times (p_{\text{coneff}})^2] + (q_{\text{effort}} \times p_{\text{coneff}})] \\ & = (1 - p_{\text{nosen}}^2) / [p_{\text{nosen}}^2 + [1 - p_{\text{nosen}}^2] + (q_{\text{effort}} / p_{\text{coneff}})] \\ & = (1 - p_{\text{nosen}}^2) / [1 + (q_{\text{effort}} / p_{\text{coneff}})] \\ & = (1 - p_{\text{nosen}}^2) / [(p_{\text{coneff}} / p_{\text{coneff}}) + (q_{\text{effort}} / p_{\text{coneff}})] \\ & = (1 - p_{\text{nosen}}^2) / [(p_{\text{coneff}} + q_{\text{effort}}) / p_{\text{coneff}}] \end{aligned}$$

and since $p_{\text{coneff}} + q_{\text{effort}} = 1$, this simplifies to:

$$(1 - p_{\text{nosen}}^2) \times p_{\text{coneff}}$$

So the fraction of 'coneff' genes existing as 'senescent' phenotypes increases as the frequency of 'nosen' genes decreases, and increases with the frequency of 'coneff' genes. Finally, the fraction of the 'coneff' genes existing as 'effort-plus-senescent' phenotypes is:

$$\frac{((q_{\text{effort}} \times p_{\text{coneff}}) \times [(q_{\text{senescent}})^2 + (2 \times q_{\text{senescent}} \times p_{\text{nosen}})])}{[F_{\text{constant}} + F_{\text{senescent}} + (q_{\text{effort}} \times p_{\text{coneff}})]}$$

and this can be expressed as:

$$\begin{aligned} & ((q_{\text{effort}} \times p_{\text{coneff}}) \times [(q_{\text{senescent}})^2 + (2 \times q_{\text{senescent}} \times p_{\text{nosen}})]) / \\ & \quad [[p_{\text{coneff}}^2 \times p_{\text{nosen}}^2] + [(1 - p_{\text{nosen}}^2) \times (p_{\text{coneff}})^2] + (q_{\text{effort}} \times p_{\text{coneff}})] \\ & = (q_{\text{effort}} \times [1 - p_{\text{nosen}}^2]) / \\ & \quad [[p_{\text{coneff}} \times p_{\text{nosen}}^2] + [(1 - p_{\text{nosen}}^2) \times p_{\text{coneff}}] + q_{\text{effort}}] \\ & = (q_{\text{effort}} \times [1 - p_{\text{nosen}}^2]) / [p_{\text{coneff}} + q_{\text{effort}}] \\ & = q_{\text{effort}} \times [1 - p_{\text{nosen}}^2] \end{aligned}$$

The fraction of 'coneff' genes existing as 'effort-plus-senescence' phenotypes increases with the frequency of 'effort' genes, and decreases with the frequency of 'nosen' genes.

The average fitness of the 'coneff' gene can thus be calculated using the average fitness of the phenotypes weighted for the fraction of the 'coneff' genes existing in each form:

$$\begin{aligned} \omega_{\text{coneff}} = & (W_{\text{constant}} \times p_{\text{nosen}}^2 \times p_{\text{coneff}}) + (W_{\text{effort}} \times q_{\text{effort}} \times p_{\text{nosen}}^2) \\ & + (W_{\text{senescent}} \times (1 - p_{\text{nosen}}^2) \times p_{\text{coneff}}) + (W_{\text{effsen}} \times q_{\text{effort}} \times [1 - p_{\text{nosen}}^2]) \dots \dots \dots (A2) \end{aligned}$$

b) 'nosen' genes.

An extensive derivation could be applied to 'nosen' genes as well, but since the argument is similar then by symmetry the fitness of 'nosen' genes must be:

$$\begin{aligned} \omega_{\text{nosen}} = & (W_{\text{constant}} \times p_{\text{coneff}}^2 \times p_{\text{nosen}}) + (W_{\text{senescent}} \times q_{\text{senescent}} \times p_{\text{coneff}}^2) \\ & + (W_{\text{effort}} \times (1 - p_{\text{coneff}}^2) \times p_{\text{nosen}}) + (W_{\text{effsen}} \times q_{\text{senescent}} \times [1 - p_{\text{coneff}}^2]) \dots \dots \dots (A3) \end{aligned}$$

Thus the fitnesses of 'coneff' and 'nosen' genotypes are not simple but depend on the frequencies of all the genes involved.

c) 'effort' genes.

The fraction of 'effort' genes existing as say 'effort' phenotypes is calculable from the frequency of copies present as homozygotes plus those as heterozygotes, all divided by the frequency of copies in all phenotypes:

$$\begin{aligned} & \{ [(2 \times q_{\text{effort}}^2) + (2 \times q_{\text{effort}} \times p_{\text{coneff}})] \times p_{\text{nosen}}^2 \} / \\ & \quad \{ \{ [(2 \times q_{\text{effort}}^2) + (2 \times q_{\text{effort}} \times p_{\text{coneff}})] \times p_{\text{nosen}}^2 \} + \\ & \quad \{ [(2 \times q_{\text{effort}}^2) + (2 \times q_{\text{effort}} \times p_{\text{coneff}})] \times [(q_{\text{senescent}})^2 + (2 \times q_{\text{senescent}} \times p_{\text{nosen}})] \} \} \end{aligned}$$

In the case of 'effort' genes, these can exist only as 'effort' phenotypes or as 'effort-plus-senescence' phenotypes. Both of these phenotypes contain 'effort' genes as homozygotes (2 copies per individual) and as heterozygotes (1 copy per individual). The above expression simplifies to:

$$\frac{\{[q_{\text{effort}}^2+(q_{\text{effort}}x p_{\text{cone}})]x p_{\text{nosen}}^2\}}{\{[q_{\text{effort}}^2+(q_{\text{effort}}x p_{\text{cone}})]x p_{\text{nosen}}^2\} + \{[q_{\text{effort}}^2+(q_{\text{effort}}x p_{\text{cone}})]x [q_{\text{senescent}}^2+(2x q_{\text{senescent}}x p_{\text{nosen}})]\}}$$

$$= \frac{\{[q_{\text{effort}}^2+(q_{\text{effort}}x p_{\text{cone}})]x p_{\text{nosen}}^2\}}{\{[q_{\text{effort}}^2+(q_{\text{effort}}x p_{\text{cone}})]x [q_{\text{senescent}}^2+(2x q_{\text{senescent}}x p_{\text{nosen}})] + p_{\text{nosen}}^2\}}$$

and since $[q_{\text{senescent}}^2+(2x q_{\text{senescent}}x p_{\text{nosen}})] + p_{\text{nosen}}^2 = 1$, this simplifies:

$$= \frac{\{[q_{\text{effort}}^2+(q_{\text{effort}}x p_{\text{cone}})]x p_{\text{nosen}}^2\}}{[q_{\text{effort}}^2+(q_{\text{effort}}x p_{\text{cone}})]}$$

$$= p_{\text{nosen}}^2$$

The fraction of 'effort' genes existing as 'effort' phenotypes is the square of the frequency of 'nosen' genes.

Since 'effort' genes can exist only as 'effort' or as 'effort-plus-senescence' phenotypes, it follows that the frequency of 'effort' genes existing as 'effort-plus-senescence' phenotypes must simply be:

$$1 - p_{\text{nosen}}^2$$

Accordingly, the average fitness of 'effort' genes can be calculated:

$$\omega_{\text{effort}} = (W_{\text{effort}}x p_{\text{nosen}}^2) + (W_{\text{effsen}}x [1 - p_{\text{nosen}}^2]) \dots \dots \dots (A4)$$

d)'senescent' genes.

As before, repetition of lengthy derivations is unnecessary because the arguments are similar. From expression (A4) for calculating the fitness of 'effort' genes, it follows that the average fitness of 'senescent' genes must be:

$$\omega_{\text{senescent}} = (W_{\text{senescent}}x p_{\text{cone}}^2) + (W_{\text{effsen}}x [1 - p_{\text{cone}}^2]) \dots \dots \dots (A5)$$

These equations are much simpler than those for the 'cone' and 'nosen' genes. Instead of there being complex four-way balances, the balances involve only two components, and this means that the fitness of 'effort' genes will always lie between that set by 'cone' and 'effort-plus-senescent' phenotypes, and the fitness of 'senescent' genes will always lie between the limits set by 'senescent' and 'effort-plus-senescent' phenotypes.

ii) Senescent genes recessive

Lengthy derivations could be repeated for each of the genes, but it follows from equations A2, A3, A4 and A5 that when senescence is recessive rather than dominant, the fitnesses are calculable from:

$$\omega_{\text{cone}} = (W_{\text{constant}} x (1 - q_{\text{senescent}}^2) x p_{\text{cone}}) + (W_{\text{effort}} x q_{\text{effort}} x (1 - q_{\text{senescent}}^2)) + (W_{\text{senescent}} x (q_{\text{senescent}}^2) x p_{\text{cone}}) + (W_{\text{effsen}} x q_{\text{effort}} x [q_{\text{senescent}}^2]) \dots \dots \dots (A2b)$$

$$\Omega_{\text{nosen}} = (W_{\text{effort}} \times [1 - p_{\text{coneff}}^2]) + (W_{\text{constant}} \times p_{\text{coneff}}^2) \dots \dots \dots (A3b)$$

$$\Omega_{\text{effort}} = (W_{\text{effort}} \times (1 - q_{\text{senescent}}^2)) + (W_{\text{effsen}} \times q_{\text{senescent}}^2) \dots \dots \dots (A4b)$$

$$\begin{aligned} \Omega_{\text{senescent}} = & (W_{\text{constant}} \times p_{\text{coneff}}^2 \times p_{\text{nosen}}) + (W_{\text{senescent}} \times q_{\text{senescent}} \times p_{\text{coneff}}^2) \\ & + (W_{\text{effort}} \times (1 - p_{\text{coneff}}^2) \times p_{\text{nosen}}) + (W_{\text{effsen}} \times q_{\text{senescent}} \times [1 - p_{\text{coneff}}^2]) \dots \dots \dots (A5b) \end{aligned}$$

Chapter 12

General Discussion and Conclusions

Chapter 12. General Discussion

Broadly speaking, the results reported in this thesis fall into 3 categories: chapters 3,4,5 and 6 consider how reproductive demands are spread through the breeding season and when natural selection acts on clutch size; chapters 7 and 8 examine differences in the quality of individuals within populations and explore their longer term implications; and the remaining chapters 9,10 and 11 make specific tests of wider assumptions commonly employed in studies relating to avian clutch size and life history theory.

It has been widely assumed that clutch size is an adaptation to the parents' abilities at a single critical stage. In chapter 3, I argue that birds are capable of shifting reproductive demands in time and suggest that critical bottlenecks are not stable in the long term and that demands may be spread over several stages. I present a mathematical framework which formalises the argument and suggests that information on the clutch-size specific reproductive demands at various stages of the breeding season would be particularly useful for answering the question of whether regular bottlenecks can occur.

The data available from the literature indeed indicate that the demands often increase with clutch size during incubation (chapter 4). Incubation can be an important phase in the regulation of clutch size. In half the studies, additional eggs could not be incubated without a depression of hatching success. Prolongation of incubation and greater loss of body condition were also recorded where clutch size was enlarged. Almost all studies found that metabolic rate was higher among birds incubating larger clutches. Field metabolic rates during incubation are only slightly lower than those during chick rearing (Tatner and Bryant 1993), and the results reviewed indicate that the act of incubation commonly entails an elevation of metabolic rate above resting levels. There was some evidence that the importance of incubation may differ between taxonomic groups, and incubating procellariiforms are unlikely to elevate metabolic rate

above resting levels. Incubation metabolic rate is also markedly higher under harsh thermal conditions.

In a case study of kittiwakes (chapter 5), I manipulated both clutch and brood size at several stages in the season and found evidence that all may be important. Daily egg survival rates were depressed when clutch size was increased, and daily chick survival rates were depressed when broods of various ages were enlarged. However, neither during incubation nor during chick rearing could any intermediate form of clutch size specific demands (e.g. loss of body condition or feather regrowth rates) be detected. Several stages of the season would seem to have been important, but the mechanism by which this was mediated is not clear from the data.

Using doubly labelled water (chapter 6), I was unable to detect increases in kittiwake energy expenditure when I increased the number of eggs incubated, though sample sizes were necessarily small. Metabolic rates were however comparable during incubation and chick rearing which is consistent with the suggestions of Tatner and Bryant (1993) : the incubation stage is demanding and expenditure is only a little below that of birds rearing chicks.

There is thus good evidence that clutch size is often set, not by any single bottleneck during chick rearing, but by several stages of the breeding season. If the birds are 'ideally free' to shift the demands of reproduction between stages within the breeding season, then bottlenecks are only stable where the demands of the other stages are independent of clutch size. The literature on incubation indicates that this is often not the case. In the study of kittiwakes, several stages during chick rearing and incubation were of importance and metabolic rates were comparable throughout. Details of the mechanism were less clear from the data.

From the results in chapter 7, it is clear that there was considerable spatial structure to the kittiwake colony, and that groups of birds showed similar performance. The physical characteristics of the nest sites also showed comparable clustering but there was no evidence of any relationship between nest site characteristics and

performance. Further, although birds were faithful to areas within the colony, there was no consistency in breeding performance at these areas between two consecutive years. Furthermore, the spatial organisation of breeding performance and nest site characteristics changed between years. Any differences in quality of adults within this colony was a transitory phenomenon.

There was consistency in breeding success of individual swifts between years, and this could account for 10-15% of all the variance in breeding success within the colony throughout the study period (chapter 8). There was however no evidence of a relationship between breeding success and survival to the following year. Using models of annual breeding success and inter-annual survival, a simulation did however indicate that these differences were negligible in accounting for the uneven distribution of lifetime reproductive success between individuals. The range of adult quality was persistent, but it was of little biological importance compared with more stochastic, environmental factors.

From these two case studies, there is evidence for a range of adult quality within the populations, but in neither case is it of major long term biological importance.

Much of life history research employs a number of implicit assumptions. In specific cases, I have tested 3 of these, and in all cases found that they are reasonable for questions of avian clutch size determination. It is commonly assumed: firstly that natural selection operates principally on arithmetic mean breeding success and that variance is of only minor importance; secondly, that natural selection on clutch size operates within the context of nutritional rather than spatial resources; and thirdly that mutation does not produce biologically important deviations from optimality.

In a simulation of swift lifetime reproductive success (chapter 9), I show that despite occupying a fluctuating environment and despite having low clutch sizes and high adult survival, there is no evidence that the lifetime reproductive success of the swifts was insured against years of bad breeding success. Had adult survival been

consistently high, then it could have provided insurance against failure in a bad year. Survival was however dependent on fluctuating annual weather conditions, and so did not serve to reduce variance in lifetime performance. In these swifts, low clutch size and high adult survival can not have been generated by natural selection to reduce variance in breeding success.

In cliff nesting kittiwakes, it is conceivable that clutch size could be influenced by the space available for the chicks (chapter 10), as much as by the nutritional resources required to rear chicks. Although nest size did differ significantly between birds with different numbers of eggs, the magnitude was exceptionally small and was the consequence rather than the cause of larger clutches. There was no evidence that the birds with larger clutches were those with ledges or space available at the edge of the nest. When brood size was enlarged, chick survival was depressed, but there was no evidence in this case that this was related to the amount of space. Given that clutch-size dependent changes in daily breeding survival rates were found throughout incubation and chick rearing (chapter 5), spatial constraints were not important in this case.

Finally, optimisation techniques which do not take mutation into account have been employed to predict the relationship between reproductive effort and age. A population genetics model which incorporated the effects of mutation produced similar predictions to optimisation in sexually reproducing organisms such as birds (chapter 11). Even if senescence itself is maladaptive and persists in equilibrium due to a balance between mutation and selection, then genes coding for a strategy which can produce the optimal response to senescence can still spread through the population. Although one of the assumptions of optimisation is violated, the models still produce robust predictions for sexually reproducing organisms such as birds.

Overall, I argue that natural selection may adjust clutch size not only in relation to the number of chicks the adults can feed, but to the parents' capacities to care for offspring at several stages in the season. I present two studies where a range of adult

quality is apparent in avian populations, but argue that it is of only minor long term biological importance. In a case study of swifts, I argue that the pattern of low reproductive rates and high survival is not due to selection for a bet-hedging strategy in their fluctuating environment. In a case study of kittiwakes, I argue that processes of clutch size regulation are not due to spatial constraints brought about by their cliff-nesting habits. I argue that optimisation models are robust in predicting increases in avian reproductive effort with age. In birds, it is not important that the models ignore mutation even when it sustains the senescence which drives selection for the increasing effort.

Tatner, P. and Bryant, D.M. 1993. Interspecific variation in daily energy expenditure during avian incubation. *J.Zool.* 231:215-232.

APPENDIX

Papers, on unrelated work, published during the
period of research for the degree of PhD