To the Graduate Council:

I am submitting herewith a dissertation written by Gareth James Russell entitled "Predicting the Appearance and Disappearance of Species: from Small Islands to Small Genera." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.

Stuart Pimm, Major Professor

We have read this dissertation, and recommend its acceptance

Accepted for the Council:

Associate Vice Chancellor and Dean of the Graduate School

PREDICTING THE APPEARANCE AND DISAPPEARANCE OF SPECIES: FROM SMALL ISLANDS TO SMALL GENERA

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Gareth James Russell

May 1996

DEDICATION

I dedicate this dissertation to my parents.

They have constantly encouraged me, even when it seemed that I would be a student forever.

ACKNOWLEDGMENTS

My time at the University of Tennessee has always been *something*—fun, stimulating, hard work or frustrating—and has usually been most of these at once. The chief architects are as follows.

James Drake, John Gittleman and Michael McKinney, my committee members, listened to and encouraged those of my ideas that were worth pursuing. Mike deserves special mention for believing (and convincing me) that I had enough interesting ideas to fill a book chapter.

Stuart Pimm, my major advisor, maintains that *all* of his students are the best. To his credit, he helps them more than most advisors as they try to 'make it so', standing head and shoulders above the crowd in the support, both scientific and material, that he provides his graduate students. Without Stuart's advice, exhortations and endless stories about Einstein, this dissertation would not consist of four published papers. In fact, it would probably not be finished.

In addition, I cannot thank Stuart enough for the opportunity to prowl around the cloud forests of Maui. In my memory the rain and mud are inextricably linked to the splendour of that fragile and unique ecosystem. Equally magical are the Everglades at 6am, as the mist rises slowly through the temporarily cool and clear air.

I feel privileged to have shared an office, a house and various drinking establishments with Hans, John, Julie, Phil, Tom and more recently Audrey and Lisa. In particular, my cohort-members John and Julie provided a perfect starting mixture of intellectual curiosity, good humour and an appreciation of the good things in life. May the white-board rise again.

Kim Norris has been my sounding board, reviewer, supporter and partner in crime for two and a half years. Without her, I would be less of a scientist and *much* less of a human being.

While at the University of Tennessee I have received financial support from the Department of Zoology (now the Department of Ecology and Evolutionary Biology) and the Science Alliance organization. For this I am grateful. Other, more specific sources of funding are acknowledged at the appropriate point within this dissertation.

ABSTRACT

In this compilation of studies I address the appearance and disappearance of species. By developing a new model of the turnover of breeding bird species on islands, I test a prediction that this turnover should decrease with increasing area of an island and also decrease with its increasing isolation. The prediction turns out to be correct, but the underlying causes are not those upon which the prediction was based. I then go on to review the status of turnover analysis at various scales of space and time, comparing the approaches taken by ecologists and paleontologists. I find that the models have much in common, but that methods and nomenclature should be standardized. I propose a set of standards, and apply an ecological model of the appearance and disappearance of breeding bird species to a paleontological dataset, where it reveals the existence of 'Lazarus' and 'Elvis' species. Finally, I analyse patterns of species extinction across genera. For mammals, I find that historical and likely future species extinctions are most likely to be drawn from species-poor genera. This also true for historical bird extinctions, but less so for likely future bird extinctions. I suggest that a change from introduced species to habitat destruction as the main cause of bird extinctions is responsible.

TABLE OF CONTENTS

Page

PART ONE
INTRODUCTION

The common threads 2
Methods and mathematics 3
Applications and conservation 4
The remainder of the dissertation 5
Other papers published while at the University of Tennessee 5
References 6

PART TWO
A CENTURY OF TURNOVER: COMMUNITY DYNAMICS AT THREE TIMESCALES

Summary 8
Introduction 10
The data 12
Calculating turnover 13
    Turnover, cumulative turnover or turnover rate? 13
    Calculation of turnover from empirical data 16
An equilibrium model 18
    Derivation 18
        A comparison with Diamond and May's model 25
    Fitting the model 26
        The failure of the equilibrium model 27
A non-equilibrium model of dynamic island biogeography 35
    Assumption of equilibrium 35
        Modifications to the equilibrium model 36

Fitting the non-equilibrium model 44
Deconstructing the non-equilibrium model 48
Discussion 57
Acknowledgments 58
References 59
Appendix 1 63
'Terrestrial' bird species found on the islands in this study 63
Appendix 2 65
Derivation of a non-equilibrium expression for turnover 65

PART THREE
TURNOVER OF BIRD COMMUNITIES ON ISLANDS DECREASES WITH INCREASING AREA AND WITH INCREASING ISOLATION: CONFIRMING MACARTHUR AND WILSON'S PREDICTIONS, BUT NOT THEIR MODEL

Introduction 71
The data 73
Records of breeding bird species 73
The biogeography of the islands 75
Restricting the dataset 80
Species, area and distance 81
Correlations among biogeographic variables 83
Number of habitats: dependent or independent variable? 84
Estimating turnover 87
Turnover area and distance 94
Short-term turnover 94
Short-term colonization and extinction probabilities 95
Pool size 96
Long-term turnover 96
Discussion 98
An apparent contradiction 98

Replacing colonization probability with pool size 99
A surprising relationship between pool size and the rescue effect—*distant* populations are more likely to be rescued 100
Testing the hypothesis 101
Acknowledgments 102
References 102
Appendix 1 106
'Terrestrial' bird species found on the islands in this study 106

PART FOUR
TURNOVER: BIOLOGICAL CHANGE AT ALL SCALES OF SPACE AND TIME

Introduction 111
Identifying turnover 112
Temporal turnover 113
Spatial turnover 115
Measuring turnover 116
Standardizing measurements 116
Intracensus turnover—time averaging and space averaging 123
Counting everything 125
Separating space and time 128
Interpreting turnover 129
Changing scales means changing processes 130
Linking space and time (metapopulation models predict both temporal and spatial turnover) 135
Modeling turnover 139
Markov expansions for repeatable events 139
Maximum likelihood applied to species 142
Maximum likelihoods applied to communities 147
Turnover applied to communities 147
The relative merits of the models 151

Markov expansions for non-repeatable events 154
Identifying 'Lazarus' species: a case study in cross-scale modeling 155
The future of turnover 158
Ecology as a 'null model' for paleontology 160
Turnover everywhere 161
Acknowledgments 161
References 161

PART FIVE
REDUCED TAXONOMIC SELECTIVITY IN THE FUTURE EXTINCTION CRISIS

Abstract 173
Introduction 173
Rarefaction—a model of random extinction 176
Selectivity—patterns of *non*-random extinction 181
Testing for selectivity 182
Selectivity in threatened genera 185
Results 186
Extinct and threatened mammals 186
Extinct and threatened birds 191
Predicting future bird extinctions 200
Selectivity by genus size and the number of genus extinctions 204
Discussion 206
Contingent selectivity 206
Phylogenetic selectivity 207
The natural history of extinctions 209
Acknowledgments 212
References 212

VITA

LIST OF TABLES

PART TWO
A CENTURY OF TURNOVER: COMMUNITY DYNAMICS AT THREE TIMESCALES

1. A sample of turnover statistics, both calculated and derived from model-fitting procedures 28

PART THREE
TURNOVER OF BIRD COMMUNITIES ON ISLANDS DECREASES WITH INCREASING AREA AND WITH INCREASING ISOLATION: CONFIRMING MACARTHUR AND WILSON'S PREDICTIONS, BUT NOT THEIR MODEL

1. A list of the islands used in this study, with associated biogeographical variables 76

PART FOUR
TURNOVER: BIOLOGICAL CHANGE AT ALL SCALES OF SPACE AND TIME

1. Processes contributing significantly to turnover at different combinations of temporal and spatial scale 132

PART FIVE
REDUCED TAXONOMIC SELECTIVITY IN THE FUTURE EXTINCTION CRISIS

1. Summary of the numerical results of an analysis of extinction selectivity for mammals 187

2. Summary of the observed selectivity in historical and likely future extinctions of mammal species 192
3. Summary of the numerical results of an analysis of extinction selectivity for birds 194
4. Summary of the observed selectivity in historical and likely future extinctions of bird species 198

LIST OF FIGURES

PART TWO
A CENTURY OF TURNOVER: COMMUNITY DYNAMICS AT THREE TIMESCALES

1. Measurements of apparent turnover (solid circles) and estimates of mean turnover (open circles) for the island of Skokholm, with the number of values contributing to each mean (solid line) 19
2. Graphic representation of turnover under equilibrium conditions 22
3. Mean turnover (solid lines) and the predictions of the equilibrium model (dotted lines) for all the islands 30
4. Predictions of one-year turnover by both the equilibrium (solid circles) and non-equilibrium (open circles) models 32
5. Graphic representation of turnover under conditions of decreasing species number 38
6. Graphic representation of turnover under conditions of increasing species number 40
7. Mean turnover (solid lines) and the predictions of the non-equilibrium model (dotted lines) for all the islands 45
8. Predictions of four-year turnover by both the equilibrium (solid circles) and non-equilibrium (open circles) models 49
9. A: Predicted non-equilibrium turnover for the island of Scolt Head, divided into intrinsic and extrinsic components 53
10. Predictions of the non-equilibrium model (thick lines) and the intrinsic turnover (thin lines) for all the islands 55

PART THREE

TURNOVER OF BIRD COMMUNITIES ON ISLANDS DECREASES WITH INCREASING AREA AND WITH INCREASING ISOLATION: CONFIRMING MACARTHUR AND WILSON'S PREDICTIONS, BUT NOT THEIR MODEL

1. A plot of predicted four-year turnover against measured four-year turnover for thirteen islands where such measurements are possible 85
2. A plot of the logarithm of the mean number of species on each island [logS (mean)] against the logarithm of the number of habitats (logH) 92

PART FOUR

TURNOVER: BIOLOGICAL CHANGE AT ALL SCALES OF SPACE AND TIME

1. Observed turnover on the island of Skokholm, calculated using the index of equation 2 119
2. Metapopulation theory explains both temporal and spatial turnover 137
3. Likelihood surfaces for three breeding bird populations on the island of Skokholm. 144
4. Likelihood surface for the entire bird community of Skokholm 148
5. The predictions of three models about turnover on the island of Skokholm 152

PART FIVE

REDUCED TAXONOMIC SELECTIVITY IN THE FUTURE EXTINCTION CRISIS

1. Extinction and sampling rarefaction curves for all mammal species 179

2. The distribution of species extinctions within different size classes of mammal genera 189
3. The distribution of species extinctions within different size classes of bird genera 196
4. The actual number of extinct bird genera (solid circle) is higher than an expected value based on randomizing the distribution of extinct species (solid diamond) 202

PART ONE

INTRODUCTION

"Observe constantly that all things take place by change, and accustom thyself to consider that the nature of the Universe loves nothing so much as to change the things which are, and to make new things like them."

Marcus Aurelius

"You could not step in the same rivers; for the other and yet other waters are ever flowing on."

Heraclitus

THE COMMON THREADS

If this dissertation has a common thread, that thread is the appearance and disappearance of species. One part of the dissertation concentrates on disappearances alone—the global extinction of bird and mammal species and the consequent extinction of their genera—and the remainder deals with *turnover*, a measure of both appearances and disappearances.

The parts of this dissertation are 'self-contained'; each has its own introduction. My purpose here is to place the studies in a wider context. Even this is almost redundant, since part four discusses the role of turnover analysis at different scales of biological inquiry, and so subsumes one of the roles this introduction might play. Instead, I will concentrate on two other themes: the theme of mathematics and methods, and the theme of applications and conservation.

METHODS AND MATHEMATICS

Some of the studies presented here share their methodology and their mathematical techniques. Models that involve *probabilities* of appearance and disappearance are becoming increasingly common in both the ecological and paleontological literature (see part four for a discussion of this). The new model of turnover presented in part two is just one example—the literature is full of others. Such models may be easily adapted to encompass different magnitudes of space and time, process usually known as a Markov expansion. The development of new probabilitistic models that apply to specific biological situations is currently one of the most productive areas of theoretical biology. I believe that similarities in these models may allow us to see similarities in the underlying biologies of the systems we look at, and any differences will help us see what is unique to each system. For example, a model recently proposed by Gilinsky and Good (1991) predicts changes in the diversity of a clade as a result of the origination and extinction of the species in that clade. Despite using probabilities of appearance and disappearance, the model is very different from those presented in this dissertation. The main reason is that Gilinsky and Good are dealing with *one time only* events—when their species are gone, they are gone forever. The models on the pages that follow this introduction address *repeatable* events—the same species can appear and disappear in an area many times (because they persist elsewhere). Comparing the mathematics of these different kinds of systems yields insight into extinction processes and their long-term

consequences. Such comparisons will, I hope, be a large part of my future research.

APPLICATIONS AND CONSERVATION

Probabilistic models are useful in an applied context because probabilities are easy to understand, and so their implications are easy to communicate to policy-makers and managers. A statement that "there is a probability p that species s will be extinct in y years" are more likely to be acted upon than a statement that "the variance in species abundance is three-quarters that of the mean abundance". This is not, however, the main practical benefit of analysing appearances and disappearances.

Those charged with conserving the living systems on our planet are coming to appreciate that change is a natural, even essential part of biological systems, and that the old conservation ethic of trying to 'freeze' a community in time is inappropriate (and may be a disaster). If we census a habitat and five years later discover that four of its species are now missing, is that a warning sign? If we protect a habitat and five years later discover that four of its species are now missing, is that a failure? Before we can assess the state of health of a community, we need to know what proportion of a community we should expect to appear and disappear under *normal* conditions. An understanding of turnover is essential, and two of the studies in this dissertation were commissioned by the Joint Nature Conservation Committee of the United Kingdom to help them answer similar questions about the biological systems in their care. A similar

development of ideas can be found in the literature of restoration—we now know that communities often require a particular sequence of *assembly*—a form of turnover—if they are to recover from disturbance.

THE REMAINDER OF THE DISSERTATION

The material in this dissertation consists of four papers in addition to this introduction, one of which is published, one of which is in press, one of which has been submitted, and one of which will be submitted shortly. I urge the reader to seek out the published papers, rather than this compilation. Each paper is a separate and self-contained part of the dissertation, and contains its own acknowledgments, bibliographic references and appendices. Reflecting the increasingly collaborative nature of science, all but one of the papers have multiple authors. This is why, in the following text, I will often refer to "we".

OTHER PAPERS PUBLISHED WHILE AT THE UNIVERSITY OF TENNESSEE

During the time that this dissertation was in progress, I was involved in a number of other, related projects. These are listed below, so that what follows this introduction may be put in the context of my overall interests.

Pimm, S. L., J. M. Diamond, T. M. Reed, G. J. Russell and J. M. Verner (1993) Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences of the USA* **90**: 10871–10875.

Curnutt, J., J. Lockwood, H.-K. Luh, P. Nott and G. Russell (1994) Hotspots and species diversity. *Nature* **367**: 326–327.

Pimm, S. L., G. J. Russell, J. L. Gittleman and T. M. Brooks (1995) The future of biodiversity. *Science* **269**: 347–350.

REFERENCES

Gilinsky, N. and I. J. Good (1991) Probabilities of origination, persistence, and extinction of families in marine invertebrate life. *Paleobiology* **17**: 145–166.

PART TWO

A CENTURY OF TURNOVER: COMMUNITY DYNAMICS AT THREE TIMESCALES

This chapter has been published as: Russell, G. J., J. M. Diamond, S. L. Pimm and T. M. Reed (1995) A century of turnover: community dynamics at three timescales. *Journal of Animal Ecology* **64**: 628–641.

SUMMARY

1. We calculated the observed species turnover of the bird communities on 13 small islands off the coast of the British Isles and the Republic of Ireland for different census intervals. For seven of these islands, the maximum intervals exceeded 80 years.

2. We developed a non-linear, asymptotic model to describe how observed turnover should change with census interval. Our assumptions were traditional ones, based upon the assumption of dynamic equilibrium in familiar island biogeography theory, even though we knew that such equilibrium is rare in these islands. Furthermore, the model considered the average dynamics of the species present and not the dynamics of the individual species.

3. This model showed that neither the observed turnover calculated over different intervals, nor the turnover rate obtained by dividing this observed turnover by the interval, are statistics that permit comparison between islands. Observed turnover increased over time, thus one year turnovers underestimated the turnovers over a decade or a century. The increase was less than linear, however, so dividing observed turnover by the number of years in its calculation produced a statistic that declined progressively with that number.

4. The model provided a significant overall fit to the data, but underestimated turnover at both the shortest and longest census intervals.

We modified the model to reduce the amount of underestimation, by incorporating the long-term changes in the number of species on each island and hence removing the assumption of equilibrium. This *non*-equilibrium model provided a much improved fit to the data, but it still failed to describe turnover at the very shortest intervals. These, however, are known from other studies to be inflated by individuals—*floaters*—that nest only once or twice on the islands.

5. The improved, non-equilibrium model made good predictions of the observed turnover over a *four*-year interval. These predictions may be used to compare islands, including those for which empirical data on four-year turnovers are sparse.

6. We divided the non-equilibrium model into an intrinsic and an extrinsic component, representing the influence of within-community and external factors respectively.

7. Even the intrinsic components of turnover are large, involving differences in species composition of 6–36% between widely separated censuses. How these intrinsic components of turnover vary from island to island is not clear because previous studies have been unable to compare turnover at different time scales. The number of islands in this study was too few for this purpose and we leave a more broadly based comparison to a future paper.

Key-words: census interval, island biogeography, non-equilibrium model.

INTRODUCTION

Turnover is the change in the composition of a biological community as a result of either or both the immigration and local extinction of species. Its magnitude is of both theoretical and practical significance, and central to debates about which theories best describe communities. Conservation efforts to protect threatened or otherwise desirable species are often directed towards maintaining the composition of a community in which they are found. In some cases, the preservation of some unchanging community is an end in itself. An understanding of turnover in the long term is crucial to these efforts. In this paper we develop a model of the way in which measurements of turnover depend upon both the interval between community censuses, and upon whether or not the total number of species in the community is changing. We test the model against data from the bird communities on thirteen small islands. Previous studies lack the temporal details we provide and these details, we argue, are essential to properly evaluate and compare estimates of community turnover.

Turnover assumed a special importance in the work of MacArthur and Wilson (1963, 1967). They interpreted previous studies on the effects of area and isolation on local communities by suggesting that immigration and extinction are continuous processes that maintain communities in *dynamic equilibrium*. This theory of island biogeography may be applied to any community which has a distinct boundary (such as that on a mountain-top, or in a body of water). It was a radical alternative to previous ideas which suggested that community

development proceeds towards a fixed 'climax' composition (e.g., Cowles 1899; Clements 1916, 1936; Gleason 1926). Confirming the evidence of Arrhenius (1921) and Mayr (1940), and following theory developed by Preston (1948, 1962a, b), the MacArthur and Wilson model predicts two relationships. These are that the number of species on an island is 1) positively related to its area, and 2) negatively related to its isolation (its distance from a source of potential immigrant species). MacArthur and Wilson (1963, p. 377) also predicted that one measure of the turnover of an island community, *turnover rate*, would decrease with both increasing area and increasing isolation, so providing the mechanisms behind the relationships.

Many subsequent studies have further demonstrated these two relationships (e.g., Lack 1969; Power 1972). These demonstrations are ambiguous, however, because the two relationships are also explicable in terms of static processes. Turnover is the key concept behind dynamic equilibrium, and turnover mechanisms are less tractable: they are best demonstrated through empirical observation of immigration and extinction rates (e.g., Simberloff 1969, 1974; Simberloff and Wilson 1969). More recently, there are studies of turnover itself (e.g., Diamond 1969, 1971, 1984a, b; Diamond and May 1977; Hunt and Hunt 1974; Jones and Diamond 1976; Lynch and Johnson 1974; Reed 1980; Schoener and Spiller 1987; Terborgh and Faaborg 1973; Williamson 1983), many of which attempt to test the effects of area and isolation on "turnover rate". By compiling and analysing a particularly detailed dataset, we 1) show that these tests are based on unreasonable assumptions about the dependence of observed turnover

upon census interval, and 2) provide a method to obtain estimates of turnover for use in comparative studies.

THE DATA

Records of nesting birds from islands off the coast of Great Britain and the Republic of Ireland are one of the most complete long-term community datasets in the world. Some of the islands have records as far back as the nineteenth century, and it is not unusual for there to be unbroken census data for 50 years. Parts of this dataset have been the subject of many previous analyses (e.g., Lack 1966, 1969, 1976; Diamond 1984a, b; Reed 1980, 1981a, b; Pimm, Jones and Diamond 1988; Pimm *et al.* 1993; Williamson 1983). It is still yielding fresh insights.

We selected a subset of thirteen islands (Bardsey, Calf of Man, Copeland, Fair Isle, The Farne Islands, Handa, Hilbre, Isle of May, Lundy, Skokholm, Scolt Head, Skomer and Steep Holm) from a larger dataset we are still compiling. These thirteen islands have reasonably large bird communities and the longest and most complete census data, derived as they are from permanent or semi-permanent bird observation stations. Pimm *et al.* (1993) used the same subset, but also included the German island of Helgoland. We exclude Helgoland because it has a distinctly different source of colonists. Summary data about these and the other islands in the dataset appear in Reed 1981a, b (a source which provides some of the data in table 1) and Pimm *et al.* 1988.

We are preparing a comparative study using even more islands. We cannot sensibly compare the many islands in this larger set—which are counted over varying intervals and with varying frequencies—unless we know something about the detailed dynamics of community turnover. This paper's principal objective is the characterization of these detailed dynamics. We wish to derive statistics that can be used confidently across the larger dataset.

We also cannot compare islands without considering which species to select. There are two factors which might obscure comparative relationships in small islands such as these. First, even a small island may have extensive cliffs surrounded by food-rich water supporting many species of pelagic feeders. Second, the amount of freshwater habitat on an island is mostly a function of its topology, the amount of rainfall, and the number of freshwater springs present. Both these factors change the effective area of the island for certain species, in a way which is largely independent of simple area measurements. We restricted our analysis accordingly by including only terrestrial species and eliminating both pelagic and freshwater feeders such as gulls, divers, waders and ducks. Birds remaining in the dataset for these islands are listed in Appendix 1.

CALCULATING TURNOVER

TURNOVER, CUMULATIVE TURNOVER, OR TURNOVER RATE?

Our analysis of turnover resembles that of Diamond and May (1977), who used the following definition:

$$\text{Turnover rate} = \frac{\text{No. of extinctions + no. of immigrations}}{\text{Total no. of species present} \times \text{census interval}} \quad (1)$$

Here, as in all cases where the islands in question are not extremely isolated, "extinction" refers simply to the disappearance of all breeding pairs of a species on an island between one year and the next. It is not only local in scope but does not necessarily imply 'true' extinction (i.e., death) but perhaps simply failure to breed or a decision to breed elsewhere. (The movement of island pairs, from the island being considered to either other islands or to the nearby mainland, does affect turnover, as we shall describe below.)

Diamond and May described mathematically what had previously been a confounding effect on estimates of turnover rate: that if community censuses are separated by two or more years, then some colonization and extinction events within this interval may go undetected. For example, species A may be present in year y and absent thereafter until year $y + n$ (where $n > 1$). A's absence between years y and $y + n$ would contribute nothing to the numerator of equation 1. As a result, turnover rate is likely to be an underestimate of the cumulative turnovers. Indeed, by chance, two widely separated censuses may find no turnover when in fact the cumulative turnovers have been substantial. We will call calculations made in non-adjacent years *apparent turnover*, to recognise these problems.

Unlike Diamond and May, we do not divide by census interval. Instead, we examine how the apparent turnover, rather than the turnover rate, changes over increasing census interval. We shall show that it is reasonable to describe apparent turnover as increasing asymptotically, following the discovery of

Diamond and May that turnover *rate* tends asymptotically towards a slope of –1. We believe that our method avoids a potentially confusing use of the word "rate" to describe a non-linear relationship. For example, Diamond (1969) describes measurements taken over a long interval as "turnover rate per 51 years", which is perfectly correct, but might tempt someone to divide these values by 51 and call them 'turnover rate per year', which would yield a severe underestimation of the actual yearly rate. More generally, we will show that neither apparent turnover nor turnover rate are statistics that permit comparisons between islands.

We will provide statistics that do permit such comparisons. Continuous counts allow us a modification not possible in most earlier studies, in that we can usually generate more than one value of apparent turnover. In a 20 year unbroken record, for example, there are 19 pairs of values separated by one year, 18 pairs of values that are separated by 2 years, and so on. We can now estimate the distributions and thus *mean* values of apparent turnover, not merely single values. The distributions may include the occasional zero value in the numerator of equation 1, but combined with the rest of the values they will still demonstrate turnover typical of the island. We calculate the mean value of all the apparent turnovers for a given census interval. For convenience, henceforth by 'turnover' we mean this *mean apparent* turnover. We use the following definitions, which are explained more fully in the text that follows:

y Year.

τ	The total number of years in a census dataset.
n	The interval over which turnover is calculated, where y is the first year of the interval and $y + n$ is the last year.
S_y, S_{y+n}	The number of species in a community in year y, or $y + n$.
E_n	The apparent *number* of extinction events over an interval n, i.e., the number of species breeding in year y that fail to breed in year $y + n$.
I_n	The apparent *number* of immigration events over an interval n, i.e., the number of species failing to breed in year y that breed in year $y + n$.
T_n	*Apparent* turnover: the turnover *per species* between two censuses separated by n years, calculated using values of E_n and I_n, the apparent numbers of extinction and immigration events.
$\overline{T}_n$	*Mean* turnover: calculated as the mean value of the apparent turnover (T_n).
$\overline{T}_1$	*Mean one-year* turnover: the value of $\overline{T}_n$ between adjacent years.

CALCULATION OF TURNOVER FROM EMPIRICAL DATA

Apparent turnovers (T_n) between any two years y and $y + n$ were calculated by comparing the presence and absence of breeding pairs of species in each of the

two years, adding the number of observed extinctions over this period (E_n) to the number of observed immigrations (I_n), and dividing by the sum of the number of species on the island in each of the two years S_y and S_{y+n}.

$$T_n = \frac{E_n + I_n}{S_y + S_{y+n}} \tag{2}$$

Clearly, for $n = 1$ (i.e., adjacent years), the procedure may in principle be carried out one less time than the total number of years in the dataset for that island (for a continuous five-year dataset, we could compare year 1 with year 2, 2 with 3, 3 with 4, and 4 with 5). Similarly, the largest interval n for which turnover can be calculated is using the first and the last year of the dataset, that is, one less than the total number of years (e.g., year 1 with year 5, so that $n = 4$). In this case there can only be one calculation. If τ is the number of years in the whole dataset, then for the range of values of n between 1 and $\tau - 1$ there is a linear decrease in the maximum number of apparent turnover values that can be calculated from $\tau - 1$ to 1. In practice, because of gaps in the data (such as occasional years when no census was carried out), we usually have slightly less than the maximum possible number of values contributing to the mean estimate. We calculated all possible apparent turnovers, and then found the mean turnover value for each n. These estimates of turnover vary in the confidence that can be placed upon them, with those of highest n, and so fewest points, being most suspect.

Figure 1 shows the individual values of apparent turnover against interval for one island (Skokholm), with the mean turnovers and the numbers of values which contributed to the means.

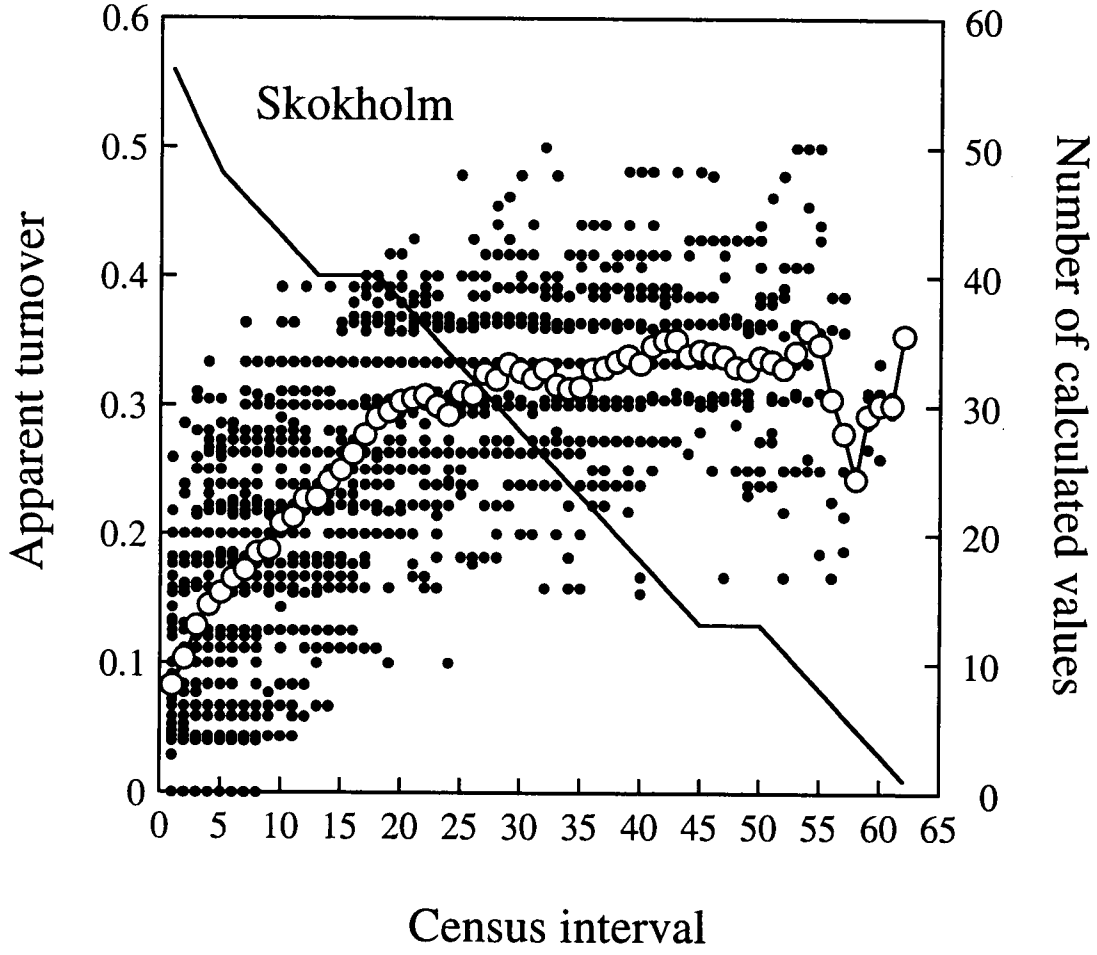
AN EQUILIBRIUM MODEL

DERIVATION

We first construct a very simple model of the way in which turnover should vary with the length of the census interval, based upon the assumption that the islands are at dynamic equilibrium (*sensu* MacArthur and Wilson). As we discuss later, we know that this assumption does not hold for most of the islands, but we would like to understand its consequences before we try to improve upon it. Following Diamond and May (1977), we use a single mean value, S_e, to describe the equilibrium distribution of values of S. Species numbers fluctuate about this value, a phenomenon that has been termed "turnover noise" (Diamond and Gilpin 1980). We do not mean to imply that the number of species is invariant, only that it may be reasonably represented by a single value. The validity of this assumption is also examined presently. The following definitions are now needed:

e_n The per-species mean extinction *probability* that a species from a given community breeds in year y but fails to breed in year $y + n$.

Figure 1. Measurements of apparent turnover (solid circles) and estimates of mean turnover (open circles) for the island of Skokholm, with the number of values contributing to each mean (solid line).


Skokholm
Apparent turnover
Number of calculated values
Census interval
0.6
0.5
0.4
0.3
0.2
0.1
0
60
50
40
30
20
10
0
0 5 10 15 20 25 30 35 40 45 50 55 60 65

i_n The per-species mean immigration *probability* that a species from a given community fails to breed in year y but breeds in year $y + n$.

$\overline{S}_y$ The mean number of species in a community over the period for which data are available. Used as an estimate of:

S_e The hypothetical equilibrium number of species in a community.

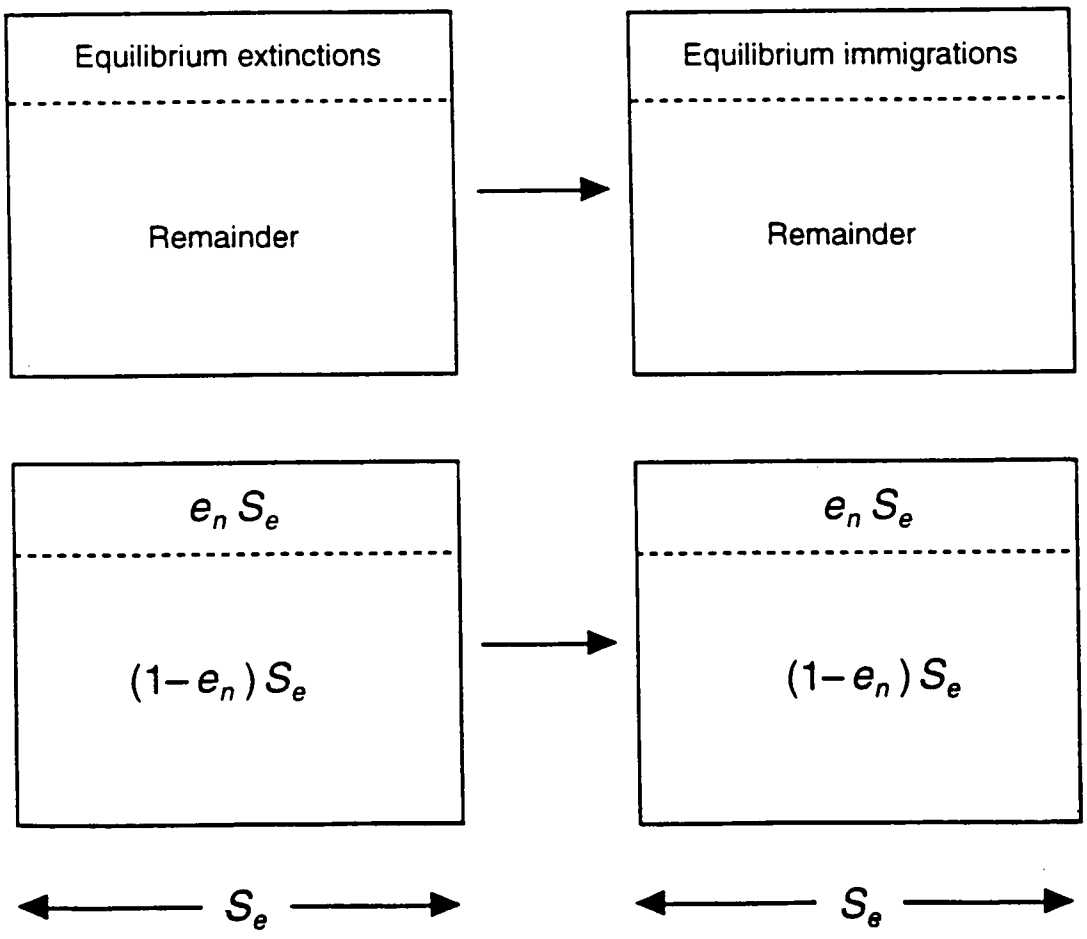
For an island at equilibrium, three things are true: the number of species is constant ($S_y = S_{y+n} = S_e$), the number of immigrations must therefore equal the number of extinctions ($I_n = E_n$), and we may estimate E_n from $e_n S_e$. Figure 2 graphically depicts this equilibrium in extinctions and immigrations. It can be seen that

$$T_{n(\mathrm{eq})} = \frac{E_n + I_n}{S_y + S_{y+n}} = \frac{2E_n}{2S_e} = \frac{2e_n S_e}{2S_e} = e_n \qquad (3)$$

Hence turnover (which by definition is per species) is equal to the mean extinction probability (also per species) over the interval n. We use the subscript (eq) to indicate that this formula depends upon the assumptions of the equilibrium model.

This equation may be used for any value of n. The series $e_1, e_2, e_3, \ldots, e_n$ is determined by the rules of probability. For adjacent years, there are four options: *present then absent* is described by e_1, so that *present then present* is described by $1 - e_1$, and *absent then present* is described by i_1, so that *absent then absent* is described by $1 - i_1$. e_n, the probability of a species being present in year y and absent in year

Figure 2. Graphic representation of turnover under equilibrium conditions. See text for definitions of symbols.


Equilibrium extinctions
Remainder
Equilibrium immigrations
Remainder
$e_n S_e$
$(1-e_n) S_e$
$e_n S_e$
$(1-e_n) S_e$
S_e
S_e

$y + n$, is the sum of the probabilities of all the possible routes from a state of presence to a state of absence over the interval n.

For an extinction event between year y and year $y + 2$, the two possible routes are *present then absent then absent* and *present then present then absent*. We assume that the probability of extinction from year y to year $y + 1$ is independent of the probability from year $y - 1$ to year y, and a similar assumption is made about the immigration probabilities. With these assumptions, the probability of the first route is e_1 multiplied by $(1 - i_1)$, and the probability of the second route is $(1 - e_1)$ multiplied by e_1. The overall probability, e_2, is the sum of these, which may be written as $e_1 + e_1 (1 - e_1 - i_1)$. This same procedure may be carried out for any pair of years. Values of e_1 to e_5 are as follows:

$$
\begin{aligned}
e_1 &= e_1 \\
e_2 &= e_1 + e_1(1 - e_1 - i_1) \\
e_3 &= e_1 + e_1(1 - e_1 - i_1) + e_1(1 - e_1 - i_1)^2 \\
e_4 &= e_1 + e_1(1 - e_1 - i_1) + e_1(1 - e_1 - i_1)^2 + e_1(1 - e_1 - i_1)^3 \\
e_5 &= e_1 + e_1(1 - e_1 - i_1) + e_1(1 - e_1 - i_1)^2 + e_1(1 - e_1 - i_1)^3 + e_1(1 - e_1 - i_1)^4
\end{aligned}
$$

This is a geometric progression with first term e_1 and common ratio $(1 - e_1 - i_1)$. n describes the term of the progression, so that e_n may be calculated for any interval:

$$
e_n = \frac{e_1\left[1 - (1 - e_1 - i_1)^n\right]}{1 - (1 - e_1 - i_1)} = \frac{e_1\left[1 - (1 - e_1 - i_1)^n\right]}{e_1 + i_1} \qquad (4)
$$

From equation 3 we know that $T_{n(eq)} = e_n$ for all values of n, so we may use equation 4 to describe how turnover varies with different census intervals. From our mean estimates of apparent turnover (that is, the mean turnovers, $\overline{T}_n$), we can apply familiar statistical procedures to estimate e_1 and i_1 for different values of n.

A comparison with Diamond and May's model

This effort is not the first attempt to model turnover. Diamond and May (1977) applied the same argument, but to the *individual* species. Their community-wide estimates of turnover recognise the actual distribution of extinction and immigration probabilities across species. In the preceding argument, these probabilities would host a further subscript indicating to which particular species a value of, say, e_1 would belong. We choose not to use this model, but assume that we can adequately model the community using mean values of immigration and extinction. We make the assumption that distributions of immigration and extinction probabilities for the *entire pool of species* can be characterised by their mean values. We doubt that this assumption is correct, but recent evidence shows that even for sporadic censuses, mean values provide reasonable data for estimating immigration and extinction rates (Clark and Rosenzweig 1994).

Inspection of the fit of Diamond and May's model (derived only for one island, Skokholm) shows that it is not particularly compelling. Perceptive readers will realise that their "explicit species" model must do at least as well as our "average

species" model. So the fits we now present will also not be "particularly compelling." Our model's simplicity, however, allows us to modify it in ways unavailable to Diamond and May. We produce an only slightly more complex model that does provide a good fit to the data, and so provides a simple and useful way of comparing islands. Our eventual objective is to find credible ways of comparing turnover across many different islands.

FITTING THE MODEL

We use the "NLIN" procedure of SAS (® SAS Institute Inc., Cary, North Carolina), which uses a least-squares method, to fit equation 4 to the data. We could do this in two ways. One would be to use the estimated mean values of turnover from our calculations, and weight them according to the number of observations that contributed to each mean. Instead, we use the entire set of observations (for Skokholm this would be all the points in Figure 1). This eliminates the need for weighting and provides a more accurate estimate of goodness-of-fit. (We recognize that, as with any time-series, the data points are not independent so that any estimates of goodness-of-fit will still be inflated to some degree. Consequently, we do not use them to assess the quality of the model.)

Out of interest, we also fit the model using the weighted means. There is a small change in the estimated parameters for the Calf of Man, but it is minor and affects none of our conclusions.

Another definition is now required:

$\hat{T}_{n(\mathrm{eq})}$ *Equilibrium* turnover: the predicted value of $\overline{T}_n$ from the fit of an 'equilibrium' model that assumes a constant number of species on each island.

Figure 3 shows both the mean turnover (solid lines) and the predictions of the fitted equilibrium model (dotted lines) for all the islands. Table 1 lists the observed mean one-year turnover value for each island ($\overline{T}_1$) and two predicted values from the equilibrium model: the one-year turnover ($\hat{T}_{1(\mathrm{eq})}$), and the *long-term* turnover ($\hat{T}_{\infty(\mathrm{eq})}$). The table also shows the mean number of species present over the entire census interval ($\overline{S}_y$), which is an estimate of the equilibrium number of species. Even though, as we noted, these *F*-values have been inflated by lack of independence in our data, the fits of the equilibrium model are extremely "significant" in all cases (the lowest *F*-value, for Hilbre, is 552.4 where $F_{0.05(2)} = 3.72$).

The failure of the equilibrium model

Although this simple model does a good job of predicting the essential features of the way in which apparent turnover varies with census interval, Figure 3 shows that it consistently underestimates turnover at extremes of census interval, and overestimates in the centre. This is more obvious in Figure 4, where we plot predicted values of one-year turnover against the observed values (the predictions of the equilibrium model are represented by the solid circles). The

Table 1. A sample of turnover statistics, both calculated and derived from model-fitting procedures. $\overline{T}_1$ is the mean one-year turnover for an island—the mean of all possible calculations of turnover between adjacent years. $\hat{T}_{1(eq)}$ is the predicted value of one-year turnover from the equilibrium model. $\hat{T}_{\infty(eq)}$ is the predicted value of asymptotic turnover from the equilibrium model. $\hat{T}_{1(ne)}$ is the predicted value of one-year turnover from the non-equilibrium model. $\hat{T}_{\infty(ne,\,in)}$ is the predicted asymptotic value of the intrinsic component of turnover from the non-equilibrium model. $\overline{S}_y$ is the mean number of species on the island over the interval for which data are available.

Island	Mean observed one-year turnover	Equilibrium model		Non-equilibrium model		Mean number of species	% change in species number per decade
		Predicted one-year turnover	Predicted asymptotic turnover	Predicted one-year turnover	Predicted asymptotic intrinsic component		
	$\overline{T}_1$	$\hat{T}_{1(eq)}$	$\hat{T}_{\infty(eq)}$	$\hat{T}_{1(ne)}$	$\hat{T}_{\infty(ne,\ in)}$	$\overline{S}_y$	
Bardsey	.073	.024	.310	.027	.256	22.1	–2.3%
Calf of Man	.091	.021	.425	.021	.583	20.4	2.1%
Copeland	.150	.094	.360	.096	.357	9.55	4.6%
Fair Isle	.077	.060	.137	.081	.090	12.3	–5.4%
Farne	.151	.117	.318	.124	.305	5.68	8.2%
Handa	.110	.048	.368	.048	.366	12.2	2.5%
Hilbre	.187	.132	.354	.132	.355	5.9	2.8%
Isle of May	.099	.055	.378	.058	.354	7.18	–1.8%
Lundy	.109	.035	.308	.069	.203	18.7	–5.8%
Scolt Head	.135	.067	.393	.072	.378	5.65	11.8%
Skokholm	.083	.034	.332	.036	.315	10.8	4.9%
Skomer	.074	.019	.406	.056	.150	23.6	10.4%
Steep Holm	.090	.034	.300	.045	.231	9.43	–4.1%

Figure 3. Mean turnover (solid lines) and the predictions of the equilibrium model (dotted lines) for all the islands.

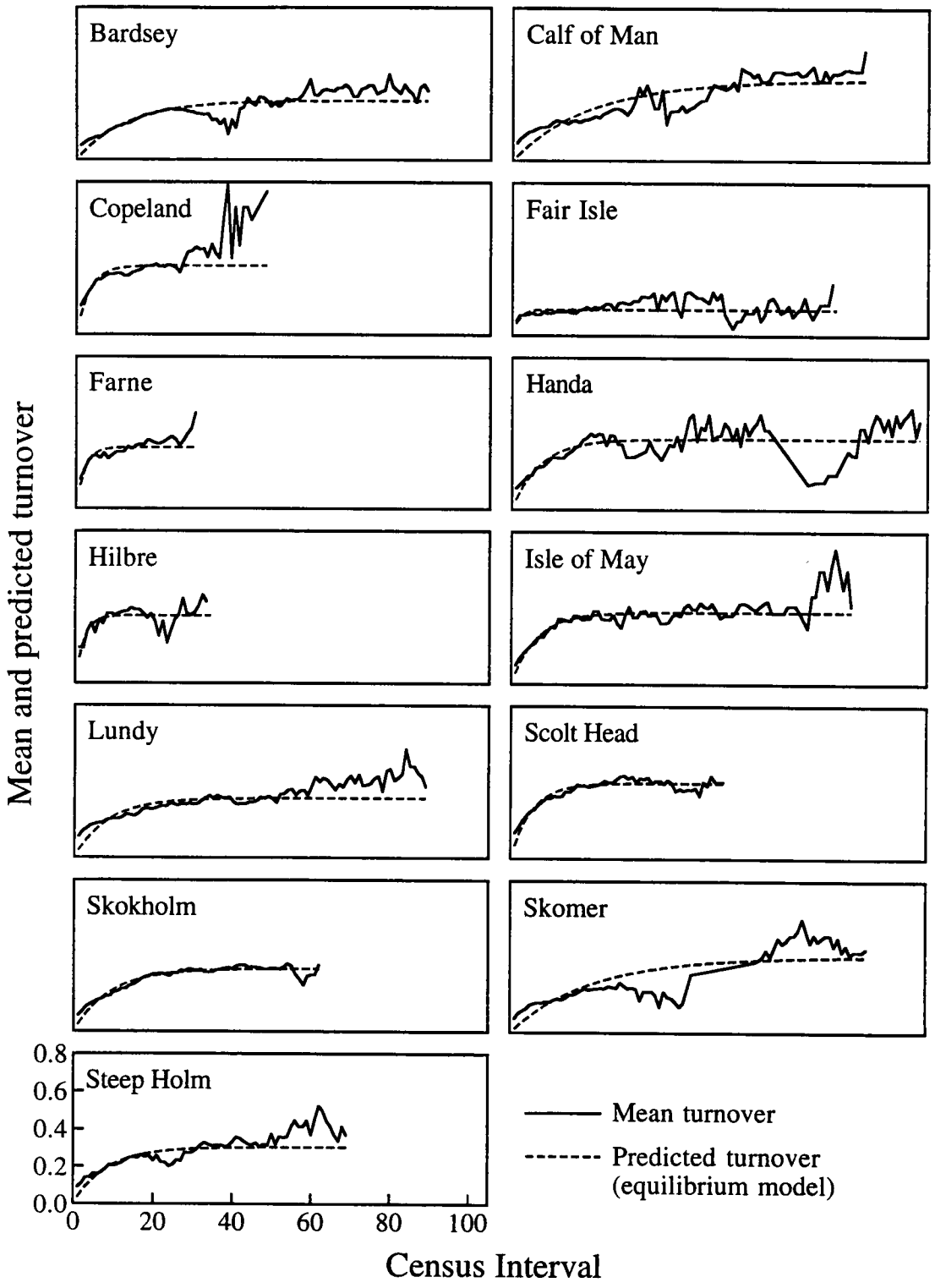
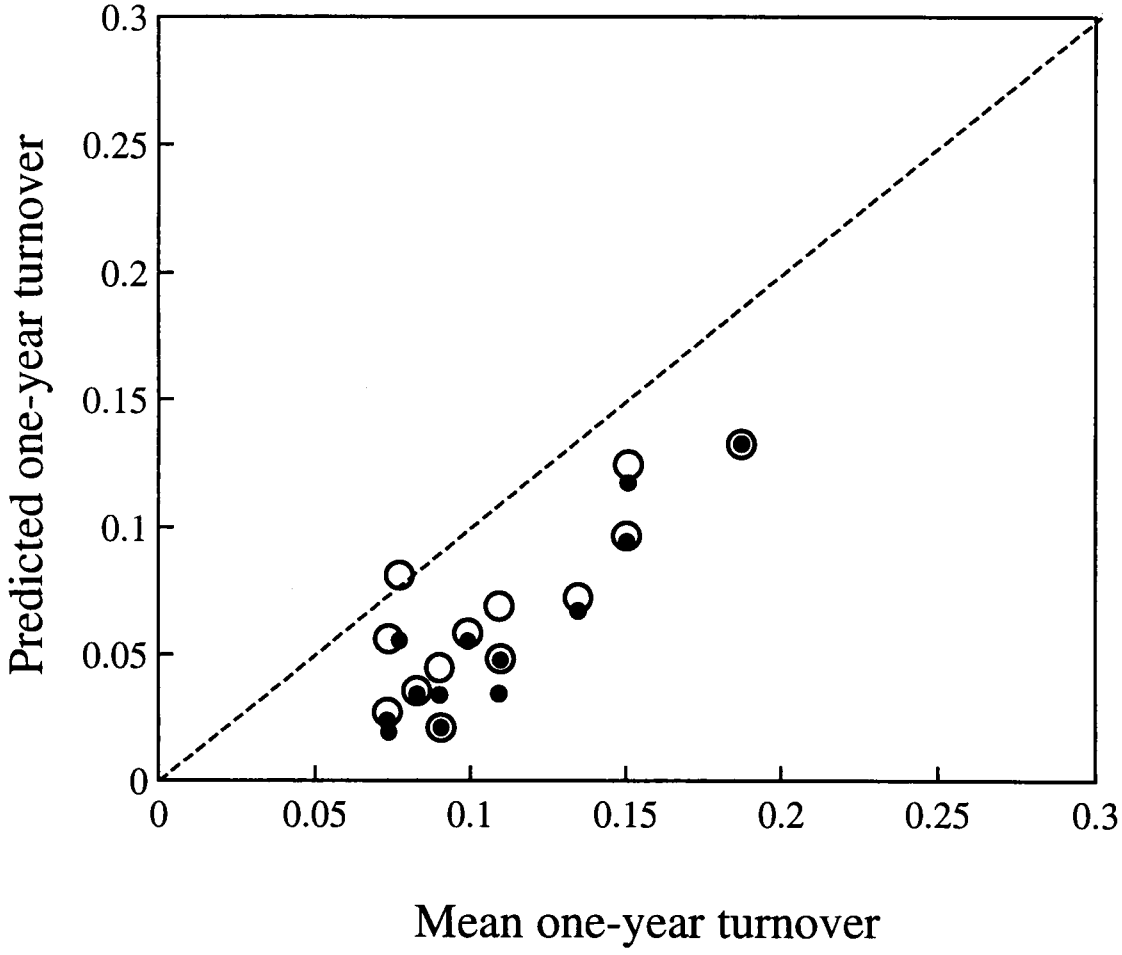

Bardsey
Calf of Man
Copeland
Fair Isle
Farne
Handa
Hilbre
Isle of May
Lundy
Scolt Head
Skokholm
Skomer
Steep Holm
Mean and predicted turnover
0.0
0.2
0.4
0.6
0.8
0
20
40
60
80
100
Census Interval
Mean turnover
Predicted turnover
(equilibrium model)

Figure 4. Predictions of one-year turnover by both the equilibrium (solid circles) and non-equilibrium (open circles) models. The dotted line represents a regression line of slope one, intercept zero, such as would be expected from a model with no systematic error.


Predicted one-year turnover
0.3
0.25
0.2
0.15
0.1
0.05
0
0
0.05
0.1
0.15
0.2
0.25
0.3
Mean one-year turnover

equilibrium model consistently underestimates the one-year turnover by approximately 0.05. How can we improve our description of the data?

We might have interpreted our simple model's failings as a consequence of our deriving mean species behaviour instead of modelling the individual species separately. As we have already noticed, Diamond and May did model the species separately, and their model also provided a poor fit to the Skokholm data. Clearly, some other processes are at work.

Inspection of the data shows that in many islands, turnover does not asymptote to a constant value as the equilibrium model predicts, but rather continues to rise as census interval increases. Since the fitting procedure is weighted towards small intervals, it 'ignores' this trend and so the fitted model consistently underestimates the data at longer intervals. The trend also has the effect of making the curve of the data at smaller intervals more gentle than predicted by the model, and as a result, the model's estimates of e_1 and i_1 are biased towards low values, because only these will generate a gentle curve. This, however, necessarily means that the curve must also start off at this low value, since when $n = 1$, $T_{n(\mathrm{eq})} = T_{1(\mathrm{eq})} = e_1$. In other words, the fitted curve is effectively 'anchored' at its initial value, and hence also underestimates the data at the smallest intervals. Both types of underestimation are most pronounced when the continued rise in turnover at long intervals is most obvious. Calf of Man and Lundy provide clear examples in Figure 3.

A NON-EQUILIBRIUM MODEL OF DYNAMIC ISLAND BIOGEOGRAPHY

ASSUMPTION OF EQUILIBRIUM

Our previous model included the assumption that the total number of species on each island can be described by the mean of a distribution, i.e., that the central tendency of this distribution does not change over time. This is not true for at least one island in this study. Using data from Skokholm between 1928 and 1967, Abbot and Grant (1976) concluded that the number of species on the island was not at equilibrium, to support a suggestion that such equilibrium is rare in high (i.e., non-tropical) latitudes. A detailed analysis by Williamson (1983) also denies an equilibrium species number. Is a changing number of species ubiquitous, or just a feature of Skokholm?

Three of the islands show a decrease in species number with time greater than 4% over a decade, and five show similarly large increases (including Skokholm). We calculated regression coefficients for species number against time and (for reasons that shall become apparent) for the natural logarithm of species number against time, for all the islands in this study.

What are the implications of either an increase or decrease in species number over time for measurements of turnover? These bird communities show only slow changes, if any, which may require intervals of fifty years or more to become detectable. Nevertheless, the effect of either rise or fall in species number

is to elevate turnover, particularly over long intervals. This will manifest itself as a failure to reach the asymptote that we expect solely from the way in which the extinction and immigration probabilities change with interval (i.e., the asymptote of the equilibrium model presented above). This constant value will be replaced by a function that describes the effect of a change in species number over time on turnover at different intervals.

The effect of changing species numbers on turnover will be more pronounced for a fall in numbers, as the following example shows: Consider a hypothetical community which is at equilibrium with ten species present. Over an interval n there are five immigrations and five extinctions. The turnover (from equation 1) is therefore (5 + 5) / (10 + 10) = 0.5. Now suppose the species number increases by one over this interval, that is, there is one additional immigration. The turnover is now (5 + 6) / (10 + 11) = 0.524, which is greater than at equilibrium. If, however, the species number *decreases* by one (an additional extinction), the turnover is now (6 + 5) / (10 + 9) = 0.579: an even greater increase above its equilibrium value. Thus, we also predict that this effect of changing species number on long-term turnover will be most pronounced in those islands showing a decrease in species number over time. (These are Bardsey, Fair Isle, Isle of May, Lundy and Steep Holm; see column 8 of table 1).

Modifications to the equilibrium model

As discussed above, we could incorporate the change in species number over time as either a linear or an exponential function of time, that is, $S = f(y)$ or

$S = f(\exp^{y})$. Both functions provide a similarly good fit to the data, but the linear function has the property that if it is negative, the predicted number of species at some point in the future will also become negative. Since negative species are clearly impossible, we choose the exponential function, which will only decrease to zero in these circumstances. (We use natural logarithms, but in fact a logarithm to any base could be used.) We incorporate the trend in species number by introducing the parameter β, where $S_y = \exp^{\beta y + c}$ (and hence $S_{y+n} = S_y \exp^{\beta n}$). Table 1 lists the trend in species numbers as the percentage change over a decade [i.e., as $(\exp^{10\beta} - 1) \times 100$].

Figs 5 and 6 show schematically how we represent the change in species number (i.e., $S_y \exp^{\beta n} - S_y$) as the result of change in both the numbers of immigrations and of extinctions. Consider first the case of decreasing species number (Figure 5). We assume that whatever process is influencing species numbers both increases the number of observed extinctions above that expected under equilibrium, and decreases the number of observed immigrations below the (same) equilibrium number. (Considering the *observed* numbers is crucial, because it means we do not have to worry about actual mechanisms, about which we have no information. For example, a breeding pair might immigrate, attempt breeding, but fail, immigrate but choose not to attempt breeding, or simply choose not to immigrate. For the purposes of measuring turnover, these distinctions do not matter.) Since the extra extinctions (which we call X) will affect the species *remaining* after the normal, equilibrium extinctions, whereas the reduction in immigrations (which we call R) will affect the normal, equilibrium

Figure 5. Graphic representation of turnover under conditions of decreasing species number. Compare with Figure 2. The ratio of the reduction in immigrations (R) to the extra extinctions (X) is the same as the ratio of the equilibrium extinctions (or immigrations: $e_n S_y$) to the remainder in year y $[(1 - e_n)S_y]$.

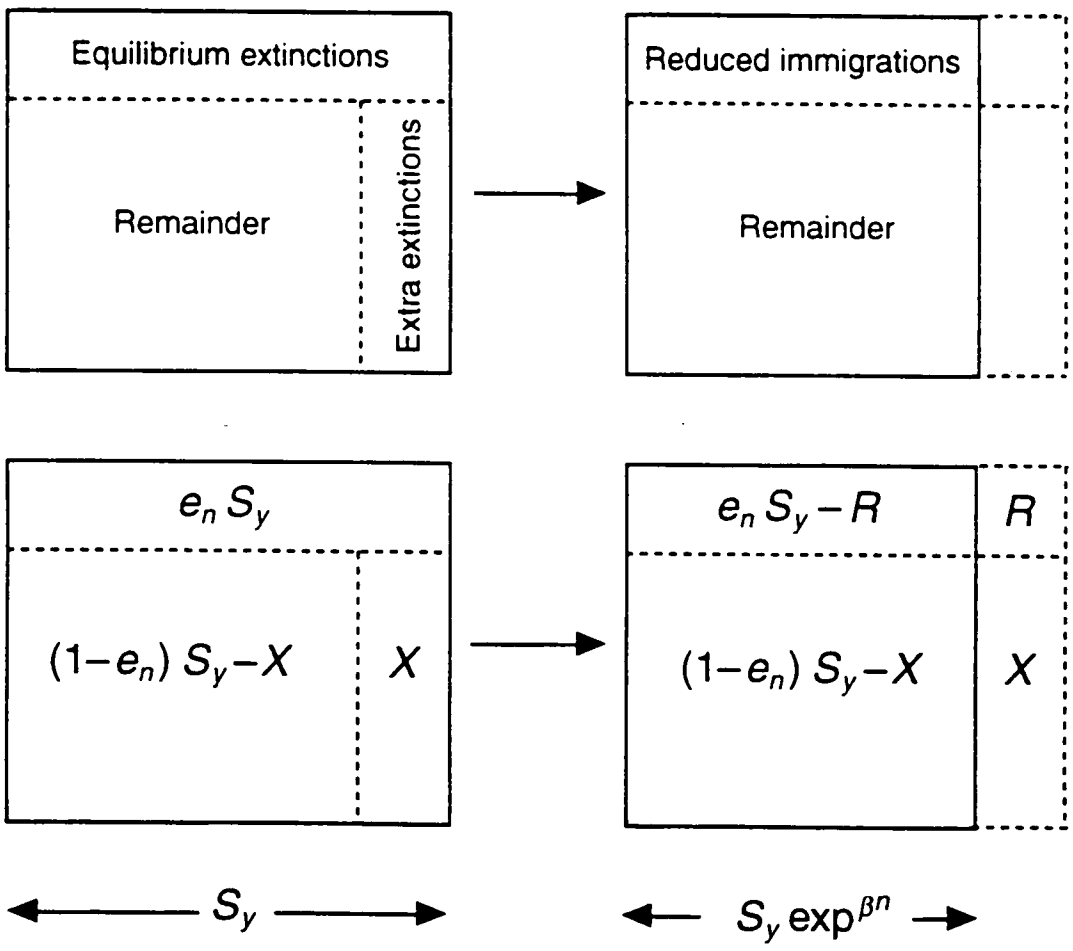
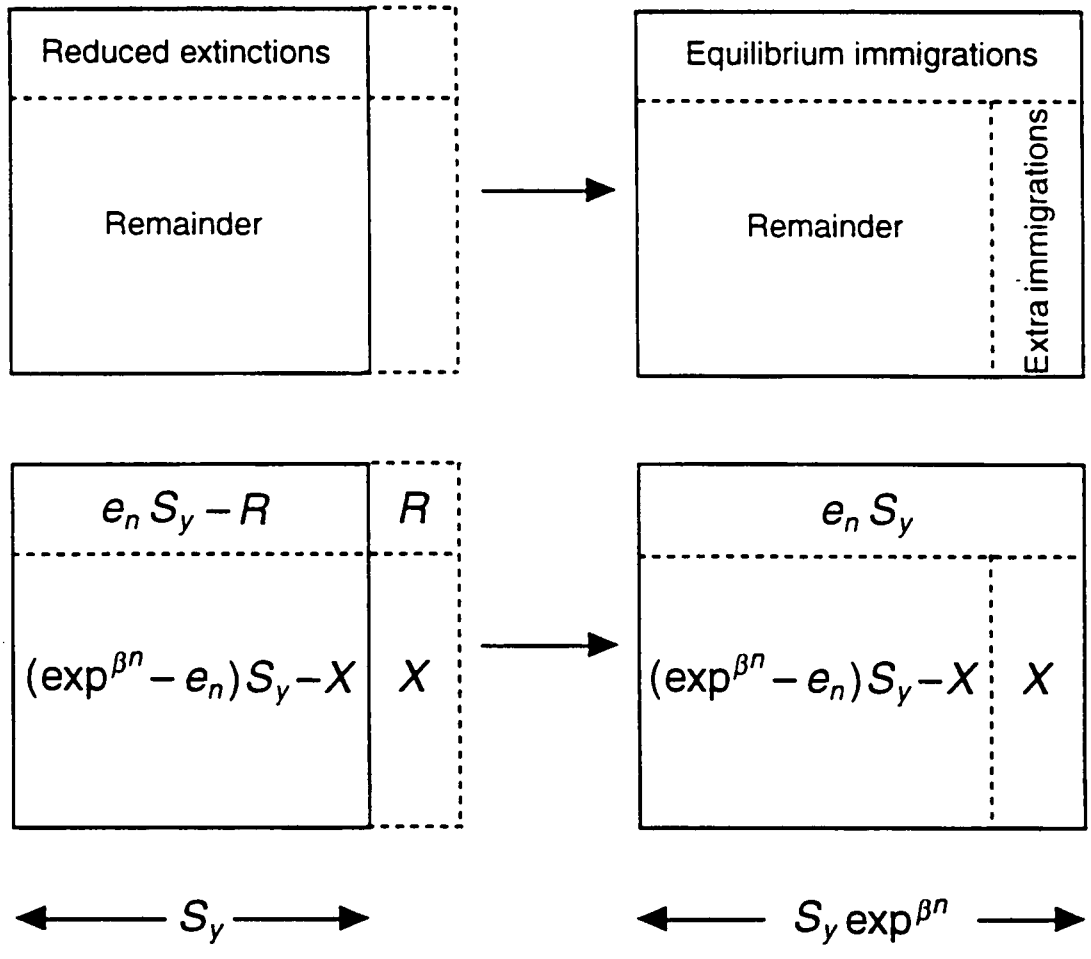

Equilibrium extinctions
Remainder
Extra extinctions
Reduced immigrations
Remainder
$e_n S_y$
$(1-e_n)\, S_y - X$
X
$e_n S_y - R$
R
$(1-e_n)\, S_y - X$
X
S_y
$S_y \exp^{\beta n}$

Figure 6. Graphic representation of turnover under conditions of increasing species number. Compare with Figs 2 and 3. In this case, the ratio of the reduction in extinctions (R) to the extra immigrations (X) is the same as the ratio of the equilibrium extinctions (or immigrations: $e_n S_y$) to the remainder in year $y + n$ $[(\exp^{\beta n} - e_n)S_y]$.


Reduced extinctions
Remainder
Equilibrium immigrations
Remainder
Extra immigrations
$e_n S_y - R$
R
$(\exp^{\beta n} - e_n) S_y - X$
X
$e_n S_y$
$(\exp^{\beta n} - e_n) S_y - X$
X
S_y
$S_y \exp^{\beta n}$

immigrations, we assume that X is the same proportion of the remainder as R is of the equilibrium immigrations. In other words,

$$\frac{X}{(1-e_n)S_y} = \frac{R}{e_n S_y}.$$

It is this proportionality that allows us to represent the reduction in species number graphically as in Figure 5. It follows that

Actual extinctions = Equilibrium extinctions + Extra extinctions

$$E = e_n S_y + X$$

and

Actual immigrations = Equilibrium immigrations – Reduction in immigrations

$$I = e_n S_y - R$$

so that

$$I + E = 2e_n S_y + X - R$$

Now consider the case of increasing species number, shown in Figure 6. This figure looks very like Figure 5, because the same reasoning applies. Here, we consider that the increase in species number is due both to an increase in the observed number of immigrations over the equilibrium number, and to a decrease in the observed number of extinctions (with the consideration of

observed numbers as important as before). Following the same rules of proportionality, we assume that the number of extra immigrations is the same proportion of the *remainder* following the equilibrium extinctions as the reduction in the number of extinctions is of the equilibrium extinctions. Using the same letter descriptions as before for the 'extra' amount (X) and for the 'reduction' (R), then in this case

$$\frac{X}{\left(\exp^{\beta n} - e_n\right)S_y} = \frac{R}{e_n S_y}.$$

from which it follows that

Actual extinctions = Equilibrium extinctions – Reduction in extinctions

$$E = e_n S_y - R$$

and

Actual immigrations = Equilibrium immigrations + Extra immigrations

$$I = e_n S_y + X$$

so that again

$$I + E = 2e_n S_y + X - R$$

and, by substitution in to equation 2, our expression for turnover in either case becomes

$$T_{n(\mathrm{ne})} = \frac{2e_n S_y + X - R}{S_y + S_{y+n}} = \frac{2e_n S_y + X - R}{S_y + S_y \exp^{\beta n}} \qquad (5)$$

We use the subscript (ne) to indicate that this formula depends upon the assumptions of the non-equilibrium model. Next we expand the values of X and R, first for when the number of species is decreasing with time, and then for when it is increasing. This expansion is presented in Appendix 2, and provides the following expressions for turnover:

$$\text{Decreasing species number}: \; T_{n(\mathrm{ne})} = \frac{-\left(\exp^{\beta n} - 1\right) + 2e_n \exp^{\beta n}}{1 + \exp^{\beta n}} \qquad (6)$$

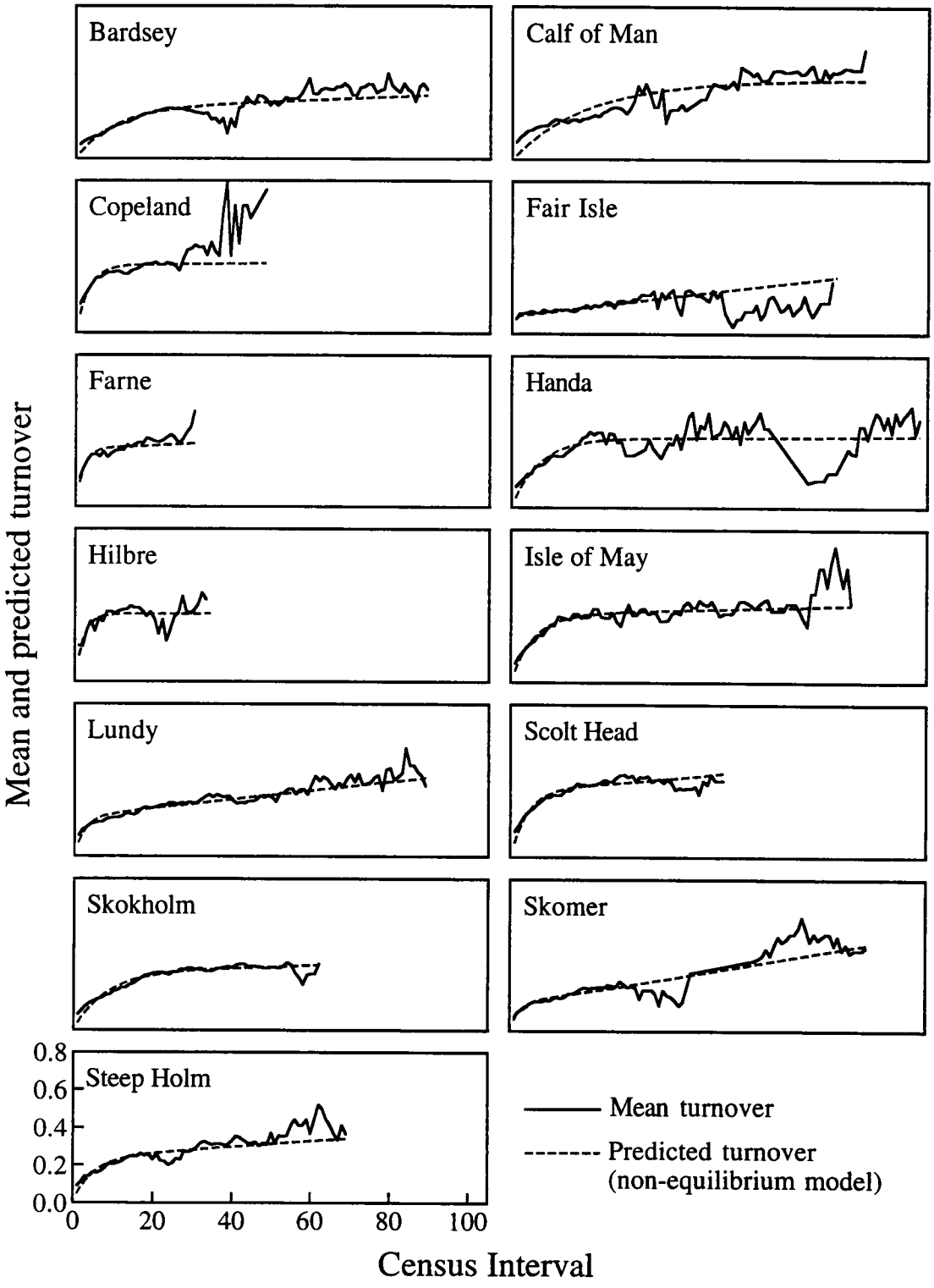
$$\text{Increasing species number}: \; T_{n(\mathrm{ne})} = \frac{\left(\exp^{\beta n} - 1\right) + 2e_n \exp^{-\beta n}}{1 + \exp^{\beta n}} \qquad (7)$$

Here, e_n is described as before by equation 3.

Fitting the non-equilibrium model

Using the regression estimates of β derived above, we fit the improved model to the data in the same way as the equilibrium model, and the results are shown in Figure 7. Again, the mean apparent turnover is represented by solid lines and the fitted non-equilibrium model by dotted lines. The new model provides a better fit to the data. This is inevitable, since the new model can only add, not subtract from the fit of the simpler model. The improvement is also seen in Figure 4 (the predictions of the non-equilibrium model are represented by *open* circles). With one exception (Calf of Man), the non-equilibrium model predicts higher one-year

Figure 7. Mean turnover (solid lines) and the predictions of the non-equilibrium model (dotted lines) for all the islands.


Bardsey
Calf of Man
Copeland
Fair Isle
Farne
Handa
Hilbre
Isle of May
Lundy
Scolt Head
Skokholm
Skomer
Steep Holm
Mean and predicted turnover
0.0
0.2
0.4
0.6
0.8
0
20
40
60
80
100
Census Interval
Mean turnover
Predicted turnover
(non-equilibrium model)

turnovers than the equilibrium model. Notice, however, that all but one of the non-equilibrium model's predictions are below the *observed* values. We shall return to this problem presently.

The improvement in fit is not easy to judge by inspection. For Fair Isle and Scolt Head the non-equilibrium model might at first appear worse than the equilibrium model, especially at longer census intervals. This is not actually the case, because these long intervals contribute fewer data points—the deviations in this region are outweighed by the smaller deviations at shorter census intervals. Other islands show a relatively small improvement (Bardsey, Farne, Hilbre, Isle of May), and two shows no visible change (Copeland, Calf of Man). These islands also show the smallest change in species number over time (see values of % change per decade in Table 1); for them, the non-equilibrium model is effectively the same as the equilibrium model. The remaining islands show much improved fits, with Lundy as the best example.

We have seen that although the non-equilibrium model is an improvement, it is not perfect—its predictions of one-year turnover still typically underestimate the observed values (Figure 4). We suspect that the answer may lie in an effect we have noticed in a detailed analysis of the times to extinction of such large-bodied birds as crows, hawks, and owls (Pimm *et al.* 1993). Populations of these species are clearly heterogenous. A proportion of pairs nest once and then (presumably) either die, or else leave and nest elsewhere, while the remainder nest repeatedly, year after year for decades. As an example, Pimm *et al.* found that on the islands in this study (plus Helgoland), 19 of 37 single-pair populations of crows lasted

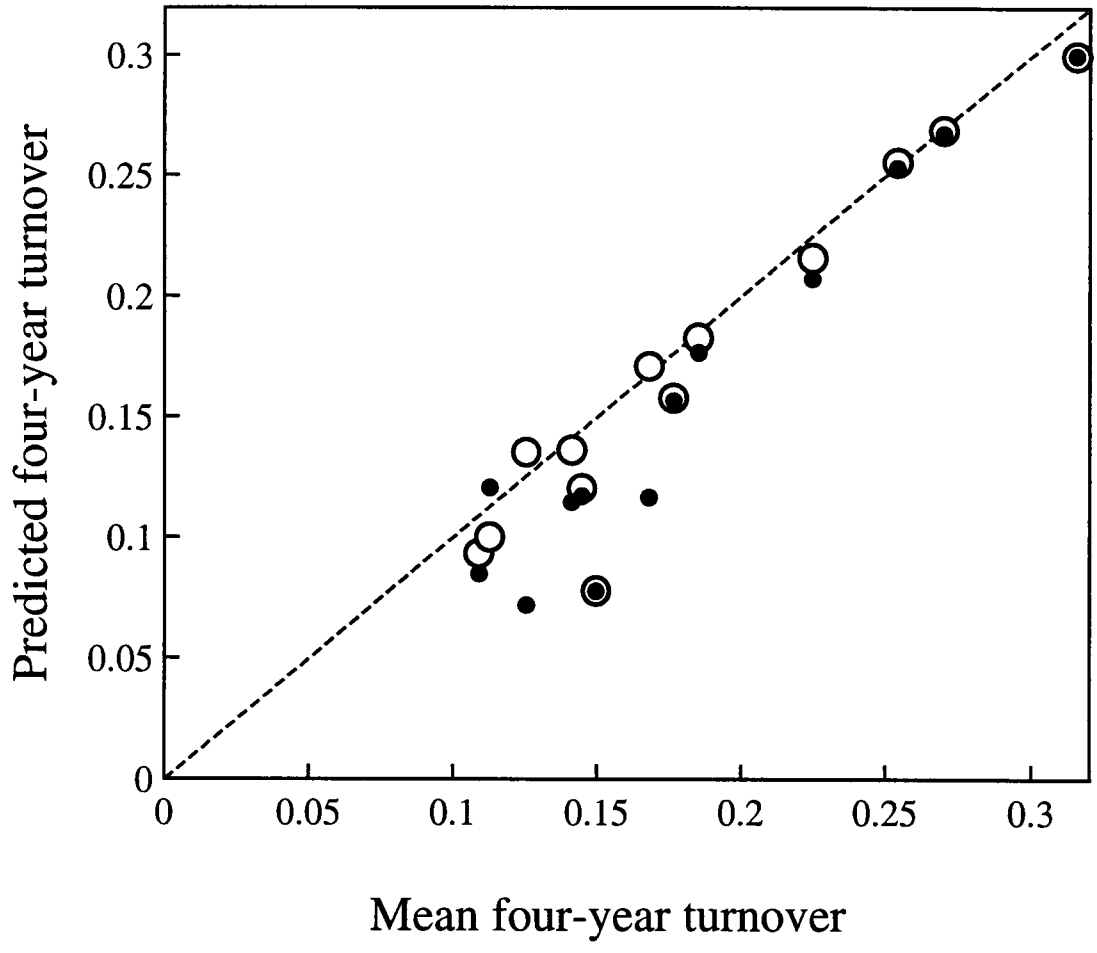
only 1 year, giving a estimate of e_1 for crows of 0.51. Assuming independence between years, we might expect that $37 \times (1 - e_1)^2 \approx 9$ pairs should last 2 years, $37 \times (1 - e_1)^3 \approx 4$ pairs should last 3 years, and so on. The probability of lasting 10 years is only $(1 - e_1)^{10} \approx 7 \times 10^{-4}$, but in reality three of the 37 one-pair populations lasted more than 10 years and one lasted more than 30 years. Clearly there is an excessive number of short-term populations, composed largely of individuals which we call *floaters*, and their effect is to inflate estimates of both e_1 and one-year turnovers.

One way to evaluate this problem is to compare observed and predicted turnovers over a slightly longer interval, say, four years. The short-term apparent extinction of floater populations will be unimportant over this interval. Figure 8 shows our analyses and they confirm our intuition: the equilibrium model seriously underestimates the observed four-year turnovers, but the non-equilibrium model provides a compelling prediction (although there is still one island—Calf of Man—which the model underestimates).

Deconstructing the non-equilibrium model

The non-equilibrium model can be thought of as having an equilibrium and a non-equilibrium component, and the good fit of this model to the data suggests that real turnovers may be thought of in a similar way. We propose that the communities on these islands exhibit dynamic behaviour (that is, turnover) on essentially three time scales.

Figure 8. Predictions of four-year turnover by both the equilibrium (solid circles) and non-equilibrium (open circles) models. The dotted line represents a regression line of slope one, intercept zero, such as would be expected from a model with no systematic error.


Predicted four-year turnover
0.3
0.25
0.2
0.15
0.1
0.05
0
0
0.05
0.1
0.15
0.2
0.25
0.3
Mean four-year turnover

a) At the shortest scale there is the year-to-year turnover of species. This is inflated by the "floaters" that may well represent individuals that move on and off the islands from year to year to nest.

b) At slightly longer intervals (approximately between 10 and 60 years, depending, as we show, on the island), apparent turnover is a cumulative function of the mean yearly immigration and extinction probabilities for the species in the communities. This is the process that defines MacArthur and Wilson's familiar model. Because it is solely the function of a particular insular community, we call this the *intrinsic component* of turnover, or just *intrinsic turnover* for short ($\hat{T}_{n(\mathrm{ne,\ in})}$). At longer intervals, this intrinsic turnover approaches an asymptotic value: the *intrinsic long-term* turnover ($\hat{T}_{\infty(\mathrm{ne,\ in})}$).

c) Most islands, however, show a change in species number over time. The rate of this change adds another function, but at longer intervals (i.e., where the intrinsic turnover has already become asymptotic). We call this function the *extrinsic* turnover, $\hat{T}_{n(\mathrm{ne,\ ex})}$, because it is mostly a function of factors *external* to the bird community (such as habitat succession or modification on the island, long-term changes in the mainland source pool, etc.). The value of the sum of the intrinsic and extrinsic components is given by the non-equilibrium model derived above, which incorporates both processes. The extrinsic component is also asymptotic, but at a longer timescale than the intrinsic component.

We can deconstruct the non-equilibrium model, and get an estimate of the intrinsic long-term turnover, by taking the values of e_1 and i_1 provided by the fit of the model and using them to calculate an asymptotic value *as if for the equilibrium model*. This value is provided by equation 4 when $n = \infty$. In this case, equation 4 may be simplified as follows: since e_1 and i_1 are probabilities, $0 \leq e_1 \leq 1$ and $0 \leq i_1 \leq 1$, so that $(1 - e_1 - i_1)$ must lie between –1 and 1. If we ignore the trivial cases where $e_1 = i_1 = 0$ and $e_1 = i_1 = 1$, then $(1 - e_1 - i_1)^{\infty} = 0$. It follows that

$$\hat{T}_{\infty(\text{ne, in})} = \frac{e_1}{e_1 + i_1} \tag{10}$$

Values of the intrinsic long-term turnover for these islands are given in Table 1. Figure 9 shows the predictions of both the entire non-equilibrium model and its intrinsic component for the island of Scolt Head. On a log/log scale, the non-equilibrium model displays two distinct convex curves representing the influence of first intrinsic and then extrinsic factors on the long-term turnover (the extrinsic component is obtained simply by subtracting the intrinsic component from the overall model). An example statistic is shown: the interval at which the extrinsic component is equal to 25% of the intrinsic component ($n_{0.25(\text{ex/in})}$). Whilst arbitrary, statistics that summarise at what interval extrinsic effects play a significant part in community dynamics may be useful in comparisons between islands, the subject of our next paper (see the Introduction). Figure 10 shows the log/log plot of both the non-equilibrium model's predictions (thick lines) and the intrinsic turnover alone (thin lines) for all the islands.

Figure 9. A: Predicted non-equilibrium turnover for the island of Scolt Head, divided into intrinsic and extrinsic components. Dotted lines represent extrapolation of the model beyond the data. B: As above, showing the interval at which the extrinsic component is at least 25% of the intrinsic component ($n_{0.25(ex/in)}$).

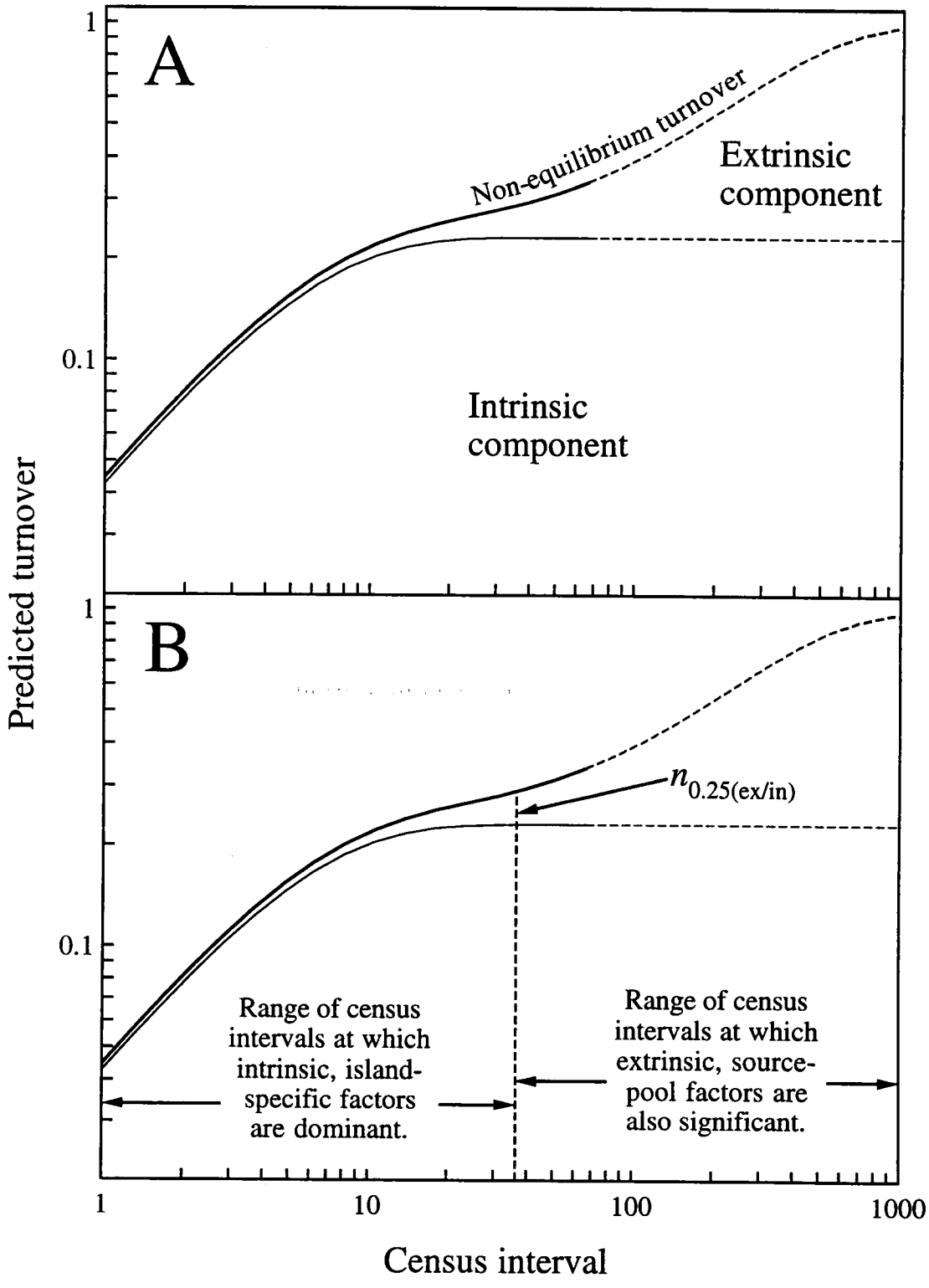
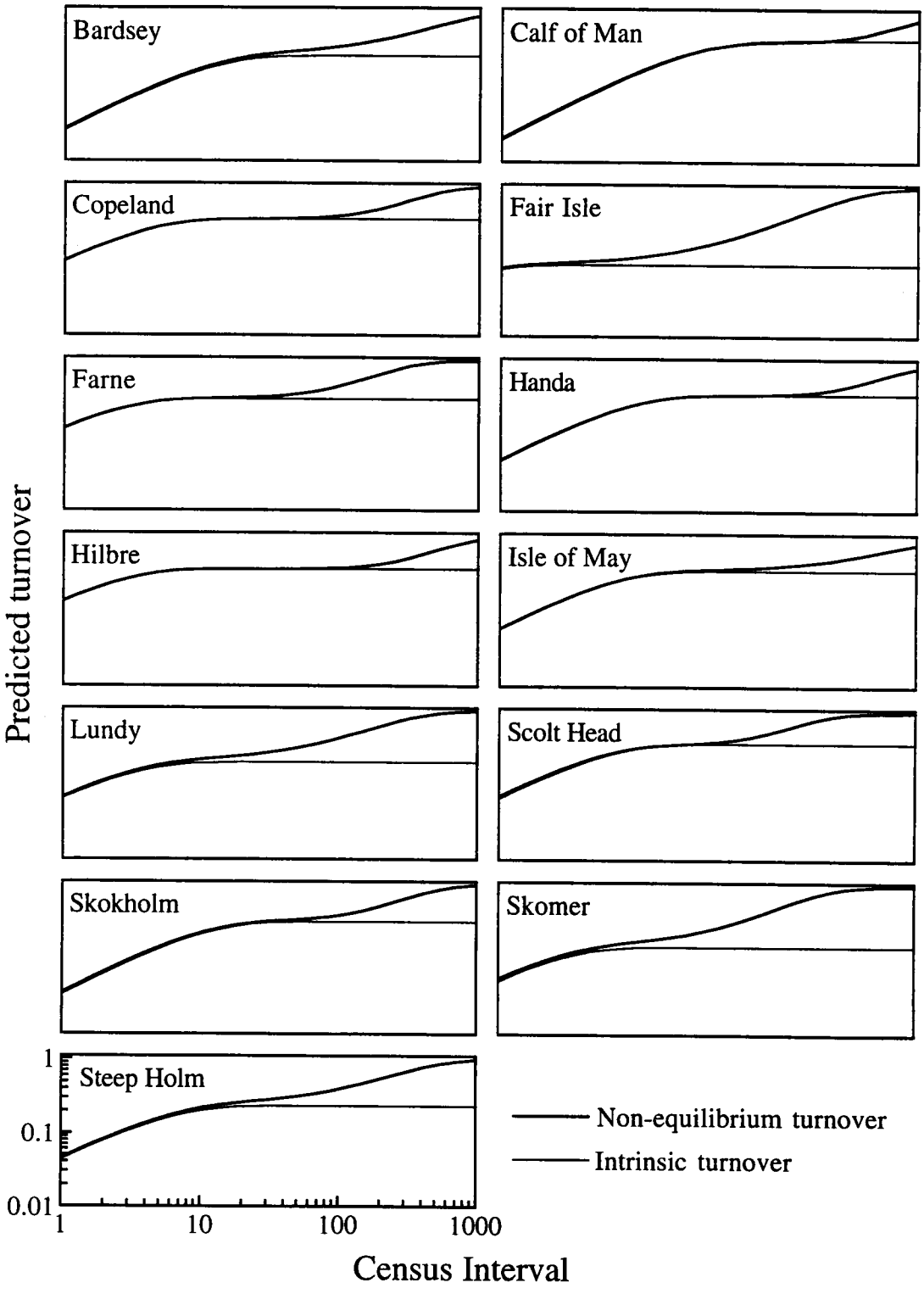

A
B
1
0.1
Predicted turnover
Non-equilibrium turnover
Extrinsic component
Intrinsic component
$n_{0.25(ex/in)}$
Range of census intervals at which intrinsic, island-specific factors are dominant.
Range of census intervals at which extrinsic, source-pool factors are also significant.
1
10
100
1000
Census interval

Figure 10. Predictions of the non-equilibrium model (thick lines) and the intrinsic turnover (thin lines) for all the islands.


Bardsey
Calf of Man
Copeland
Fair Isle
Farne
Handa
Hilbre
Isle of May
Lundy
Scolt Head
Skokholm
Skomer
Steep Holm
Predicted turnover
1
0.1
0.01
1
10
100
1000
Census Interval
Non-equilibrium turnover
Intrinsic turnover

DISCUSSION

In discussing their model, Diamond and May identify three characteristics of turnover that they "neglected" without suggesting their possible effects: 1) correlations between species' presences and absences, 2) serial correlations within species, and 3) temporal variation in extinction and immigration probabilities. These features should undoubtedly be examined for the magnitude of their influence on measurements of turnover, and incorporated into a model if necessary. However, by examining the magnitudes of the devations between their model's predictions and data, the authors also suggest that a "trend in S^* is related to the *main* cause of the misfits to our simplified theory" (our italics). It is just this effect of a trend in species number that our non-equilibrial model addresses.

Within the range of data available, the non-equilibrial component of the model provides a marked improvement over the equilibrium model in those situations where there is a significant trend in species number. On the time scales we consider here, most islands show a trend in species number. Both models underestimate turnover at the very shortest timescales (< 4 years) for reasons to do with the ephemeral nesting habits of some individuals within each species.

The interesting questions are still unanswered. Island biogeographers need to know how turnover varies with island size and isolation. Those charged with managing communities would like an estimate of how quickly their communities will change and by how much. The conclusions of this paper are that the

simplest statistics are of limited use. Apparent turnover increases over time, so that one year turnovers underestimate the turnovers over a decade or a century. The increase is not linear, however, so dividing apparent turnover by the number of years in its calculation still does not produce a statistic one can use for comparison. Moreover, the turnovers calculated over the shortest intervals are inflated by "floaters" and so are a poor guide to what one would expect over an interval of just a few years.

The equilibrium model gives rather more useful insight. By fitting the model to the data, we can estimate the long-term, asymptotic turnover and, furthermore, estimate how many years of observation data we will need before that turnover is realised. (Visual inspection of Figure 3 suggests that somewhere between a decade and a half century is required before apparent turnover is not increasing perceptibly.) The non-equilibrium model suggests that we must incorporate another feature into the models and so separate components of intrinsic and extrinsic turnover if we are to characterize turnover sensibly. To answer the questions of how "turnover varies with island size and isolation" requires more than one simple measure of turnover. These measures are now in hand. We will answer the questions elsewhere.

ACKNOWLEDGMENTS

The authors would like to thank M. E. Gilpin and J. Bell for comments on earlier drafts of the manuscript. Funding for this research was provided by the Joint Nature Conservation Committee of the United Kingdom.

REFERENCES

Abbot, I. and P. R. Grant (1976) Non–equilibrial bird faunas on islands. *American Naturalist* **110**: 507–528.

Arrhenius, O. (1921) Species and area. *Ecology* **9**: 95–99.

British Ornithologists' Union (1992) *Checklist Of Birds Of Britain And Ireland*. 6th. ed. British Ornithologists' Union, Tring.

Clark, C. W. and M. L. Rosenzweig (1994) Extinction and colonization processes: parameter estimates from sporadic surveys. *American Naturalist* **143**: 583–596.

Clements, F. E. (1916) Plant succession: an analysis of the development of vegetation. *Carnegie Institute Publication* **242**. Washington, DC.

Clements, F. E. (1936) Nature and the structure of the climax. *Ecology* **24**: 252–284.

Cowles, H. C. (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* **27**: 95–117, 167–202, 281–308, 361–391.

Diamond, J. M. (1969) Avifaunal equilibria and species turnover rates in the channel islands of California. *Proceedings of the National Academy of Sciences of the USA* **64**: 57–63.

Diamond, J. M. (1971) Comparison of faunal equilibrium turnover rates on a tropical and a temperate island. *Proceedings of the National Academy of Sciences of the USA* **68**: 2742–2745.

Diamond, J. M. (1984a) "Normal" extinctions of isolated populations. *Quaternary Extinctions: a prehistoric revolution* (eds. Martin, P. S. and R. G. Klein), pp. 824–862. University of Arizona Press, Tucson, AZ.

Diamond, J. M. (1984b) Historic extinctions: a rosetta stone for understanding prehistoric extinctions. *Extinctions* (ed M.H. Niteki), pp. 191–246. University of Chicago Press, Chicago, IL.

Diamond, J. M. and M. E. Gilpin (1980) Turnover noise: contribution to variance in species number and prediction from immigration and extinction curves. *American Naturalist* **115**: 884–889.

Diamond, J. M. and R. M. May (1977) Species turnover rates on islands: dependance on census interval. *Science* **197**: 226–270.

Gibbons, D. W., J. B. Reid and R. A. Chapman (1993) *The New Atlas Of Breeding Birds In Britain And Northern Ireland: 1988–1991*. Poyser, Berkhamstead.

Gleason, H. (1926) The individualistic concept of the plant association. *Bulletin of the Torry Botanical Club* **53**: 1–20.

Hunt, G. L. and M. W. Hunt (1974) Trophic levels and turnover rates: the avifauna of Santa Barbara Island, California. *Condor* **76**: 363–369.

Jones, H. L. and J. M. Diamond (1976) Short-time-base studies of turnover in breeding bird populations on the Californian channel islands. *Condor* **78**: 526–529.

Lack, D. L. (1966) *Population Studies of Birds*. Oxford University Press, Oxford.

Lack, D. L. (1969) The number of bird species on islands. *Bird Study* **16**: 193–209.

Lack, D. L. (1976) *Island Biology Illustrated by the Land Birds of Jamaica*. University of California Press, CA.

Lynch, J. F. and N. K. Johnson (1974) Turnover and equilibria in insular avifaunas, with special reference to the California channel Islands. *Condor* **76**: 370–384.

MacArthur, R. H. and E. O. Wilson (1963) An equilibrium theory of insular zoogeography. *Evolution* **17**: 373–387.

MacArthur, R. H. and E. O. Wilson (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

Mayr, E. (1940) The origin and history of the bird fauna of Polynesia. *Proceedings of the Sixth Pacific Scientific Congress* **4**: 197–216.

Pimm, S. L., J. M. Diamond, T. M. Reed, G. J. Russell and J. M. Verner (1993) Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences of the USA* **90**: 10871–10875.

Pimm, S. L., H. L. Jones and J. M. Diamond (1988) On the risk of extinction. *American Naturalist* **132**: 757–785.

Power, D. M. (1972) Numbers of bird species on Californian islands. *Evolution* **26**: 451–463.

Preston, F. W. (1948) The commonness, and rarity, of species. *Ecology* **29**: 254–283.

Preston, F. W. (1962a) The canonical distribution of commonness and rarity I. *Ecology* **43**: 185–215.

Preston, F. W. (1962b) The canonical distribution of commonness and rarity II. *Ecology* **43**: 410–432.

Reed, T. M. (1980) Turnover frequency in island birds. *Journal of Biogeography* **7**: 329–335.

Reed, T. M. (1981a) *A study of populations of landbirds on the islands around Britain.* D. Phil. Thesis. University of Oxford, UK.

Reed, T. M. (1981b) The number of breeding landbird species on British islands. *Journal of Animal Ecology* **50**: 613–624.

Schoener, T. W. and D. A. Spiller (1987) High population persistence in a system with high turnover. *Nature* **330**: 474-477.

Simberloff, D. S. (1969) Experimental zoogeography of islands. A model of insular colonization. *Ecology* **50**: 296–314.

Simberloff, D. S. (1974) Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics* **5**: 161–182.

Simberloff, D. S. and E. O. Wilson (1969) Experimental zoogeography of islands. The colonization of empty islands. *Ecology* **50**: 278–296.

Terborgh, J. and J. Faaborg (1973) Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk* **90**: 759–779.

Williamson, M. H. (1983) The land-bird community of Skokholm: ordination and turnover. *Oikos* **41**: 378–384.

APPENDIX 1

"TERRESTRIAL" BIRD SPECIES FOUND ON THE ISLANDS IN THIS STUDY

For definition of "terrestrial", see text. Common names, scientific names and taxonomic sequence are taken from Gibbons, Reid and Chapman (1993). Scientific names follow the guidelines of the British Ornithologists' Union (1992).

Sparrowhawk	*Accipiter nisus*
Buzzard	*Buteo buteo*
Kestrel	*Falco tinnunculus*
Peregrine	*Falco peregrinus*
Red Grouse	*Lagopus lagopus*
Red-legged Partridge	*Alectoris rufa*
Grey Partridge	*Perdix perdix*
Quail	*Coturnix coturnix*
Pheasant	*Phasianus colchicus*

Rock Dove	*Columba livia*
Stock Dove	*Columba oenas*
Woodpigeon	*Columba palumbas*
Collared Dove	*Streptopelia decaocto*
Cuckoo	*Cuculus canorus*
Little Owl	*Athene noctua*
Short-eared Owl	*Asio flammeus*
Nightjar	*Caprimulgus europaeus*
Skylark	*Alauda arvensis*
Sand Martin	*Riparia riparia*
Swallow	*Hirundo rustica*
House Martin	*Delichon urbica*
Meadow Pipit	*Anthus pratensis*
Rock Pipit	*Anthus petrosus*
Yellow Wagtail	*Motacilla flava*
Grey Wagtail	*Motacilla cinerea*
Pied Wagtail	*Motacilla alba*
Wren	*Troglodytes troglodytes*
Dunnock	*Prunella modularis*
Robin	*Erithacus rubecula*
Black Redstart	*Phoenicurus ochruros*
Whinchat	*Saxicola rubetra*
Stonechat	*Saxicola torquata*
Wheatear	*Oenanthe oenanthe*
Blackbird	*Turdus merula*
Song Thrush	*Turdus philomelos*
Mistle Thrush	*Turdus viscivorus*
Grasshopper Warbler	*Locustella naevia*
Sedge Warbler	*Acrocephalus schoenobaenus*
Whitethroat	*Sylvia communis*
Blackcap	*Sylvia atricapilla*
Chiffchaff	*Phylloscopus collybita*
Willow Warbler	*Phylloscopus trochilus*
Goldcrest	*Regulus regulus*
Spotted Flycatcher	*Muscicapa striata*
Great Tit	*Parus major*
Magpie	*Pica pica*
Chough	*Pyrrhocorax pyrrhocorax*
Jackdaw	*Corvus monedula*
Rook	*Corvus frugilegus*
Carrion and Hooded Crow	*Corvus corone*

Raven	*Corvus corax*
Starling	*Sturnus vulgaris*
House Sparrow	*Passer domesticus*
Tree Sparrow	*Passer montanus*
Chaffinch	*Fringilla coelebs*
Greenfinch	*Carduelis chloris*
Goldfinch	*Carduelis carduelis*
Siskin	*Carduelis spinus*
Linnet	*Carduelis cannabina*
Twite	*Cardeulis flavirostris*
Redpoll	*Carduelis flammea*
Bullfinch	*Pyrrhula pyrrhula*
Yellowhammer	*Emberiza citrinella*
Reed Bunting	*Emberiza schoeniclus*
Corn Bunting	*Miliaria calandra*

APPENDIX 2

DERIVATION OF A NON-EQUILIBRIUM EXPRESSION FOR TURNOVER

When the species number is decreasing with time, i.e., $\beta < 0$ (see Figure 5),

$$X = (1-e_n)S_y - (1-e_n)S_y \frac{S_y \exp^{\beta n}}{S_y}$$

$$= (1-e_n)S_y\left(1-\exp^{\beta n}\right)$$

$$R = e_n S_y - e_n S_y \frac{S_y \exp^{\beta n}}{S_y}$$

$$= e_n S_y\left(1-\exp^{\beta n}\right)$$

so that by substitution into equation 5,

$$T_{n(\mathrm{ne})} = \frac{2e_n S_y + (1-e_n)S_y\left(1-\exp^{\beta n}\right) - e_n S_y\left(1-\exp^{\beta n}\right)}{S_y + S_y \exp^{\beta n}}$$

$$= \frac{2e_n + (1-e_n)\left(1-\exp^{\beta n}\right) - e_n\left(1-\exp^{\beta n}\right)}{1+\exp^{\beta n}}$$

$$= \frac{1+\exp^{\beta n}(2e_n - 1)}{1+\exp^{\beta n}}$$

When the species number is increasing with time, i.e., $\beta > 0$ (see Figure 6),

$$X = \left(S_y \exp^{\beta n} - e_n S_y\right) - \left(S_y \exp^{\beta n} - e_n S_y\right)\frac{S_y}{S_y \exp^{\beta n}}$$

$$= \left(\exp^{\beta n} - e_n\right)S_y\left(1 - \frac{1}{\exp^{\beta n}}\right)$$

$$= \left(\exp^{\beta n} - e_n\right)S_y\left(1 - \exp^{-\beta n}\right)$$

$$R = e_n S_y - e_n S_y \frac{S_y}{S_y \exp^{\beta n}}$$

$$= e_n S_y\left(1 - \frac{1}{\exp^{\beta n}}\right)$$

$$= e_n S_y\left(1 - \exp^{-\beta n}\right)$$

so that (again) by substitution into equation 5,

$$T_{n(\mathrm{ne})} = \frac{2e_n S_y + \left(\exp^{\beta n} - e_n\right)S_y\left(1 - \exp^{-\beta n}\right) - e_n S_y\left(1 - \exp^{-\beta n}\right)}{S_y + S_y \exp^{\beta n}}$$

$$= \frac{2e_n + \left(\exp^{\beta n} - e_n\right)\left(1 - \exp^{-\beta n}\right) - e_n\left(1 - \exp^{-\beta n}\right)}{1 + \exp^{\beta n}}$$

$$= \frac{\exp^{\beta n} + 2e_n \exp^{-\beta n} - 1}{1 + \exp^{\beta n}}$$

We can test these formulations by estimating their values for the equilibrium condition $\beta = 0$, when turnover should be equivalent to e_n, and in the limit as n approaches infinity, when turnover should be unity.

For decreasing species number, if $\beta = 0$ then $\exp^{\beta n} = 1$, so that

$$T_{n(\mathrm{ne})} = \frac{1+1(2e_n-1)}{1+1} = \frac{2e_n}{2} = e_n$$

and if $\beta < 0$ and $n \to \infty$, then $\exp^{\beta n} \to 0$, so that

$$T_{n(\mathrm{ne})} \to \frac{1+0(2e_n-1)}{1+0} = \frac{1}{1} = 1$$

For increasing species number, if $\beta = 0$ then $\exp^{\beta n} = \exp^{-\beta n} = 1$, so that

$$T_{n(\mathrm{ne})} = \frac{1+2e_n(1)-1}{1+1} = \frac{2e_n}{2} = e_n$$

and if $\beta > 0$ and $n \to \infty$, then $\exp^{\beta n} \to \infty$ and $\exp^{-\beta n} \to 0$, so that

$$T_{n(\mathrm{ne})} \to \frac{\exp^{\beta n}+0-1}{1+\exp^{\beta n}} \to 1$$

Furthermore, we can show that the expressions for turnover differ only in the signs of certain terms: if we expand the expression for decreasing species number,

$$T_{n(\mathrm{ne})} = \frac{1+\exp^{\beta n}(2e_n - 1)}{1+\exp^{\beta n}} = \frac{1+2e_n \exp^{\beta n} - \exp^{\beta n}}{1+\exp^{\beta n}} = \frac{-\left(\exp^{\beta n} - 1\right) + 2e_n \exp^{\beta n}}{1+\exp^{\beta n}}$$

we see that it is similar in form to the expression for increasing species number,

$$T_{n(\mathrm{ne})} = \frac{\exp^{\beta n} + 2e_n \exp^{-\beta n} - 1}{1+\exp^{\beta n}} = \frac{\left(\exp^{\beta n} - 1\right) + 2e_n \exp^{-\beta n}}{1+\exp^{\beta n}}$$

Since we know the sign of β that applies to each of these we could write a combined expression, but feel that little would be gained by the resulting, more complicated form.

PART THREE

THE TURNOVER OF BIRD COMMUNITIES ON SMALL ISLANDS: CONFIRMING MACARTHUR AND WILSON'S PREDICTIONS, BUT NOT THEIR MODEL

INTRODUCTION

MacArthur and Wilson (1963, 1967) proposed a model to explain the number of species on islands. Their novel suggestion was that island communities can be understood as a dynamic equilibrium between extinction and colonization. The model predicts that the number of species will increase with the area of an island and decrease with its distance from a source of colonizing species. At the time of their suggestion, empirical evidence for these relationships was well-established (Arrhenius 1921, Mayr 1940, Williams 1943, Ripley 1944, Darlington 1957) and there were a number of non-dynamic models to explain them. For example, Lack (1976—see also Lack 1969) proposed that the number of species on oceanic islands is determined by the islands' "ecological poverty", a term which Lack himself coined and described as "deliberately vague". (It seems to be a measure of the number of habitats, or perhaps ecologial niches, available for colonizing species to exploit.) The unique feature of the MacArthur and Wilson model is that it predicts turnover, a change in composition of a community over time, and further predicts that this turnover will decrease with both area and distance.

MacArthur and Wilson's predictions about turnover have never been properly tested. One reason is that turnover data are harder to come by than estimates of species richness, because repeated censuses are needed. More importantly though, many authors have misunderstood the relationship between observed turnover and census interval. The relationship is crucial, because most empirical data do not come from identical intervals, and so must be standardized before

comparisons can be made. Prior to 1977, a number of authors had already noticed that the relationship is non-linear and asymptotic: turnover increases with census interval, but not indefinitely (or equivalently, turnover rate plotted against census interval tends to a slope of –1: see Jones and Diamond 1976). Diamond and May (1977) demonstrated the way in which this non-linear relationship arises by considering how probabilities of colonization and extinction of species over one year can be expanded to consider longer intervals. Unfortunately, most studies purporting to test MacArthur and Wilson's predictions were either published before this (e.g., Diamond 1969), or were published subsequently but ignore the implications of the non-linear relationship (e.g., Schoener 1983). Implicitly or explicitly, they assume a linear relationship. We shall demonstrate presently that that assumption leads to systematic errors in estimates of turnover.

This paper represents the first time that an appropriate non-linear model, based on Diamond and May (1977) and extended by Russell *et al.* (1995), has been used to standardize and compare turnovers across a large subset of islands. We investigate avian biogeography of 42 British and Irish islands. As well as various estimates of turnover, our variables include mean species richness, area, distance from the mainland, number of habitats and maximum elevation.

THE DATA

RECORDS OF BREEDING BIRD SPECIES

Our data consist of records of breeding terrestrial species on many of the small islands of the United Kingdom and the Republic of Ireland. Some of the data are in the form of abundances (number of pairs), and others are in the form of records of presence or absence. The analyses presented here use presence/absence data, in the form of community matrices where each row represents a species, and each column a census year. Abundance data can, or course, be converted to presence/absence data.

There are four reasons why the datasets used in this paper are of unusually high quality:

1) Some of these islands have permanent or semi-permanent bird observatories, and the others are censused frequently and systematically.

2) Most of the islands are small enough that the entire area can be searched.

3) Breeding pairs are relatively conspicuous.

4) Bird-watchers typically put more effort into finding rare species. While this tendency can introduce systematic bias into estimates of abundance, it is beneficial when estimating presence or absence.

The nature of these data was reviewed by Russell *et al.* (1995), although some new data have been added since that analysis. At least some censuses have been performed on 71 islands. We select a subset of 41 islands that have been censused at least four times, including the thirteen analysed by Russell *et al.* (1995). We list the islands in Table 1, along with summary island biogeographic data that we will discuss presently.

The data are not complete. Sometimes there are species-year combinations where no census was made, and sometimes the census-maker was unsure whether a breeding pair of the species was present. For censuses where the original data were only in the form of presence/absence records, we can do nothing about such missing records. For censuses where we have abundance counts, however, there is the possibility of interpolation. For example, the record of the number of breeding pairs of Sedge Warbler (*Acrocephalus schoenobaenus*) on Skomer between 1981 and 1990 is 16, 31, 11, 15, 18, 'no census', 'no census', 29, 30, 36. These numbers suggest that the species was also breeding in 1986 and 1987.

We follow Pimm *et al.* 1993 by using formal rules for interpolating missing data. For a gap of x years, we add the number of breeding pairs in the year immediately before the gap to the number of breeding pairs immediately after the gap. We infer breeding if this number is equal or greater than $(x + 1) \times 2$. Thus for a gap of one year the criterion is $(1 + 1) \times 2 = 4$, and so we assume continuous breeding if the sequence is 2_2, 1_3 or 3_1. For a gap of two years the criterion is $(2 + 1) \times 2 = 6$, and we assume continuous breeding if the sequence is

3__3, 2__4, 4__2, 1__5 or 5__1, and so on. We never assume breeding if the estimate for one of the adjacent years is zero.

If the uncensused years are at the beginning or end of a dataset, so that there is a single adjacent year for which we have data, we use a similar but more conservative rule. In this case, we look at the number of breeding pairs in only that adjacent year, and apply the same criterion as before. Thus, for a single missing year at the end of a species' record, we assume continuous breeding if the number of pairs in the previous year is at least $(1 + 1) \times 2 = 4$. For two missing years, we infer breeding if the number of pairs in the previous year is at least $(2 + 1) \times 2 = 6$.

When interpolation is not possible, either because the data were originally in the form of presence/absence records or because the above criteria for interpolation are not met, the we use a notation to represent 'missing datum'. Missing records in a given year may lead to its exclusion from one or more analyses (see below).

THE BIOGEOGRAPHY OF THE ISLANDS

Table 1 lists a number of biogeographic variables for the islands in this study. Latitude, longitude, area, distance from the mainland, number of habitats, maximum elevation and pool size for 35 of these 41 islands were presented in Reed 1981. We added these measurements for the remaining islands, plus one alternative measure of distance.

Latitude (°N)— estimated from Ordnance Survey maps and gazetteers.

Table 1. A list of the islands used in this study, with associated biogeographical variables. °W is the longitude of each island in degrees and frations of a degree West of Greenwich—negative numbers indicate degrees East of Greenwich. °N is the latitude of each island in degrees and fractions of a degree North of the equator. *A* is the area of each island in hectares. *H* is the number of habitats on each island (see text for details). D_1 is the shortest distance in kilometers from the island to the nearest mainland (Great Britain or Eire). D_2 is the shortest distance in kilometers from the island to the nearest landmass that is at least five times its area *and* closer to the mainland. E is the maximum elevation on the island. P_1, P_2 and P_3 describe the estimated number of species in the pool of available colonizers for ech island. The sources of the data are P_1—Diamond (unpublished), P_2—Reed (1981b) and P_3—this paper (see text for details).

Island	Abbr.	°W	°N	A	H	D_1	D_2	E	P_1	P_2	P_3
Bardsey	BD	4.8	52.77	179.8	19	3	3	167	132	45	31
Calf of Man	CM	4.08	54.05	249.5	18	53	0.5	127.9	132	36	36
Canna	CN	6.6	57.05	1046.6	18	39	14.5	210.2	130	46	29
Coll	CL	6.72	56.17	7418.1	22	14	10.5	103.3	130	51	29
Copeland	CP	5.53	54.68	32	11	1.5	1.5	33.2	132	25	16
Coquet Island	CQ	1.57	55.33	6.5	7	—	—	6.1	—	—	4
Eigg	EG	6.08	56.88	3160.2	26	11.5	11.5	392.6	—	67	51
Faeroe Isles	FS	7	62	140000	27	319	319	—	153	—	14
Fair Isle	FI	1.63	59.53	765	19	125.5	85.5	216.9	147	32	14
Farne	FR	1.63	55.62	29	7	2.4	2.4	17	123	—	6
Flannan Isles	FN	7.61	58.28	—	—	114	29.5	80	—	—	35
Foula	FL	2.08	60.13	1336.5	17	173.5	22	418.2	147	31	17
Grassholm	GH	5.72	51.4	8.9	6	15.5	11.5	44.5	—	3	—
Handa	HN	5.22	58.38	310.2	18	0.5	0.5	133.9	130	26	19
Hascosay	HS	0.98	60.6	1728.4	8	247	0.8	26.8	147	20	—
Hilbre	HL	3.22	53.38	6.5	12	1	1	9.1	132	10	9
Inchmickery	IN	3.22	56	1.4	7	3.4	—	14.6	—	8	—
Isle of May	IM	2.53	56.2	48.6	11	7.5	7.5	36.5	123	21	11
Isles of Scilly	IS	6.3	49.92	1640	26	40.5	40.5	49	164	—	28
Lindisfarne	LF	2.78	55.68	541.9	17	1.25	1.25	21	123	35	24
Lundy	LN	4.7	51.2	452.1	21	18	18	141.9	164	49	24
Mingulay	MG	7.62	56.8	610.8	14	86	50	271.4	—	18	13
Muck	MK	6.17	56.83	642.3	21	6	6	137.4	—	41	28
North Rona	NR	5.83	59.33	119.9	10	72.5	71.5	108.2	—	8	9
Orkney Isles	OI	3.11	59.02	—	—	11	11	479	—	—	58
Out Skerries	OS	0.73	60.4	265.3	11	235	14	51.8	—	13	9

Table 1 (continued).

Island	Abbr.	°W	°N	A	H	D_1	D_2	E	P_1	P_2	P_3
Puffin	PF	4.03	53.32	28.3	6	7	0.5	49.7		14	
Raasay	RS	6.03	57.4	6360.1	22	6.5	6.5	443.6		79	50
Rhum	RM	6.43	57	10692.2	25	22	22	810.1	130	74	47
St. Agnes	SA	6.33	49.9	109.4	16	40.5	46	24.1	164	29	17
St. Kilda	SK	8.55	57.82	853.3	14	163	64	121	130	23	11
Sanday	SN	6.57	55.3	426.5	16	—	—	58.8	—	—	9
Scolt Head	SC	-0.32	52.97	334.1	9	0.5	0.5	12.2	164	24	9
Shetland Islands	ST	1.25	60.39	—	—	168	168	450	—	—	28
Shiant Isles	SN	6.34	57.89	231	11	31.5	19	125	130	—	—
Skokholm	SK	5.28	51.70	97.2	15	3.5	3	51.8	164	29	16
Skomer	SM	5.26	51.65	292.4	18	1	1	78.9	164	42	28
Steep Holm	SH	3.1	51.35	19	8	5	5	78	164	25	12
Tiree	TR	6.85	56.52	7652.9	24	36	21.5	140.1	—	53	35
Tory	TY	7.2	55.27	331.4	12	10.5	10.5	82.3	105	19	11
Trischen	TS	—	—	100	—	11	11	—	—	—	7

Longitude (°W)—estimated from Ordnance Survey maps and gazetteers.

Area (*A*)—total area above high tide line, estimated from 1:2500 Ordnance Survey maps and gazetteers.

Number of habitats (*H*)—based upon Fuller's (1974) classification of habitat types, amended for island environments. The numbers of habitats on the islands were estimated from published and unpublished sources that cover the period from which bird data are available. The criterion for inclusion was that a habitat type be at least 0.2 ha in area.

Distance to mainland (D_1)—measured as the shortest distance in kilometers from the island shore to the nearest mainland shore (Britain or the Rebublic of Ireland).

Distance to nearest larger island (D_2)—measured as the shortest distance in kilometers from the island shore to the nearest landmass in the direction of the mainland that is at least five times the size of the island in question. For 24 out of the 41 islands, this is the mainland itself.

Elevation (*E*)—the maximum elevation on an island in meters, estimated from Ordnance Survey maps and gazetteers.

Pool size (P_{1-3})—Various estimates of the number of species available for colonization of a given island. P_1 is taken from Diamond (unpublished), P_2 is taken from Reed 1981b, and P_3 we generated ourselves as will explain presently.

RESTRICTING THE DATASET

When investigating how the number of species on these islands varies with variables such as area and distance, we restrict our data in certain ways.

Russell *et al.* (1995) pointed out that "even a small island may have extensive cliffs surrounded by food-rich water supporting many species of pelagic feeders. Second, the amount of freshwater habitat on an island is mostly a function of its topology, the amount of rainfall, and the number of freshwater springs present. Both these factors change the effective area of the island for certain species, in a way which is largely independent of simple area measurements." Since our purpose is to test a theory which makes predictions based on area, we only include 'terrestrial' bird species. That is, we eliminate both pelagic and freshwater feeders such as gulls, divers, waders and ducks. (Note: we include Woodcock even though it is taxonomically a wader, because it forages in damp forest rather than standing water.) Birds remaining in the dataset for these islands are listed in Appendix 1.

As mentioned above, on some years on some islands there may be species for which the census data are ambiguous or missing, even after interpolation. Our estimates of the species number in those years are uncertain. To minimize the effect of this uncertainty, we do not include these years when calculating mean species number over time, the change in species number over time, or turnover.

The model presented by MacArthur and Wilson assumes that the community on an island is in (dynamic) equilibrium, so that the number of species should be

approximately constant (S_{eq}). Some of these islands, however, show a significant trend in species number over time, as measured by β where β is the slope of a linear regression of ln S against year (an exponential model is to be preferred to a linear one, since extrapolation of a linear model allows the possibility of a negative number of species). For all analyses involving mean species number, we exclude eleven islands where the absolute value of β is greater than 0.0095, that is, where there is more than a 10% change in species number per decade.

SPECIES, AREA AND DISTANCE

MacArthur and Wilson proposed that the number of species is greater on large islands (because of a reduced extinction rate), and on islands that are close to the mainland (because of an increased colonization rate). The form of the species-area relationship is usually given as $S = cA^z$, where S is the mean number of species on an island, A is the area of that island, and c and z are constants (Preston etc.). Other forms for the relationship are possible (Connell?), but the 'power' form given here is appropriate when, as for our data, the areas under consideration range over a number of degrees of magnitude. The parameters c and z can be estimated as the intercept and slope respectively of a plot of log$S$ against log$A$.

The islands in this study also encompass several orders of magnitude of distance from the mainland, so we favour a power form for the species-distance relationship. If area and distance from the mainland are independent, we can express the proposed dependence of S on A and D as follows:

$$S = c_1 A^{z_1} c_2 D^{z_2} = c_3 A^{z_1} D^{z_2} \quad (1)$$

For our estimate of the equilibrium species number, we used the mean species number ($\overline{S}$) for those islands showing less than 10% change in species number per decade. We tested the model by means of a multivariate linear regression using log-transformed variables.

$$\log \overline{S} = \log \hat{c}_3 + \hat{z}_1 \log A + \hat{z}_2 \log D + \varepsilon \quad (2)$$

where ε is the error term. The fit of the model was significant ($p < 0.0001$) with both A and D contributing significantly. MacArthur and Wilson also predict the sign of each relationship, so to test their theory we examine the estimated parameters $\hat{z}_1$ and $\hat{z}_2$ and test their significance with a one-tailed test. The estimate for the coefficient of the area term, $\hat{z}_1$, is 0.29 ($p << 0.001$), which is of the correct sign and consistent with published values of this parameter for other island faunas (Rosenzweig 1995). The estimate for the coefficient of the distance term, $\hat{z}_2$, is –0.18 ($p = 0.037$), which is also of the correct sign.

MacArthur and Wilson's model is able to predict the number of breeding bird species on the islands in this study. The lower significance of the distance relationship may be attributed to the high mobility of birds relative to the distance of most of these islands. As we pointed out in the introduction, however, there are other theories that predict species-area and species-distance relationships. One of these theories supposes that larger and less distant islands have a greater habitat diversity, and that this alone explains the number of bird species (Lack 1969). Before proceeding to test predictions about turnover which

are unique to MacArthur and Wilson's theory, we shall examine more closely some alternative explanations for species-area effects.

CORRELATIONS AMONG BIOGEOGRAPHIC VARIABLES

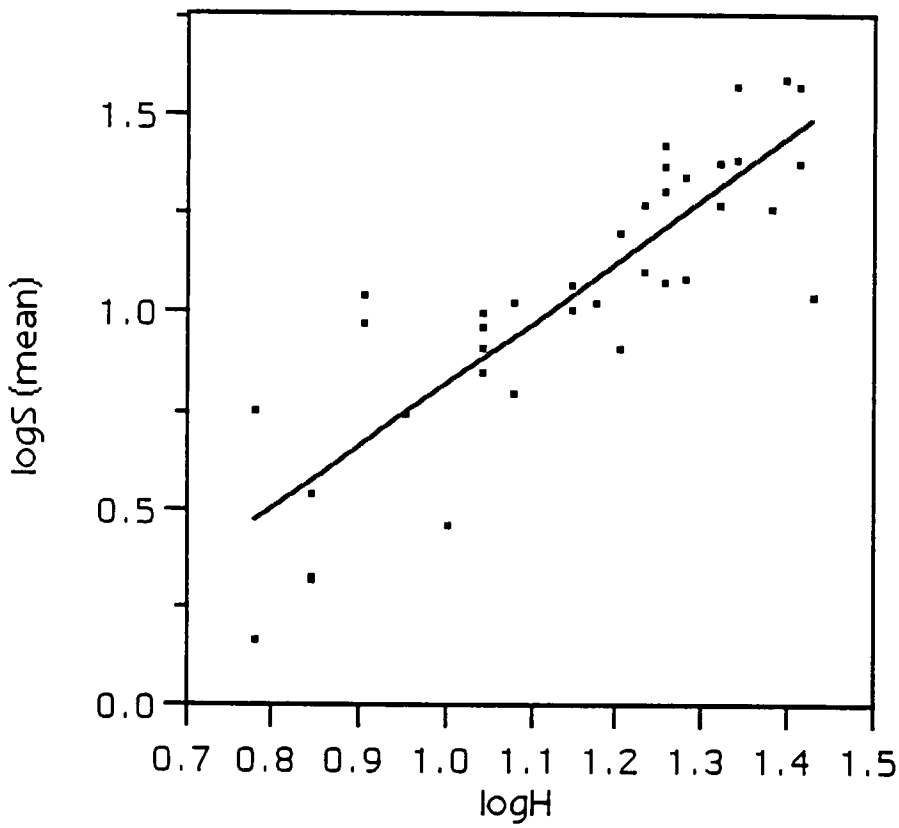
Reed (1981b), in his analysis of a related set of British and Irish islands, noted that some island biogeographic variables may be correlated. There is no relationship between area and distance for either Reed's or our islands. But for the islands that Reed analyzed, maximum elevation increases as island area increases ($r = 0.804$). This correlation is confirmed by our dataset ($r = 0.687$, $p < 0.0001$). Since it is statistically incorrect to include highly-correlated variables in a regression model, we exclude elevation from all further analyses, noting that this does not mean it plays no role.

Latitude and longitude are both independent of area and distance, and so can reasonably be included in a model. However, we find no relationships between the mean number of species on an island and either latitude or longitude, even when we include these variables with area and distance in a multivariate analysis. The very small range of longitudes involved make the lack of a discernible effect unsurprizing. The ~12° spread of latitudes from St. Agnes to the Faroe Isles, however, is enough to suggest a possible decrease in diversity in more northern islands (Rapoport's Rule). That we do not observe such a decrease may again be a reflection of a limited range of latitudes. In addition, most of these islands experience a relatively mild, maritime climate that reduces the climatic effects of latitude.

NUMBER OF HABITATS: DEPENDENT OR INDEPENDENT VARIABLE?

A number of authors have speculated that faunal species-area relationships in fact reflect the greater underlying habitat diversity of larger islands (e.g., Lack 1975), and that we might more profitably explore species-habitat relationships. Indeed, a plot of $\log \overline{S}$ against the logarithm of the number of habitats ($\log H$) on each island reveals a close, relationship (Figure 1: $p < 0.0001$). This does not, however, prove a causal relationship. As far as birds are concerned, 'number of habitats' is a crude measure of the number of plant species. Plant species independently exhibit patterns of island biogeography—indeed, they are the subject of one of the earliest investigations of the species-area relationship (see Rosenzweig 1995). We fit a model similar to that in equation 1 above, except with number of habitats rather than mean number of species as the dependent variable. This overall model is significant ($p < 0.0001$), and one-tailed tests for the variables in the model show that area contributes strongly ($p < 0.0001$) and distance contributes moderately ($p < 0.078$). We do not expect much of a distance relationship for plants in these islands, since the islands are not very isolated and plant propagules—seeds—are extremely mobile whether borne by the wind or by birds. Nevertheless, the island biogeography of habitats clearly mirrors that of breeding birds. So the relationship between number of bird species and number of habitats may be nothing more than a correlation brought about by similar dependencies on area and isolation, or it may be a mixture of correlation and the causal relationship proposed by Lack. We cannot separate out the effects with the available data.

Figure 1. A plot of predicted four-year turnover against measured four-year turnover for thirteen islands where such measurements are possible.


logS (mean)
1.5
1.0
0.5
0.0
0.7 0.8 0.9 1.0 1.1 1.2 1.3 1.4 1.5
logH

Whatever the relationships between number of habitats, area and isolation, no model that contains area and isolation as predictor variables should also contain number of habitats. To further demonstrate this point, we fit a model that predicts number of species using number of habitats, area and isolation as if they were three independent variables (all log-transformed). In this model, only habitat is a significant contributor. Reed (1981b) included both area and number of habitats in his analysis of the biogeography of these islands. Fitting a model that used number of habitats, area, isolation, elevation and latitude as independent predictor variables, he concluded that number of habitats, area and isolation contributed significantly to the overall model. Reed did not publish the significance level for each variable, but number of habitats explained approximately 75% of the variability in species number—area and distance contributed only about 6% between them. Since our purpose is to test a theory that specifically invokes area and isolation, we choose to ignore number of habitats in our further analyses (remaining mindful of its importance).

ESTIMATING TURNOVER

Following Russell *et al.* 1995, we calculate turnover of breeding species on these islands using the conventional formula

$$T_n = \frac{E_n + I_n}{S_y + S_{y+n}} \tag{3}$$

where E_n is the number of observed extinctions over a period n, I_n is the number of observed colonizations, S_y is the number of breeding species in census year y and S_{y+n} is the number of breeding species in census year $y + n$. If there are x censuses for a given island, there are ${}^{x}C_2 = x!/(x-2)!\,2!$ possible pairwise combination of census years. After interpolation, we eliminate census years where records are still ambiguous or missing, and calculate the turnover for every remaining pairwise combination.

Our aim is compare turnover across islands. Since turnover is dependent upon the interval over which it is measured, we must compare the same intervals. There are two ways to do this. After calculating turnover over all possible intervals provided by the data for each island, we might only use those intervals that are common to a suitably large sample of the islands. This was the approach of Diamond (1971) and Lynch and Johnson (1974). The predictions made by MacArthur and Wilson, however, apply to short-term turnovers, whereas the Diamond and the Lynch and Johnson studies examine intervals of 55 and 51 years respectively. An obvious candidate interval is one year. Unfortunately there are few datasets where sufficient censuses were carried out in consecutive years.

Alternatively, we can standardize the measurements to an appropriate interval. Many comparative studies of turnover (e.g., Schoener 1983) have attempted to do this by using the following procedure:

$$\text{Unit turnover} = \text{Observed turnover} \times \frac{\text{Unit interval}}{\text{Observed interval}} \qquad (4)$$

For example, if we wanted to estimate yearly turnover we would multiply weekly turnover by 52, or divide the turnover over a decade by ten. This approach assumes a linear relationship between turnover and census interval. But as Diamond and May (1977) showed, turnover increases asymptotically with census interval. (They actually considered turnover *rate*, which tends to a slope of –1 at long intervals.) Hence if the observed interval is less than the unit interval, a linear approach overestimates unit turnover; if the observed interval is greater, it underestimates. To correctly standardize turnover measurements, that is, to obtain measures of 'unit turnover', we must employ a model of the nonlinear relationship between turnover and census interval.

Russell *et al.* (1995) presented two models of turnover in terms of the probabilities of colonization and extinction for particular species. The first model assumes that species number is at equilibrium, whereupon the number of species is approximately constant ($S_y = S_{y+n} = S_{eq}$), the number of colonizations will equal the number of extinctions ($I_n = E_n$), and we may estimate E_n from $e_n S_{eq}$ where e_n is the per-species probability of extinction over the interval n. From this it follows that

$$T_{n,eq} = \frac{E_n + I_n}{S_y + S_{y+n}} = \frac{2E_n}{2S_{eq}} = \frac{2e_n S_{eq}}{2S_{eq}} = e_n \qquad (5)$$

By means of a Markov expansion, we can express e_n (and hence $T_{n,eq}$) in terms of the probabilities of colonization and extinction over one year (i_1 and e_1 respectively):

$$T_{n,eq} = e_n = \frac{e_1\left[1-(1-e_1-i_1)^n\right]}{e_1+i_1}. \qquad (6)$$

Russell *et al.* fit this model to the turnover data for thirteen islands, all of which are included in our dataset. They noticed that the model tends to underestimate turnover at both the longest and shortest intervals, and to overestimate at intermediate values. One the reasons for this is that some islands show sufficient change in species number over time to call into question the assumption of an equilibrium species number. If species numbers are not approximately constant over times of many years or decades, turnovers will be inflated (irrespective of whether the trend is up or down). This inflation becomes progressively more severe over longer census intervals.

The influence of a changing species number requires a modification to the model. Russell *et al.* (1995) presented a 'non-equilibrium' model which incorporates the estimated parameter β. We assume that $S_y = \exp^{\beta y}$, and estimate β as the slope of a plot of ln$S$ against time. Depending upon whether the number of species on the island is increasing or decreasing over the period for which censuses are available:

$$T_{n(\mathrm{ne})} = \frac{-\left(\exp^{\beta n} - 1\right) + 2e_n \exp^{\beta n}}{1 + \exp^{\beta n}} \qquad \text{(Decreasing species number)} \qquad (7)$$

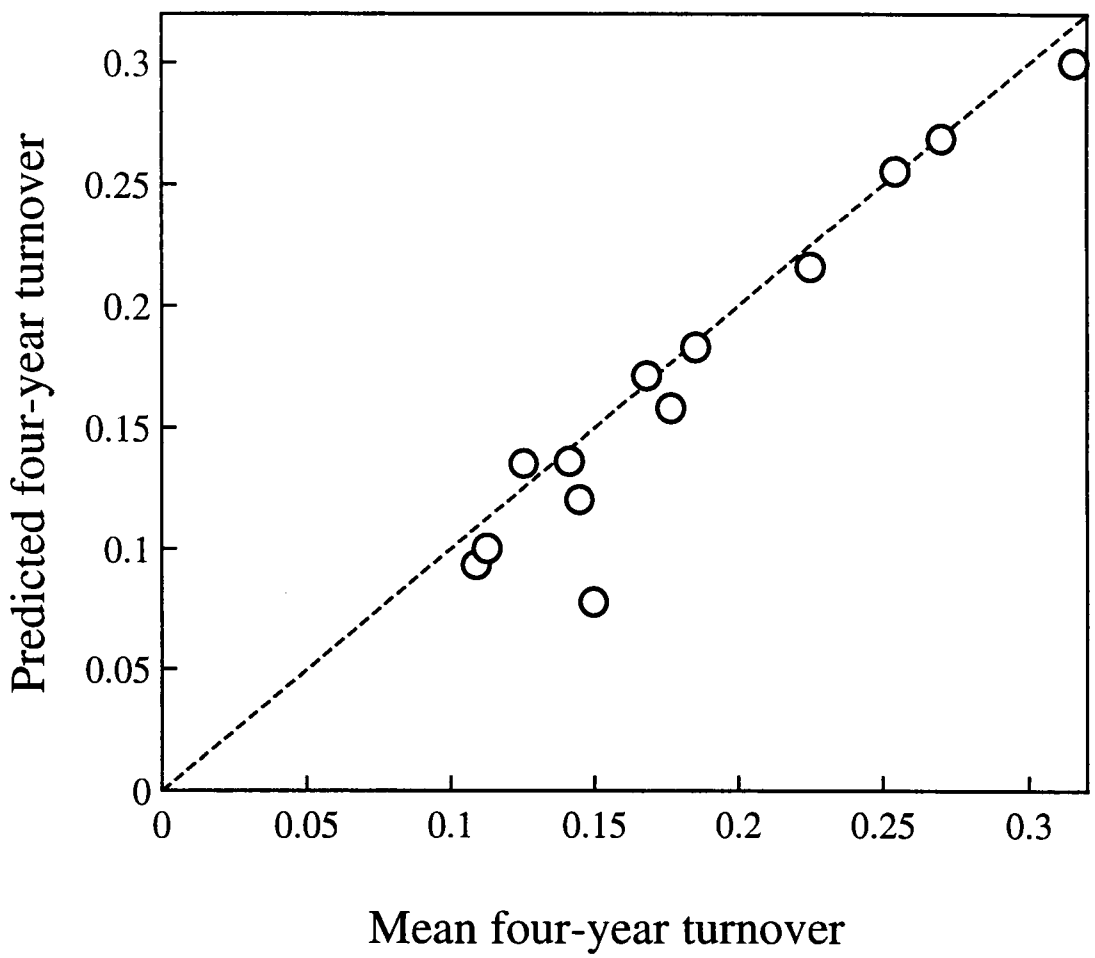
or

$$T_{n(\mathrm{ne})} = \frac{\left(\exp^{\beta n} - 1\right) + 2e_n \exp^{-\beta n}}{1 + \exp^{\beta n}} \qquad \text{(Increasing species number).} \qquad (8)$$

where e_n is still given by equation 4. This model makes fits the observed data better than the equilibrium model, particularly at long intervals, but still understimates one-year turnovers.

The tendency of both the equilibrium and the non-equilibrium model to underestimate one-year turnovers can be traced to certain species that are occasionally represented by breeding pairs that only last one or two years. Pimm *et al.* (1993) determined that these pairs (which they called "floaters") were persisting for a period shorter than expected (based on observations of longer-lasting pairs of the same species on the same islands). Floaters inflate the short-term turnover in a way that the above model does not take into account (since it assumes that all pairs have the same colonization and extinction probabilities). The influence of floaters means that we should examine turnover over a slightly longer interval—just long enough to remove their influence, but short enough to still be representative of the sort of turnover about which MacArthur and Wilson made predictions. Our previous analysis (Russell *et al.* 1995) suggested that four-year turnover is appropriate, and again, these data confirm it. Figure 2 shows a

Figure 2. A plot of the logarithm of the mean number of species on each island [logS (mean)] against the logarithm of the number of habitats (logH). The line has a slope of 1.55 ($p < 0.0001$).


Predicted four-year turnover
0.3
0.25
0.2
0.15
0.1
0.05
0
0
0.05
0.1
0.15
0.2
0.25
0.3
Mean four-year turnover

plot of predicted four-year turnovers against calculated values for those 13 islands where such direct calculations are possible.

In our investigation of the biogeography of turnover that shall present next, we use the estimates of four-year turnover provided by fitting the non-equillibrium model each of the 41 islands in our study.

TURNOVER, AREA AND DISTANCE

SHORT-TERM TURNOVER

MacArthur and Wilson's model makes two specific predictions about short-term turnover. Firstly, the turnover of a species assemblage on an island should be lower on larger islands, because the rate of extinction will be lower. Secondly, turnover should also be lower on more distant islands, because the rate of colonization will be lower. A small, near island may have the same number of species as a large far island, but will have a much higher turnover rate.

We propose a model of the way in which four-year turnover depends upon area and distance that has the same form as the species-area-distance model above (equation 3).

$$T_{4,\mathrm{ne}} = c_4 A^{z_3} D^{z_4} \qquad (9)$$

We use this 'power' form for the same reasons as in the species-area-distance model—so that when we estimate the parameters by fitting a multivariate linear

model, we normalize area and distance measurements by log-transformation. Furthermore the distribution of our estimates of $T_{4,ne}$ is right-skewed, so log-transformation is appropriate here also. Thus we fit the model

$$\log T_{4,ne} = \log \hat{c}_4 + \hat{z}_3 \log A + \hat{z}_4 \log D + \varepsilon \qquad (10)$$

This model is significant overall ($p < 0.0001$) with both area and distance contributing significantly and with the predicted sign. The estimated area coefficient, $\hat{z}_3$, is –0.143 ($p = 0.0022$, one-tailed test), and the estimated distance coefficient, $\hat{z}_4$, is –0.148 ($p = 0.0134$, one-tailed test). So the model appears to confirm the predictions of MacArthur and Wilson that short-term turnover will decrease as both area and distance increases.

SHORT-TERM COLONIZATION AND EXTINCTION PROBABILITIES

We can test MacArthur and Wilson's model further, because it is based on predictions about the way in which colonization and extinction rate vary with island area and isolation. They suggested that the extinction rate is lower on larger islands, and that the colonization rate is higher on nearer islands. The turnover models used in these analyses generate estimates of these parameters in the form of one-year probabilities—i_1 and e_1—so we can also test the basis for the predictions. We still have the problem of floaters, so it would be sensible to assess how i_4 and e_4 (rather than i_1 and e_1) vary with area and distance. When $n = 4$, e_4 is obtained from e_1 by means of equation 6 and i_4 from i_1 by means of the equivalent expression

$$i_n = \frac{i_1\left[1-(1-e_1-i_1)^n\right]}{e_1+i_1}. \qquad (11)$$

We fit two models similar to equation 10 above, except that in place of T_4 we used log-tranformations of our extimates of i_4 and e_4 respectively. We find that extinction probability decreases as both area and distance increase, and that colonization probability shows no relationship with either area or distance. Thus the result for turnover can be explained by the variation in extinction probability alone.

POOL SIZE

It should be immediately apparent that our estimates of i_1 and e_1 allow us to estimate the effective pool size for the islands in this study. At equilibrium, $S_y = S_{eq}$, $I_n = E_n$, $I_n = i_n (P - S)$ and $E_n = e_n S$. Assuming that $n = 1$, it follows that

$$P = S\left(1+\frac{e_1}{i_1}\right) \qquad (12)$$

Table xx lists our estimates of pool size, along with those from three (two) other studies.

LONG-TERM TURNOVER

If a turnover model is asymptotic, long-term turnovers can be represented by the value of this asymptote (T_∞). For the equilibrium model of equation 5, when $n = \infty$, $(1 - e_1 - i_1)^n = 0$ and so $T_{\infty,eq} = e_1/(e_1 + i_1)$. We know, however, that the

equilibrium model does a poor job of predicting long-term turnovers, and the non-equilibrium model is to be preferred.

The non-equilibrium model has the following feature: if there is *any* change in species number over time (i.e., if $\beta \neq 0$), the asymptotic value of the model is unity ($T_{\infty,ne} = 1$). But we can divide non-equilibrium turnover into two components—an intrinsic component, $T_{n,ne\ (int)}$, which is solely the product of year-to-year colonization and extinction events, and an extrinsic component, $T_{n,ne\ (ext)}$, which is the additional turnover caused by a changing number of species (so that $T_{n,ne} = T_{n,ne\ (int)} + T_{n,ne\ (ext)}$). The intrinsic component can be thought of as the equilibrium model which lies at the heart of the non-equilibrium model. We can extract the intrinsic component by applying equation 5 (the equilibrium model) to the estimates of i_1 and e_1 obtained by fitting the non-equilibrium model.

It follows that intrinsic long-term turnover for the non-equilibrium model is given by $e_1/(e_1 + i_1)$, and extrinsic long term turnover by $1 - [e_1/(e_1 + i_1)]$. Russell *et al.* (1995) also proposed another statistic, $n_{0.90\ (int)}$, the interval required for intrinsic turnover to reach 90% of its long-term value. This statistic is easily calculated—it is the value of n that satisfies the equation

$$\frac{e_1\left[1-(1-e_1-i_1)^n\right]}{e_1+i_1} = 0.9\frac{e_1}{e_1+i_1}, \qquad (12)$$

which occurs when

$$n = \frac{-1}{\log(1 - e_1 - i_1)}. \qquad (13)$$

The model of MacArthur and Wilson make no predictions about long-term turnover. Nevertheless, we determine if either intrinsic long-term turnover or $n_{0.90\,(\text{int})}$ show a relationship with area or distance by the usual procedure of a multivariate linear regression using log-transformed variables. We find no significant relationships.

DISCUSSION

AN APPARENT CONTRADICTION

Our results show an apparent contradiction. On the one hand, our species-area-distance analysis shows that both area and distance contribute as expected to determining the number of bird species on islands. If the assumptions of MacArthur ad Wilson's model are correct, the species-distance component is caused by a reduction in the yearly colonization rate I_1 for more distant islands, and that this is caused by a reduction in the per-species colonization probability i_1. Our turnover-area-distance analysis, however, shows that while area and distance both contribute as expected to determining the short-term turnover of bird species on islands, this is due only to a variation in extinction probability with both area and distance, and not to any systematic variation in colonization probability. Unexpectedly, extinction probability decreases with increasing distance, as well as decreasing with increasing area.

If the per-species colonization probability i_1 does not vary systematically with distance (or area), does this mean that the yearly colonization rate I_1 does not vary? On a given island $I_1 = i_1 (P - S)$. We propose that it is the pool size P that varies. A glance at Table xx will show that our estimates of pool size are far less than those made by previous authors. We belive that our pools reflect biological reality. In general, our estimates of i_1 are greater than our estimates of e_1. If we were to calculate I_1 as $i_1 (P - S)$ using these previous estimates of pool size, and E_1 as e_1S, we would find that $I_1 >> E_1$. This cannot be so—we know that some of our islands are effectively at an equilibrium species number, and even those that show some change in species number over time show much less than this difference between colonizations and extinctions would suppose. For most islands we obtain sensible values for I_1 only by assuming a small value for P.

REPLACING COLONIZATION PROBABILITY WITH POOL SIZE

By applying MacArthur and Wilson's model implicitly assumes that all species have the same species pool, and that the difference in the number of colonizations per year between islands is a function of a difference in the per-species colonization probability. We propose that it is more useful to consider different islands to have effective species pools of different size, such that the average colonization probability of the species in each pool is approximately the same across different pools. The distinction is subtle—rather than saying that all species could make it out to an island in any given year but few make it to the more distant ones, we are saying that fewer species can make it out to a distant

island in a given year, but those that can have a relatively high probability of doing so.

A SURPRIZING RELATIONSHIP BETWEEN POOL SIZE AND THE RESCUE EFFECT—*DISTANT* POPULATIONS ARE MORE LIKELY TO BE RESCUED

We can now explain the species-distance effect in a different way—distant islands have less species because there are less species that make the attempt to reach them. The species-area effect may still be explained in the conventional way, as due to a lower per-species extinction probability on larger islands. But does our new model explain the strange observation that the average per-species extinction probability is higher on near islands? By considering pools instead of colonization probabilities, an pattern unnoticed by MacArthur and Wilson becomes obvious. This pattern has to do with the rescue effect as proposed by Brown and Kodric-Brown. The rescue effect refers to populations where the orginal pairs disappear, but are replaced *within the year* (rescued) by other pairs of the same species. This makes population appear to be continuous. In our proposal, islands that are closer to the mainland have a bigger species pool, in which many species will be competitors. We propose that the probability of a given population becoming extinct is independent of distance, but that the probability of its being rescued by another population of the same species is lower on near islands because of the large number of other species that could take its place. Any potential rescuers will have to fight for the vacated spot with numerous other species. By comparison, a distant island receives a fairly small

but predictable set of potential colonizers each year, and the chance that a population will be rescued is greater. Thus the probability of observing an extinction will be higher on near islands, even though the probability of an actual extinction is lower.

TESTING THE HYPOTHESIS

Clearly, this hypothesis needs to be tested. There are two way to do this. The most obvious involves a detailed examination of the biology of the species on these islands. We can examine the set of species that *regularly* colonizes each island, and so estimate the the yearly pool size independently. If the hypothesis is reasonable, we will find that there is a set of species that regulalrly make the trip to more distant islands (as well as close ones), and a set that only makes an attempt to reach close islands. We might call these sets the 'middle-distance migrants' and the 'island-hoppers' respectively.

Another way to test the hypothesis is to try to determine the actual extinction probability for the species on an island, rather than the observed probability that may hide 'rescues'. An intriguing method for doing this has recently been proposed (Clark and Rosenzweig 1994, Rosenzweig and Clark 1994). So until our hypothesis has been tested, we can say that the predictions concerning the way in which species number and short-term turnover vary with island area and distance made by MacArthur and Wilson are supported by these data. Some of the assumptions underlying the predictions, however, are clearly incorrect. In the

future we should look to a modified version of their model if we wish to explain the biogeography of terrestrial bird communities on British and Irish islands.

ACKNOWLEDGMENTS

The authors would like to thank J. Drake, J. Gittleman and M. McKinney for comments on earlier drafts of the manuscript. Funding for this research was provided by the Joint Nature Conservation Committee of the United Kingdom and the Pew Foundation Program for Scholars in Conservation and the Environment.

REFERENCES

Arrhenius, O. (1921) Species and area. *Ecology* **9**: 95–99.

British Ornithologists' Union (1992) *Checklist Of Birds Of Britain And Ireland*. 6th. ed. British Ornithologists' Union, Tring.

Clark, C. W. and M. L. Rosenzweig (1994) Extinction and colonization processes: parameter estimates from sporadic surveys. *American Naturalist* **143**: 583–596.

Darlington, P. J. (1957) *Zoogeography*. John Wiley, New York.

Diamond, J. M. (1969) Avifaunal equilibria and species turnover rates in the channel islands of California. *Proceedings of the National Academy of Sciences of the USA*, **64**, 57–63.

Diamond, J. M. (1971) Comparison of faunal equilibrium turnover rates on a tropical and a temperate island. *Proceedings of the National Academy of Sciences of the USA* **68**: 2742–2745.

Diamond, J. M. and R. M. May (1977) Species turnover rates on islands: dependance on census interval. *Science* **197**: 226–270.

Fuller, R. J. (1974) Ornithological Sites Register. *British Trust for Ornithology News* (supplement): 1–8.

Gibbons, D. W., J. B. Reid and R. A. Chapman (1993) *The New Atlas Of Breeding Birds In Britain And Northern Ireland: 1988–1991*. Poyser, Berkhamstead.

Hunt, G. L. and M. W. Hunt (1974) Trophic levels and turnover rates: the avifauna of Santa Barbara Island, California. *Condor* **76**: 363–369.

Jones, H. L. & Diamond, J. M. (1976) Short-time-base studies of turnover in breeding bird populations on the Californian channel islands. *Condor* **78**: 526–529.

Lack, D. L. (1969) The number of bird species on islands. *Bird Study* **16**: 193–209.

Lack, D. L. (1976) *Island Biology Illustrated by the Land Birds of Jamaica*. Blackewll Scientific, Oxford.

Lynch, J. F. and N. K. Johnson (1974) Turnover and equilibria in insular avifaunas, with special reference to the California channel Islands. *Condor* **76**: 370–384.

MacArthur, R. H. and E. O. Wilson (1963) An equilibrium theory of insular zoogeography. *Evolution* **17**: 373–387.

MacArthur, R. H. and E. O. Wilson (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

Mayr, E. (1940) The origin and history of the bird fauna of Polynesia. *Proceedings of the Sixth Pacific Scientific Congress* **4**: 197–216.

Pimm, S. L., J. M. Diamond, T. M. Reed, G. J. Russell and J. M. Verner (1993) Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences of the USA* **90**: 10871–10875.

Pimm, S. L., H. L. Jones and J. M. Diamond (1988) On the risk of extinction. *American Naturalist* **132**: 757–785.

Power, D. M. (1972) Numbers of bird species on Californian islands. *Evolution* **26**: 451–463.

Preston, F. W. (1948) The commonness, and rarity, of species. *Ecology* **29**: 254–283.

Preston, F. W. (1962a) The canonical distribution of commonness and rarity I. *Ecology* **43**: 185–215.

Preston, F. W. (1962b) The canonical distribution of commonness and rarity II. *Ecology* **43**: 410–432.

Reed, T. M. (1981a) *A study of populations of landbirds on the islands around Britain.* D. Phil. Thesis. University of Oxford.

Reed, T. M. (1981b) The number of breeding landbird species on British islands. *Journal of Animal Ecology* **50**: 613–624.

Ripley, S. D (1944) The bird fauna of the West Sumatra islands. *Bulletin of the Museum of Comparative Zoology* **94**: 305–430.

Rosenzweig, M. L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Rosenzweig, M. L. and C. W. Clark (1994) Island extinction rates from regular censuses. *Conservation Biology* **8**: 491–494.

Russell, G. J., J. M. Diamond, S. L. Pimm and T. M. Reed (1995) A century of turnover: community dynamics at three timescales. *Journal of Animal Ecology* **64**: 628–641.

Schoener, T. W. (1983) Rate of species turnover decreases from lower to higher organisms: a review of the data. *Oikos* **41**: 372–377.

Williams, C. B. (1943) Area and the number of species. *Nature* **152**: 264–267.

APPENDIX 1

"TERRESTRIAL" BIRD SPECIES FOUND ON THE ISLANDS IN THIS STUDY

For definition of "terrestrial", see text. Common names, scientific names and taxonomic sequence are taken from Gibbons, Reid & Chapman (1993). Scientific names follow the guidelines of the British Ornithologists' Union (1992).

White-tailed Eagle	*Haliaeetus albicilla*
Hen Harrier	*Circus cyaneus*
Goshawk	*Accipiter gentilis*
Sparrowhawk	*Accipiter nisus*
Buzzard	*Buteo buteo*
Golden Eagle	*Aquila chrysaetos*
Kestrel	*Falco tinnunculus*
Merlin	*Falco columbarius*
Peregrine	*Falco peregrinus*
Red Grouse	*Lagopus lagopus*
Ptarmigan	*Lagopus mutus*
Red-legged Partridge	*Alectoris rufa*
Grey Partridge	*Perdix perdix*
Quail	*Coturnix coturnix*
Pheasant	*Phasianus colchicus*
Woodcock	*Scolopax rusticola*
Rock Dove	*Columba livia*
Stock Dove	*Columba oenas*
Woodpigeon	*Columba palumbas*
Collared Dove	*Streptopelia decaocto*
Turtle dove	*Streptopelia turtur*
Cuckoo	*Cuculus canorus*
Barn Owl	*Tyto alba*
Little Owl	*Athene noctua*
Tawny Owl	*Strix aluco*
Long-eared Owl	*Asio otus*
Short-eared Owl	*Asio flammeus*

Snowy Owl	*Nyctea scandiaca*
Nightjar	*Caprimulgus europaeus*
Swift	*Apus apus*
Skylark	*Alauda arvensis*
Sand Martin	*Riparia riparia*
Swallow	*Hirundo rustica*
House Martin	*Delichon urbica*
Meadow Pipit	*Anthus pratensis*
Rock Pipit	*Anthus petrosus*
Yellow Wagtail	*Motacilla flava*
Grey Wagtail	*Motacilla cinerea*
Pied/White Wagtail	*Motacilla alba*
Dipper	*Cinclus cinclus*
Wren	*Troglodytes troglodytes*
Dunnock	*Prunella modularis*
Robin	*Erithacus rubecula*
Black Redstart	*Phoenicurus ochruros*
Whinchat	*Saxicola rubetra*
Stonechat	*Saxicola torquata*
Wheatear	*Oenanthe oenanthe*
Ring Ouzel	*Turdus torquatus*
Blackbird	*Turdus merula*
Song Thrush	*Turdus philomelos*
Redwing	*Turdus iliacus*
Mistle Thrush	*Turdus viscivorus*
Grasshopper Warbler	*Locustella naevia*
Sedge Warbler	*Acrocephalus schoenobaenus*
Lesser Whitethroat	*Sylvia curruca*
Whitethroat	*Sylvia communis*
Blackcap	*Sylvia atricapilla*
Chiffchaff	*Phylloscopus collybita*
Willow Warbler	*Phylloscopus trochilus*
Goldcrest	*Regulus regulus*
Spotted Flycatcher	*Muscicapa striata*
Long-tailed Tit	*Aegithalos caudatus*
Coal Tit	*Parus ater*
Blue Tit	*Parus caeruleus*
Great Tit	*Parus major*
Treecreeper	*Certhia familiaris*
Magpie	*Pica pica*
Chough	*Pyrrhocorax pyrrhocorax*

Jackdaw	*Corvus monedula*
Rook	*Corvus frugilegus*
Carrion and Hooded Crow	*Corvus corone*
Raven	*Corvus corax*
Starling	*Sturnus vulgaris*
House Sparrow	*Passer domesticus*
Tree Sparrow	*Passer montanus*
Chaffinch	*Fringilla coelebs*
Greenfinch	*Carduelis chloris*
Goldfinch	*Carduelis carduelis*
Siskin	*Carduelis spinus*
Linnet	*Carduelis cannabina*
Twite	*Cardeulis flavirostris*
Redpoll	*Carduelis flammea*
Bullfinch	*Pyrrhula pyrrhula*
Snow bunting	*Plectrophenax nivalis*
Yellowhammer	*Emberiza citrinella*
Reed Bunting	*Emberiza schoeniclus*
Corn Bunting	*Miliaria calandra*

PART FOUR

TURNOVER: BIOLOGICAL CHANGE AT ALL SCALES OF SPACE AND TIME

This chapter will be published as: Russell, G. J. (1996) Turnover: biological change at all scales of space and time. *Biodiversity Dynamics: Turnover Of Populations, Species And Higher Taxa* (ed. McKinney, M. L.). Columbia University Press, Columbia, NY.

NOTE. This part of my dissertation will be published as a chapter in an edited volume (see previous page). A number of times I refer to other chapters in this volume, for example: "Schopf and Ivany, Chapter 9". The reader who wishes to follow up these references should search out the appropriate chapter in:

McKinney, M. L. (1996) *Biodiversity Dynamics: Turnover Of Populations, Species And Higher Taxa*. Columbia University Press, Columbia, NY.

INTRODUCTION

In this chapter I will argue for turnover as an underappreciated and underutilized property of all biological systems. Currently, study of turnover is piecemeal. Turnover is defined, measured and modeled in many different ways, depending upon the discipline, the scale of measurement and whether this measurement is over time or space. Where models are similar, they seem to have been arrived at independently. I will demonstrate that:

1) Turnover may be found in all biological systems.

2) Turnover can be measured in a similar way over time and space.

3) Turnover can be measured in a similar way at different scales.

4) In some circumstances, turnover can be modeled in a similar way at different scales.

None of these propositions are new. Together, however, they make a compelling case for turnover as one of the most useful phenomena for comparative biological study.

I will illustrate the propositions above using the most commonly recognized type of biological turnover—the difference in species composition of two communities. My arguments are divided into four main sections. In the first section I discuss the nature of turnover—what is it, and where might we expect

to find it? In the second section I discuss the measurement of turnover, and show that the methods currently in use have much in common. In the third section I review some recent attempts to model temporal turnover in a particular type of community, and show that these models share a key mathematical technique. In the fourth section I apply one of these ecological models to a paleontological dataset, and show that the model is useful at this scale also.

There are other types of turnover. Since I am an ecologist by training, this chapter demonstrates a bias towards ecological examples—for this I apologize. Fortunately, this predisposition is balanced by Chaper 8, in which Norman Gilinsky addresses turnover at different scales from his perspective as a paleontologist. I start with ecological scales of space and time and expand my view to the longer timespans and often wider spaces of the fossil record. Gilinsky begins with higher taxonomic levels—families and orders—at a global scale, and focusses down upon the species, decades and hectares that constitute much of ecology. But turnover is more general still. In the concluding section of this chapter, I will argue that turnover is a property of all biological systems, and that methods for measuring and modeling turnover should be the same wherever it is found.

IDENTIFYING TURNOVER

I propose that in ecology, turnover be defined simply as the difference in composition between two community censuses. This utilitarian approach does

not distinguish between space and time, and I will try to show that when measuring community differences, there is no reason to make such a distinction.

TEMPORAL TURNOVER

The first ecologists to study biological communities held polarized opinions. Some maintained that communities develop over time through a predictable "succession" of stages, culminating in a persistent set of species called the climax (Cowles 1899; Clements 1916, 1936). A succession is driven by interactions between species; for example, an early-colonizing species might modify the soil in such a way as to allow the later colonization of a less tolerant species. Clearly, communities in different environments will have different successional sequences and reach different climax compositions. As a corollary, early versions of the theory implied that all communities in the same environment will exhibit the same successional sequence and reach the same climax.

Others proposed that communities are the chance result of the independent dynamics of species (e.g., Gleason 1926). In this view, the ranges occupied by species are determined largely by environmental factors, with little biotic interaction. The community at a particular place consists of those species whose ranges intersect there, and there is no predictable succession or climax.

We now know that neither of these views are wholly correct. Partly predictable successional sequences do occur. At the same time, species do move, often independently, in response to environmental changes. The composition of a

community is determined not only by climate and soil conditions, but also by a unique sequence of species replacements that is, at least in part, a function of species interactions. This sequence is commonly called an *assembly history*, distinguishing it from a more deterministic succession (for example, see Drake 1991; Luh and Pimm 1993.) But all these viewpoints imply that communities change their composition over time. Even the staunchest supporters of succession acknowledge that communities are constantly being 'knocked back' from their climax state by environmental forces, after which they return to the climax through a process of 'secondary' succession. All types of community change over time can be classified under the heading of temporal turnover.

MacArthur and Wilson (1963, 1967) proposed a theory that combines these opposing viewpoints and makes testable predictions about temporal turnover. Using islands as their example system, they suggested that communities develop towards an equilibrium of species richness, but not of species composition. According to their theory, community development is not wholly deterministic like a successional sequence, but a function of probabilistic processes of colonisation and local extinction. Equilibrium is reached not when these processes cease, but when they balance each other. Turnover may still be considerable. This theory has been supported by empirical observation of colonisation and extinction (e.g., Simberloff 1969, 1974; Simberloff and Wilson 1969), and under certain assumptions, models based on these processes have yielded good predictions of both species richness and turnover (e.g., Diamond 1969, 1971, 1984a, b; Diamond and May 1977; Hunt and Hunt 1974; Jones and

Diamond 1976; Lynch and Johnson 1974; Reed 1980; Schoener and Spiller 1987; Terborgh and Faaborg 1973; Williamson 1983).

At longer timescales, increased study of fossils during the eighteenth and nineteenth centuries (e.g., Cuvier 1812; see Mayr 1982 for a review) revealed that the communities of the past were made up of very different species from those we know today. Temporal turnover is evident in almost all fossil communities (although see Brett and Baird 1995). More recent analyses (e.g., Sepkoski 1981) also indicate that the total number of species has varied dramatically. The origination and extinction of species are responsible for these changes.

SPATIAL TURNOVER

If we census the community found at two different places and find different species compositions, then according to the definition presented earlier, we are seeing turnover. But the existence of spatial turnover is perhaps not obvious. Turnover is often defined, either explicity or implicity, as changes in 'a community'. Some might argue that in the temporal example we are indeed censusing the 'same' community (albeit at different times), but that in the spatial example we are censusing different communities. It is easy to visualize the sequence that leads from a set of species at time t to a different set of species at time $t + n$. Over time, species come and go in the area we are observing. There is an obvious continuity. It is less easy to visualize the sequence that leads from a set of species in one place to a set of species in another. Why might we make this distinction? To see temporal turnover, we need only sit and wait, but to see

spatial turnover, we must move ourselves. Because of this, we tend to view space and time differently. If we do move from one community to another, however, species 'appear' and 'disappear' just as they do over time. I suggest that if were concerned with differences in species composition, then calling two communites separated by time 'the same', and two communities separated by space 'different' is not a useful distinction.

Both kinds of community comparison also have this in common: on average, the greater the separation in time or space, the greater the difference in species composition. (This pattern becomes noisy but still recognizable if there are cyclic appearances and disappearances of particular species in time, or alternating community patches in space). So again, it makes sense to treat temporal and spatial turnover a similar manner. In the remainder of this chapter, I will use the term 'temporal turnover' for changes in community composition over time, the term 'spatial turnover' for changes in community composition over space.

MEASURING TURNOVER

STANDARDIZING MEASUREMENTS

Ecological turnover is a result of the appearances and disappearances of species. The most widely used index of temporal turnover for two censuses performed at different times has been

$$\text{Turnover rate} = \frac{\text{Number of appearances} + \text{number of disappearances}}{\text{Total number of species present} \times \text{census interval}}. \quad (1)$$

(e.g., Diamond and May 1977; Schoener 1983). This index consists of two parts: a measure of change (the numerator) and a method of standardization (the denominator). The measure of change is straightforward—simply add the number of species that either appear or disappear when comparing the two censuses. The standardization has two parts. First, divide by the sum of the number of species in both censuses. This converts the change into a proportion of the total set of species (allowing us to compare the turnover in communities of different size). Then, divide by the census interval. The index now describes the proportion of the community that changed per time unit (which is why it is called turnover *rate*).

Recently, Russell *et al.* (1995) proposed the form

$$\text{Turnover} = \frac{\text{Number of extinctions} + \text{number of immigrations}}{\text{Total number of species present}}. \quad (2)$$

This index standardizes turnover by community size, but not by interval (and so is not a rate). Their reason for not dividing by census interval is that the relationship of turnover to interval is asymptotically non-linear. Diamond and May showed that for breeding birds on islands, turnover *rate* declines hyperbolically to a slope of –1. Gingerich (1983) noticed that metrics which calculate paleontological extinction rate (a component of turnover rate) also show a negative relationship with interval.

Figure 1 shows a plot of observed turnover (as measured by equation 2) against census interval. The data are yearly censuses of breeding bird populations from the island of Skokholm. (We will see more of these data later in the Chapter. They are the same data used by Diamond and May [1977], where equation 1 was used to calculate turnover.) The figure shows the turnover for every possible pairwise comparison of years. The data are clearly asymptotic. In this particular dataset we can observe year to year turnover directly, since there are many pairs of censuses separated by only one year. But this may not always be the case, and in a later section I will show that calculation of turnover *rate* is misleading when the only census data available are separated by long intervals.

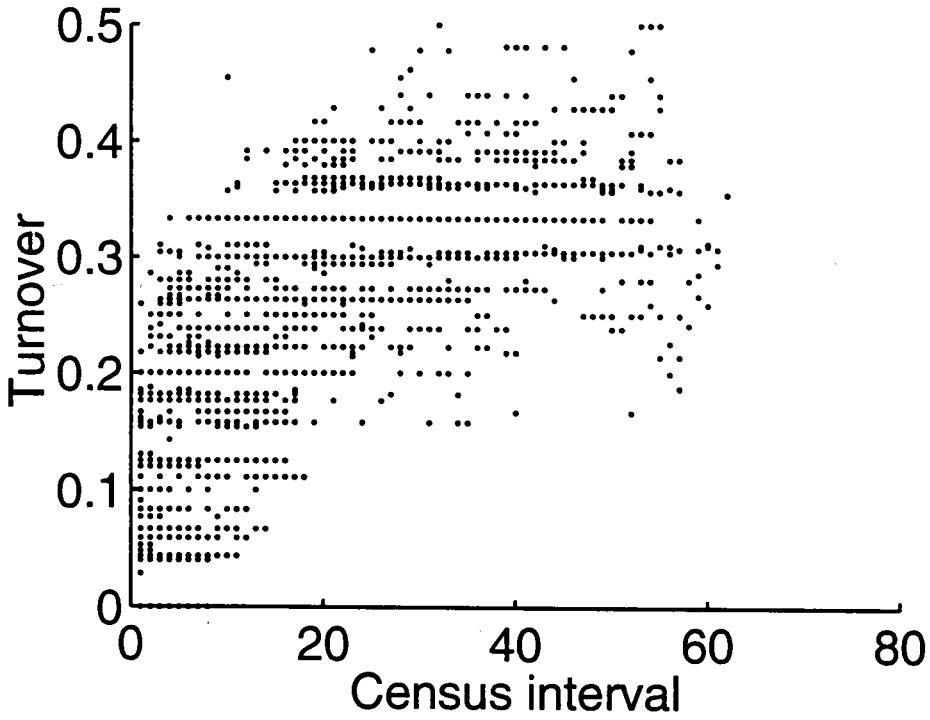
In paleontology there are a variety of turnover indices. Oliver and Pedder (1994) identify three alternatives, attributed to Roth (1987), McGhee (1988) and Oliver (1990) respectively. I have changed the words for easier comparison with the ecological indices above, and to prevent prejudgement about the processes involved.

$$\text{Turnover rate} = \frac{\text{Number of appearances} + \text{Number of disappearances}}{\text{Length of stratigraphic stage}} \quad (3)$$

$$\text{Turnover rate} = \frac{\text{Number of appearances} - \text{Number of disappearances}}{\text{Length of stratigraphic stage}} \quad (4)$$

$$\text{Turnover rate} = \frac{\text{Number of disappearances}}{\text{Number of genera present (in stratigraphic stage)}} \times 100 \quad (5)$$

Figure 1. Observed turnover on the island of Skokholm, calculated using the index of equation 2. Points represent the turnover for every possible pairwise combination of census years.


0.5
0.4
0.3
0.2
0.1
0
Turnover
0
20
40
60
80
Census interval

These, like the ecological indices, are measures of community turnover. They should not be confused with the taxonomic turnover (see Simpson 1944; Stanley 1979; Sepkoski 1981, 1984, 1987 and Gilinsky—Chapter 8). Their similarity to the ecological indices is immediately apparent. The first model is most similar; the numerator is the same, but is standardized by time and not by community size. The second model is like the first, but the number of disappearances is *subtracted* from the number of appearances. Both models use as their interval the stage: a somewhat arbitrary period of time that may be anything from one to twenty million years in length. Standardization thus gives the turnover rate per million years. The third model is described by Oliver and Pedder (1994) as being equivalent to what they call "proportional extinctions". In this case, the number of disappearances is standardized by community size, except that size is defined in terms of the number of genera, rather than species. Indeed, extinction indices show a similar distribution of forms to turnover indices, from the simple number of extinctions (E) through extinction rate (E/t where t is time) and proportional extinctions (E/D where D is diversity) to a proportional extinction rate ($E/[D \times t]$) (Foote 1994).

There is, however, an important difference between all these paleontological indices and the ecological indices of equations 1 and 2. In ecological turnover, there is one census at the beginning of the interval and one at the end. In the paleontological indices, *all* appearances and disappearances within the interval are counted. We might call the indices *pairwise* and *cumulative* turnover

respectively. Species which appear and disappear within the interval are included in paleontological turnover but not in ecological turnover.

The difference between pairwise and cumulative turnover is profound. In cumulative turnover, the relationship between 'appearances plus disappearances' and census interval will be positive and approximately linear—as we look at a greater timespan, we will see a proportional increase in the total number of appearance and disappearance events within that time. Dividing by census interval becomes sensible in these circumstances. Conversely, dividing by the total number of species becomes difficult to justify. In pairwise turnover, standardizing by the number of species (or genera) means that the maximum possible turnover—when every taxon in an initial census is not present in a second—is unity. In cumulative turnover, the total number of appearances plus disappearances can be greater than the total number of species. Dividing by the number of species could produce a turnover that is greater than unity (and hence not a proportion).

There is, of course, nothing to stop us from calculating cumulative turnover in ecology, or pairwise turnover in the fossil record. But from here onwards, I will restrict my discussion to pair-wise turnover.

So we can measure turnover, using a similar index, over days, years, decades, millennia or less consistent units such as stratigraphic stages. What if we want to measure turnover across kilometers, patches or biomes? Existing approaches to community change over space reveal a unique set of indices. Cody (1975) defined

alpha diversity as the number of species at a given time in "a small patch of habitat within an extensive and uniform stand of the same type" (see also Whittaker 1960, 1970). If the composition of the community changes over space, then the rate at which we pick up new species along a transect provides a measure called *beta diversity* (the differences between local communities, or patches). We can also measure *gamma diversity* (the differences between larger areas, such as biogeographic provinces). Confusingly, alpha diversity is a measure from one area, whereas beta and gamma diversity are spatially comparative measures. But rather than calculating beta or gamma diversity, there is no reason why we cannot use the index of turnover shown in equation 2. The index works for any kind of community difference.

INTRACENSUS TURNOVER—TIME AVERAGING AND SPACE AVERAGING

Whether turnover is spatial or temporal, there are a number of practical difficulties associated with measuring it 'in the field'. Temporal turnover is the difference in species composition of two communities at different points in time. Spatial turnover is the difference in species composition of two communities at different points in space. But what is a point in time, or a point in space?

Censusing a community takes a certain amount of time, and the longer the time, the more likely that there will be some changes in species composition while the census is being conducted—some *intracensus* turnover. Suppose we want to measure the turnover (i.e., the *intercensus* turnover) of a community over an interval of one year. Ideally, we would conduct our census on the same day in

each of two consecutive years. But what if, for some reason, each census takes a month to complete? Clearly, there may be some turnover as the census is being taken. If so, each census will tend to pick up more species than if the species composition of the community remained constant during the census period. The species lists from both the first and second censuses will be longer than if we had just looked at one day. The intercensus turnover will therefore tend to underestimate the true yearly turnover.

In paleontological studies the sampling has been done for us by the physical processes of sedimentation, and the problem of intracensus turnover is acute enough to have the special name of "time averaging". Time averaging refers to the fact that even relatively thin slices of rock typically contain sediments that differ in age by thousands of years (see Schindel 1982 for a discussion of the effects of different sampling schemes). The greater the time-averaging, the more intracensus turnover and the less (apparent) intercensus turnover there will be. It would perhaps be wise if all pairwise turnover studies include, as a summary statistic, the ratio of the intracensus interval to the intercensus interval. The smaller this ratio, the better.

So in an ideal world, we would measure temporal turnover by censusing a defined area over the smallest possible interval of time. By analogy, we should measure spatial turnover by censusing the smallest possible area (over a defined time interval). Ecologists often talk about 'point diversity', but typically they mean the number of species in a certain 'homogenous' area (i.e., alpha diversity). In principle, we could actually measure point diversity. The procedure might be

something like this: a we observe an very small area, in the form of a column of small diameter rising from the ground, and for a fixed length of time we record the species of every organism that intersects the column, even if only for an instant. This procedure is not as bizarre as it sound—plant ecologists already employ a similar approach in the form of a 'point transect'. If we want to include more mobile organisms in our census, though, the procedure is rather inefficient—we might have to wait a very long time before getting a decent sample of species. So instead, the census method used is exactly the same as for measuring temporal turnover—a count of all the species in a certain area.

Once again, we have the problem of intracensus turnover. Suppose we census two 100ha plots separated in space by 200m. If the plots are squares, 1km on each side, do we mean that edge of one plot and the edge of the other are 200m apart? Or that the *centers* of each plot are 200m apart, in which case there would be an overlap of 80%? This problem might be called 'space averaging', and as with time averaging our goal should be to minimize the ratio of intracensus to intercensus turnover. In this case we would try to minimize the ratio of the area sampled to the distance between the samples.

COUNTING EVERYTHING

Empirical studies of community turnover are beset by incomplete species lists. Sepkoski (1994) estimated the total number of species present during the Cenozoic as ~600 000. The number of fossil species from this period is ~40 000, which is < 7%. Schopf (1978) has pointed out that species with the highest

probability of forming indentifiable fossils, such as intertidal, sediment-dwelling macrofauna, can reach ~40% representation, but for many terrestrial species the probability of fossilization is close to zero. The problem of inadequate sampling can be reduced by instead counting higher taxa such as genera or families. The dynamics of such taxa correlate fairly well with those of their constituent species (Sepkoski 1992; Bambach and Sepkoski 1992; Jablonski 1995) but they have a much more consistent preservational record. Unfortunately, the species or population remains the dominant unit of study in ecology, and emphasis on different taxonomic levels remains a stumbling block for the integration of paleontology with ecology.

The limited sampling provided by the fossil record has profound consequences for the interpretation of paleoecological community dynamics. If fossils represent a random sample of *individuals*, the species content of this sample will be biased towards those species which are most abundant (McKinney in press). The smaller the sample, the stronger the bias; Sepkoski (1994) estimates that 90% of fossil individuals come from the most abundant 0.5% of fossilizable species. If the sampling is over a large area, there will also be a bias towards those species which are widespread. These may be the same species that were abundant: in both fossil and contemporary data there is a correlation between abundance and geographic range (Russell and Lindberg 1988; Gaston 1994; Brown 1995).

So in most circumstances, paleoecologists are studying only the most abundant and/or widespread species (even if the fossils include 40% of the extant species at that time). Much ecological evidence suggests that such species are less prone

to extinction (Gaston 1994 and references within). The same is true of populations at a more local scale (Goodman 1987; Pimm *et al.* 1993). The often overlooked consequence of this is that the fossil record describes the dynamics of a peculiarly persistent subset of species. Turnover in this subset will be much lower than in the community as a whole (McKinney and Allmon 1995), and may explain some examples of apparent 'community stasis' in the fossil record (e.g., Brett and Baird 1995; Alroy, Chapter 12).

Ecologists often accuse paleontologists of poor quality data (personal observation; see also Jackson 1988). These critics overlook the equally obvious fact that no ecological field studies ever consider an entire, natural community. Through constraints of time, budget and taxonomic knowledge, we study birds on islands, bacteria and protists in laboratory flasks, or the complete but artificial communities of a computer program. (The closest approach to a field study of a complete community is the recording by Simberloff and Wilson [1969] of the colonization of arthropod species onto several defaunated mangrove islands.) Assemblages such as 'birds' may represent far less than 7% of the total species richness, given the large number of unknown invertebrate and bacteria species we believe to inhabit the soil (World Conservation Monitoring Centre 1992). Indeed, if the total number of species on the planet is conservatively estimated at 30 million (Pimm *et al.* 1995), the 9770 recognized extant bird species (Sibley and Monroe 1990, 1993) represent a meagre 0.03%.

Should we ignore the turnover of assemblages and wait until we know the details of every species in a community? The current rate at which these very

species are being lost (Pimm *et al.* 1995) does not allow us that luxury. Conservation biologists, for practical reasons, often turn to single species as indicators of the 'health' of entire communities (e.g., Thomas *et al.* 1973; Soulé and Kleppel 1988). An assemblage can provide information, if not on the whole community, then at least on community-*level* dynamics, providing a more powerful diagnostic tool than the status of a single species (Fry *et al.* 1986; Block *et al.* 1986; Kremen 1992).

SEPARATING SPACE AND TIME

It may be difficult to distinguish between spatial and temporal turnover. If there is a limitation on the number of personnel available to collect census data for a study of spatial turnover, it may not be possible to census all the different areas at the same time. The same census takers may have to move from one site to another, sampling them sequentially. While a careful experimental design can minimize this problem, there will always be an element of temporal turnover in the data.

In paleontological data, there is always some error associated with age estimates (whether by radiometric methods or by stratigraphic correlation). When comparing fossils from different areas, it is sometimes hard to be sure that we are looking at exactly the same time period. If we are not, we will again introduce temporal noise into any spatial patterns.

One type of fossil sampling method is to take all the fossils from a vertical column of rock (usually called a core). The age of the rock, and hence of the fossils trapped within, is an increasing function of depth. So by sampling at different depths in the core, we should detect any temporal turnover. But this may not be all we are detecting. Sediments deposited on a sea floor can be brought by an ocean current from several hundred kilometers away. A shift in ocean currents can change the source of sediment to a new area, far enough away from the first to have a completely different species composition. If one of these changes has occurred in the area sampled by a core, different parts of the core will effectively be sampling different areas (as well as different times). It is often possible to detect substantial changes in sediment origin, especially if sampling is not limited to a core but covers a larger area (so that a picture of spatial changes may be built up). But at a fine scale, undetected vagaries of sedimentation will introduce spatial noise into a temporal pattern.

As mentioned above, spatial and temporal dynamics are often correlated (again, see Brown 1995 for a review of the ecological evidence). This is a mixed blessing. It may be virtually impossible to filter out the unwanted 'noise' while leaving the 'pattern' of interest, but at the same time the 'noise' may be similar enough to the 'pattern' that the combined signal may still represent the pattern.

INTERPRETING TURNOVER

There are two aspects to interpreting turnover. One aspect is understanding what processes are involved. What are the 'appearances' and 'disappearances'

that we observe? The second aspect is linking these processes—showing how the observed patterns of turnover arise from them.

CHANGING SCALES MEANS CHANGING PROCESSES

Appearances and disappearances come in two forms. An appearance can represent the *colonization* of a preexisting entity into the area of observation, or the *origination* of something new. Similarly, a disappearance can represent *local extinction* from just the area of observation, or *global extinction*. At the ecological scale of bird assemblages on islands, the entity is usually a population of breeding pairs of a given species. In this case, appearances represent the formation of one or more breeding pairs where previously there were none. The individuals may have come from another population (on another island or on the mainland), or they may have been already present on the island as part of a non-breeding population. Disappearances represent the dissolution of all breeding pairs of that species, due any combination of a) death, b) movement of some individuals away, or c) the failure or decision by a pair not to breed in a given year.

At the paleoecological scale of an assemblage of foraminiferan species in a stratigraphic core, appearances can describe either colonization (to the area sampled by the core) or the origination of a new species. (Or perhaps both: Gould and Eldredge [1977; also see Gould 1980] have argued that most apparently rapid transitions from one form to another in the fossil record are actually records of invasions from an isolated population that has undergone

evolutionary change in an undetected location before reappearing to replace the maternal population—an colonization following an unseen origination.) Disappearances can from the core represent local extinction or global extinction.

The important difference between these processes is that colonizations and local extinctions can happen repeatedly, whereas originations and global extinctions cannot. In the next few paragraphs I will show that if we observe temporal turnover at certain scales, we may simultaneously observe the effects of colonizations, originations, local extinctions and global extinctions!

We saw that for bird breeeding assemblages on small islands, where the timescale is measured in years or decades and the spatial scale in kilometers, appearance usually represents colonization and disappearance usually represents local extinction. Originations of new species are rare enough that on an ecological timescale of decades, their influence is negligible. Also, very few species are endemic to areas of only a few hectares. Distant islands or otherwise isolated areas have disproportionately more endemics, but in general, an extinction from a very small area will be a local extinction. Community dynamics at these scales are the result of only two processes (Table 1: upper left-hand box).

If we extend the just the timescale to thousands of years or more, it is tempting to think that the first assumption becomes increasingly inappropriate—that appearances may also be due to the evolutionary origination of new species within the area of observation. But if the area is small enough, such evolutionary events are still rare. Soulé (1980) has documented the smallest islands on which

Table 1. Processes contributing significantly to turnover at different combinations of temporal and spatial scale. Parentheses indicate the special case of 'mass extinctions'.

	Ecological time	Geological time
Local community	Immigration	Immigration
	Local extinction	Local extinction
Wider community	Immigration	Immigration
	Local extinction	Local extinction
		Origination
	(Global extinction)	Global extinction
Global community		Origination
	(Global extinction)	Global extinction

autochthonous speciation is known to have occurred for various taxa. For birds and mammals, that island is Madagascar, with an area of ~600 000 km^2. (This is also why, as mentioned earlier, most apparent originations observed in the fossil record are probably colonizations; the originations occurred elsewhere.) So we still need consider only two processes (upper right-hand box).

What if we return to a short, ecological timescale but consider a large area (say, a continent)? At this short timescale there will still be negligible originations, even in a large area, but does global extinction become more likely with the increased area? It does, but with the following caveat. Global diversity has increased since the beginning of life, so the total number of originations must have been more than the total number of global extinctions (Raup 1994). So if originations are rare over short time periods, global extinctions must *on average* be rarer still (Gilinsky and Good 1991). But there is a complication—there have been episodes in the history of life when the rate of extinction has, for a short while, vastly exceeded the rate of origination. During these so-called "mass extinction" events, global extinctions may be relatively common even over short time periods. Thus there are either two or three processes contributing to turnover (center left-hand box).

Consider both a large spatial scale and an extended timescale (millions of years). Originations and global extinctions now play an important part. But, if the spatial scale is anything less than global, colonization and local extinction must still play a role. There are four processes contributing to turnover (center right-hand box).

Finally, if we extend the spatial scale to include the entire planet, all appearances must be the result of origination, and all extinctions must be global. There can be only two processes. Still, over short time periods their impact will be low except for occasional peaks in rate of global extinction (lower left-hand box). It is only over long intervals that both will have a significant impact (lower right-hand box).

I present Table 1 as 'food for thought'. It suggests that at intermediate scales of space and time, temproal turnover requires a complex, four-parameter explanation, but that at restricted scales of space and/or time and for the global community at geological timescales, just one process of appearance and one process of disappearance are important. There is the intriguing hint that models of turnover at these extreme scales might look rather similar. Just such a conclusion has already been reached for models of diversity, rather than turnover: Sepkoski (1991a, b) has attempted to model the overall pattern of diversification of life on earth using a logistic model that is more usually applied to population dynamics.

LINKING SPACE AND TIME (METAPOPULATION MODELS PREDICT BOTH TEMPORAL AND SPATIAL TURNOVER)

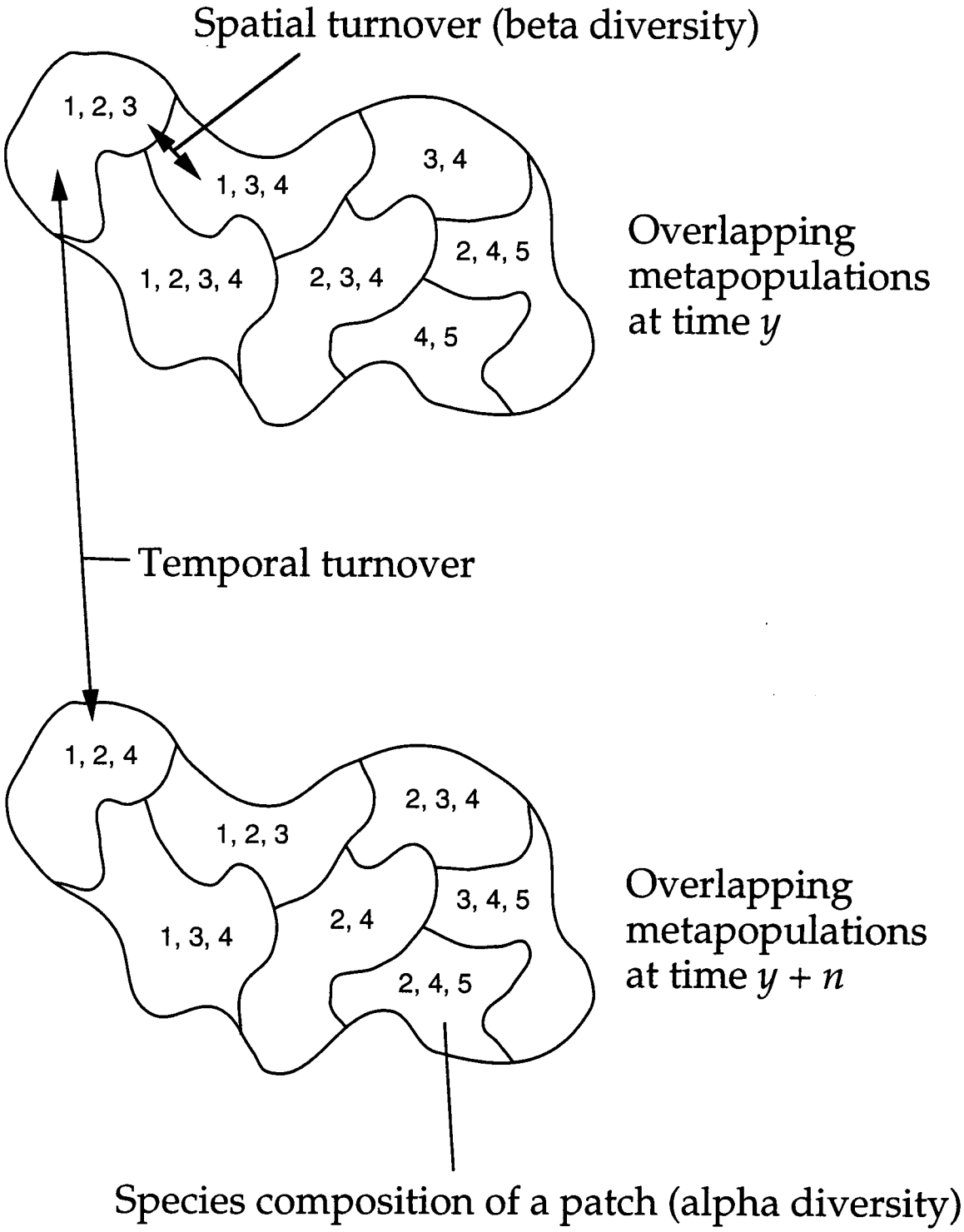
Turnover need not be applied solely to communities. I am going to preempt the concluding section of this chaper a little by briefly considering a different form of turnover. The spatial distribution (range) of most species changes over time. If we represent the range as a formally defined metapopulation (Levins 1970), or

even if we divide a continuous population into an array of arbitrary locations (rasterization), then we will be able to measure a presence/absence pattern of local populations over time (Maurer 1994; Maurer and Nott—Chapter 3). This might be called *range turnover* (Curnutt *pers. comm.*).

Metapopulations, in either the formal or loose sense described above (Harrison 1994 and Chapter 2), provide a simultaneous explanation of spatial and temporal community turnover. The metapopulation of one species may exhibit turnover of its local populations (range turnover). A given geographical area will contain portions of the metapopulations of *many* species. Assuming that their ranges do not overlap completely, different subsets of the area (patches) contain different subsets of species (local communities). As we move from patch to patch we encounter different communities. But if we stay in one patch for a while, the set of species will also change. The idea of species as metapopulations predicts both spatial and temporal turnover. Figure 2 represents this graphically: at each point in time, the distribution of each of species 1–5 is patchy, and for species 1, 2, 3 and 5, this patchy distribution changes between times y and $y + n$.

Spatial and temporal turnover are united in the idea of the 'shifting mosiac', identified empirically by Watt (1947) and now a cornerstone of landscape ecology. Perhaps the utility of metapopulation models lies as much in their ability to unite these different forms of community change as in their ability to explain the dynamics of any one species.

Figure 2. Metapopulation theory explains both temporal and spatial turnover.


Spatial turnover (beta diversity)
1, 2, 3
1, 3, 4
3, 4
2, 4, 5
1, 2, 3, 4
2, 3, 4
4, 5
Overlapping metapopulations at time y
Temporal turnover
1, 2, 4
1, 2, 3
2, 3, 4
3, 4, 5
1, 3, 4
2, 4
2, 4, 5
Overlapping metapopulations at time $y + n$
Species composition of a patch (alpha diversity)

MODELING TURNOVER

Might mathematical models of turnover, as a function of appearance and disappearance processes, be similar at different scales? In this section I will present some models that were developed for ecological data. Significantly, all the models use a similar and characteristic mathematical technique for dealing with repeatable appearances and disappearances.

MARKOV EXPANSIONS FOR REPEATABLE EVENTS

For many kinds of appearance and disappearance (sometimes called 'birth and death') processes, we can express the probability that each event will occur over a given interval of time in terms of the probability that it will occur over a unit interval of time. For example, over the last 400 years mammals species have had, on average, a yearly extinction probability of $\sim 3.5 \times 10^{-5}$. We can easily calculate the probability that a species will become extinct in n years by simply multiplying this probability by n. If a mammal species is extant in 1996, the probability that it will have disappeared by 2050 is $54 \times 3.5 \times 10^{-5} \approx 0.002$.

As I noted above, such global extinctions can happen only once. A more complicated example is provided by breeding populations of birds on islands. In this case, 'disappearance' is simply the failure by a particular species to breed on an island when it had bred before. The species is still breeding somewhere, and may return to the island to breed again, so the disappearance is a local extinction. If a species breeds in a particular year, we can describe the probability that it will

not breed at a point n years into the future, in terms of the probabilities of local extinction and of colonisation over *one* year. The expression, which is called a Markov expansion, is

$$\delta_n = \frac{\delta_1}{\lambda_1 + \delta_1}\left[1 - (1 - \lambda_1 - \delta_1)^n\right] \quad (6)$$

where δ_1 is the probability of observing a local extinction over one year, λ_1 is the probability of observing a colonization over one year, and δ_n is the probability of observing a local extinction when comparing two years separated by n years.

Note that this is *not* the probability that a local extinction will occur at any time during this interval. It is the probability that a species will be breeding in the first year and not in the year that is n years later. It may have come and gone many times in between. We saw the same distinction when comparing methods of measuring turnover in a previous section—paleontologists tend to look at a span of time, ecologists tend to compare two moments in time.

Since colonization may also be temporary (it may be followed by a local extinction), then a similar expression exists for λ_n, the probability of observing a colonization over an interval n:

$$\lambda_n = \frac{\lambda_1}{\lambda_1 + \delta_1}\left[1 - (1 - \lambda_1 - \delta_1)^n\right] \quad (7)$$

Both expressions use the same two variables, λ_1 and δ_1. Note that λ_1 and δ_1 are not expected to be the same, even if the number of species in the assemblage

remains approximately constant. This is because the extinction probability applies to the species in the assemblage, and the colonization probability to the species *not* in the assemblage. Also, the probability of a species being present in year y and in year $y + n$ is simply $(1 - \delta_n)$, and the probability of a species being present in year y and in year $y + n$ is $(1 - \lambda_n)$.

There is one more wrinkle to this story. All the breeding pairs of a species might cease breeding in one year, but be replaced *before the next year* by more pairs of the same species. This is especially likely if the number of breeding pairs is small. In this case, a local extinction has clearly occurred, but unless we can recognise individual birds, we will not observe it. Let us express the probability of a 'real' local extinction over one year as μ_1, to distinguish it from the probability of an 'observed' local extinction (δ_1). Although we do not see some of the 'real' extinctions, we can still estimate the value of μ_1. To observe a local extinction, not only must the breeding population fail, but *no new population must colonize*. Thus δ_1, the probability of observing a local extinction, is given by $\mu_1(1 - \lambda_1)$ so that μ_1 is given by $\delta_1 /(1 - \lambda_1)$. In the next section I will show that if we observe a species over time we can estimate λ_1, δ_1, and hence also μ_1.

The distinction between 'real' and observed local extinctions only applies to certain kinds of data, and is useful only if we want to know the probability that a given set of individuals will fail. Often we simply want the probability that the population will fail; whether or not there is turnover of individuals is not an issue. In such cases we calculate only δ_1.

Why is this mathematical technique so useful? Unit probabilites such as λ_1 and δ_1 are standardized by time, and allow us to compare different species or communities. If we are lucky, our census data will be from adjacent time periods and we will be able to estimate λ_1 and δ_1 directly (e.g., Rosenzweig and Clark 1994). It is much more likely that our data will be irregularly spaced, and may never include adjacent time units. Markov expansions can be used *backwards* to estimate unit probabilities from observations over longer intervals (Clark and Rosenzweig 1994). There are three types of model.

MAXIMUM LIKELIHOODS APPLIED TO SPECIES

The first type of model addresses the species in a community separately. By looking at the patterns of appearances and disappearances over time, we can estimate λ_1 and δ_1 for each species. We will then have distributions of these probabilities, and principle we could then describe the behaviour of the community in terms of these distributions. We can estimate λ_1 and δ_1 by fitting the Markov expressions above to the sequences of presence and absence for each species, using a maximum likelihood approach. (Likelihood is the probability of obtaining the observed data, given a particular model. Likelihood differs from usual statistical probability, which is the probability that a particular model is correct, given the observed data. If a model is formulated in terms of probabilities, calculating likelihoods is straightforward.)

Suppose we have the following sequence:

Time unit	1	5	6	9	11	12	16	18
Presence or absence?	A	P	P	A	P	A	A	P

This sequence has as its likelihood function

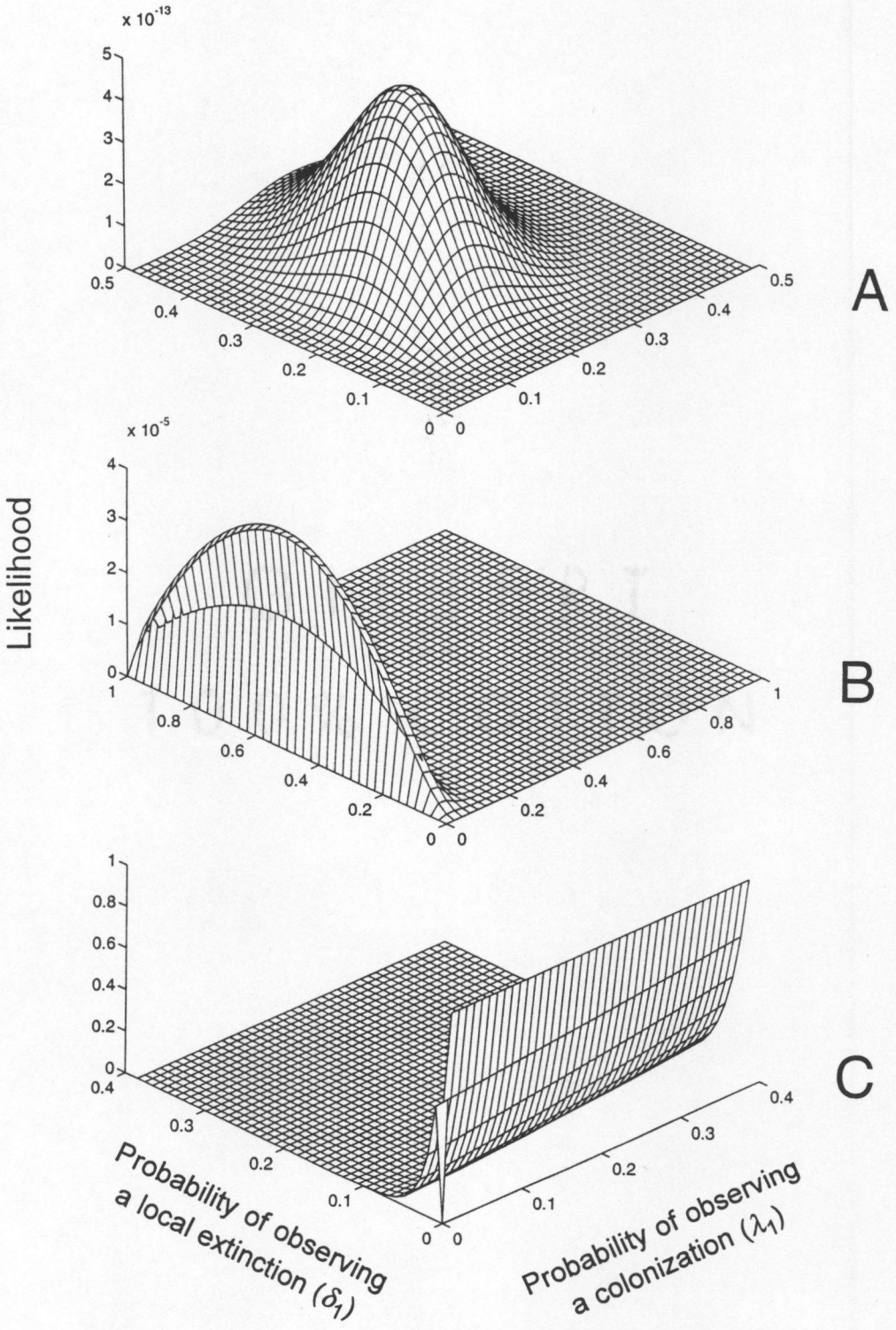
$$L = \lambda_4 \cdot (1-\delta_1) \cdot \delta_3 \cdot \lambda_2 \cdot \delta_1 \cdot (1-\lambda_4) \cdot \lambda_2 \tag{8}$$

that is to say, the product of the probabilities of each transition. I have shown that we can represent all of these transition probabilities in terms of just δ_1 and λ_1. The maximum likelihood estimators (MLE's) are obtained by finding those values of λ_1 and δ_1 which produce the largest value of L.

Such MLE's are obtained by using a non-linear maximization algorithm that searches the space of all possible values if λ_1 and δ_1, 'homing in' on those that provide the highest value of L. There are either two or three constraints on the possible values. Since λ_1 and δ_1 are probabilities, they are constrained to be within the ranges $0 \leq \lambda_1 \leq 1$ and $0 \leq \delta_1 \leq 1$. For mathematical reasons, there is also a constraint that $(\lambda_1 + \delta_1) \leq 1$. Furthermore, if we are then going to calculate μ_1 from $\delta_1 / (1 - \lambda_1)$, then δ_1 must lie in the range $0 \leq \delta_1 \leq (1 - \lambda_1)$.

Estimates obtained by this method vary widely in the confidence we can place in them, depending upon the quality of the data. Figures 3A–3C show the likelihood surfaces for combinations of colonization and extinction probability for three the bird species—buzzard (*Buteo buteo*), robin (*Erithacus rubecula*) and skylark (*Alauda arvensis*)—on the island of Skokholm (see Russell *et al.* 1995 for a

Figure 3. Likelihood surfaces for three breeding bird populations on the island of Skokholm: A—Buzzard, B—Robin, C—Skylark. See text for details.


x 10^-13
5
4
3
2
1
0
0.5
0.4
0.3
0.2
0.1
0
0
0.1
0.2
0.3
0.4
0.5
A
x 10^-5
4
3
2
1
0
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
B
1
0.8
0.6
0.4
0.2
0
0.4
0.3
0.2
0.1
0
0
0.1
0.2
0.3
0.4
C
Likelihood
Probability of observing a local extinction (δ_1)
Probability of observing a colonization (λ_1)

more complete description of these data). The first points of interest are the extremely small values of the likelihoods for the buzzard and robin. This is because Skokholm has census data for many years, so that these likelihoods are the product of many individual probabilities. If our data are extensive, likelihood values can be fantastically low, but it is not their absolute values that matter. The point of this (and indeed all) statistical techniques is to find the *best* model that describes the data. What is important is the value of the maximum likelihood *relative to the likelihoods for other combinations of parameters*. I could normalise the likelihoods, or use logarithms, but no particular purpose would be served in this case.

The next point is that the confidence we place in these MLE's can vary widely. For example, the surface for the buzzard shows a clear maximum, but for the robin the surface is more of a ridge—there is considerable uncertainty as to the value of δ_1, the extinction probability. The reason is that there are only two years when robins were present, and so only two years when we could observe an extinction. The skylark shows an even more extreme surface topology—in this case the MLE of δ_1 is zero, whereupon all the possible values of λ_1 have the same likelihood. This surface is produced because skylarks are always present on Skokholm. It is clear that the probability of extinction when present must be very low, but we can discern nothing about the probability of colonization because the species has to be absent before it can colonize! It is possible to calculate formal confidence intervals for maximum likelihood estimates of this kind, although the procedure is rather complicated.

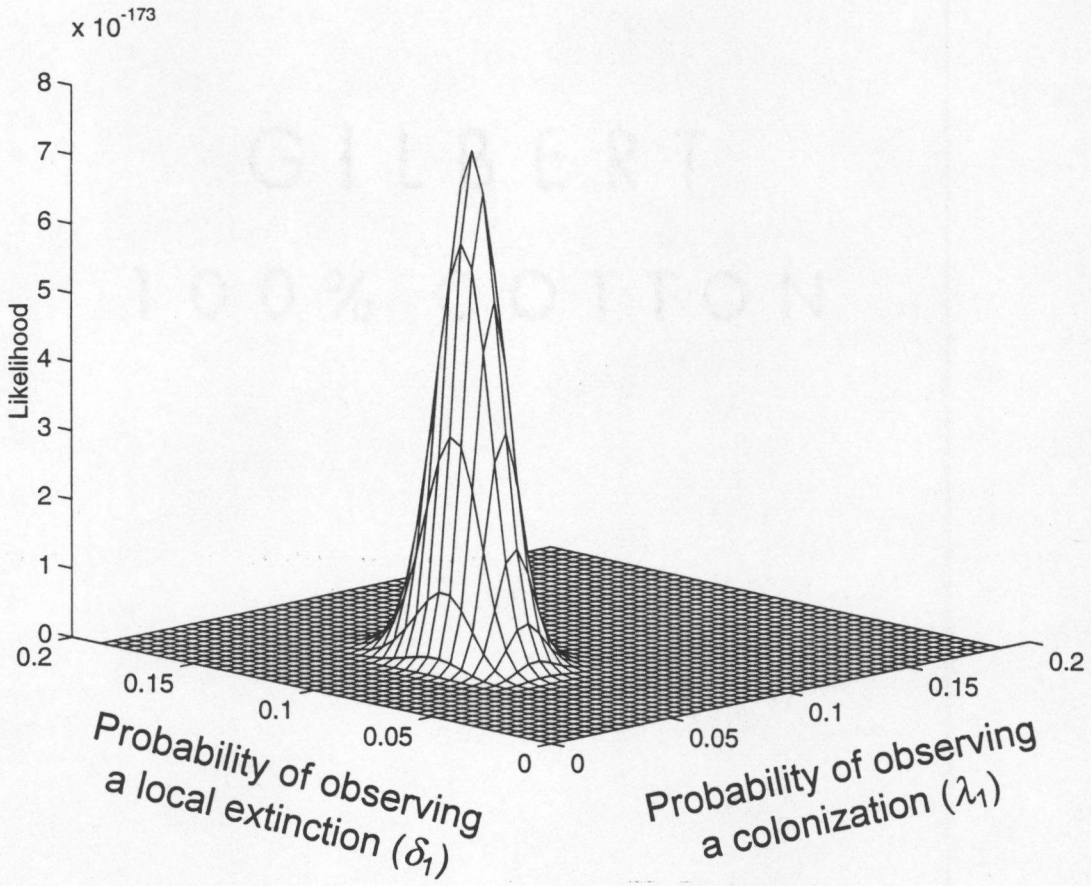
MAXIMUM LIKELIHOODS APPLIED TO COMMUNITIES

The second type of modeling approach addresses the community as a whole. We effectively assume that a community can be characterised by average species values. There will be an average appearance probability and an average disappearance probability for the community. Why do this, instead of the species-by-species approach? We might not have enough data to analyse species separately. Clark and Rosenzweig (1994) applied the maximum likelihood model (as described above) to entire plant assemblages on small Australian islands, rather than to the species. The number of years for which census data are available is so few that reliable estimates for each species are unobtainable. (Even in the Skokholm dataset we had to elimate some estimates for some species for this reason.) When we consider an entire assemblage, we search for those estimates of λ_1 and δ_1 that, if applied to *every species* in the assemblage, give the highest probability of obtaining the assemblage data. The likelihood surface usually shows an unambiguous maximum—Figure 4 shows the likelihood surface for the bird community on Skokholm.

TURNOVER APPLIED TO COMMUNITIES

The third type of approach makes the same assumption about average probabilities as the second approach (with the same advantages and disadvantages). But instead of estimating these average probabilities directly, we can use a model of the expected turnover that they give rise to. The description of turnover in equation 2 can be written symbolically as

Figure 4. Likelihood surface for the entire bird community on Skokholm.


x 10^-173
Likelihood
8
7
6
5
4
3
2
1
0
0.2
0.15
0.1
0.05
0
Probability of observing a local extinction (δ_1)
0
0.05
0.1
0.15
0.2
Probability of observing a colonization (λ_1)

$$T_n = \frac{E_n + I_n}{S_y + S_{y+n}} \tag{9}$$

where T_n is *apparent* turnover—the observed turnover per species between two censuses separated by n years, E_n is the observed number of extinctions over this interval, I_n is the observed number of colonizations, y is the time of the first census and S_y and S_{y+n} are the numbers of species at the times of the first and second censuses.

If we assume an equilibrium species richness, three things are approximately true: the number of species is constant ($S_y = S_{y+n} = S_{eq}$), the number of colonizations must therefore equal the number of extinctions ($I_n = E_n$), and we may estimate E_n from $\delta_n S_{eq}$ where δ_n is the mean per-species extinction probability: the probability that a species from a given community breeds in year y but fails to breed in year $y + n$. Hence

$$T_{n,eq} = \frac{E_n + I_n}{S_y + S_{y+n}} = \frac{2E_n}{2S_{eq}} = \frac{2\delta_n S_{eq}}{2S_{eq}} = \delta_n \tag{10}$$

where we can represent δ_n in terms of λ_1 and δ_1 as given by equation 2.

Russell *et al.* also present a 'non-equilibrium' model which takes into account change in species number over time (a phenomenon which will inflate turnovers especially at longer intervals). If β is the slope of a plot of ln (species number) against time (an exponential, rather than linear, regression is used to prevent the possibility of a negative number of species), then

$$T_{n,\mathrm{ne}} = \frac{\frac{\beta}{|\beta|}\left(\exp^{\beta n} - 1\right) + 2\delta_n \exp^{\frac{-\beta}{|\beta|}\beta n}}{1 + \exp^{\beta n}} \tag{11}$$

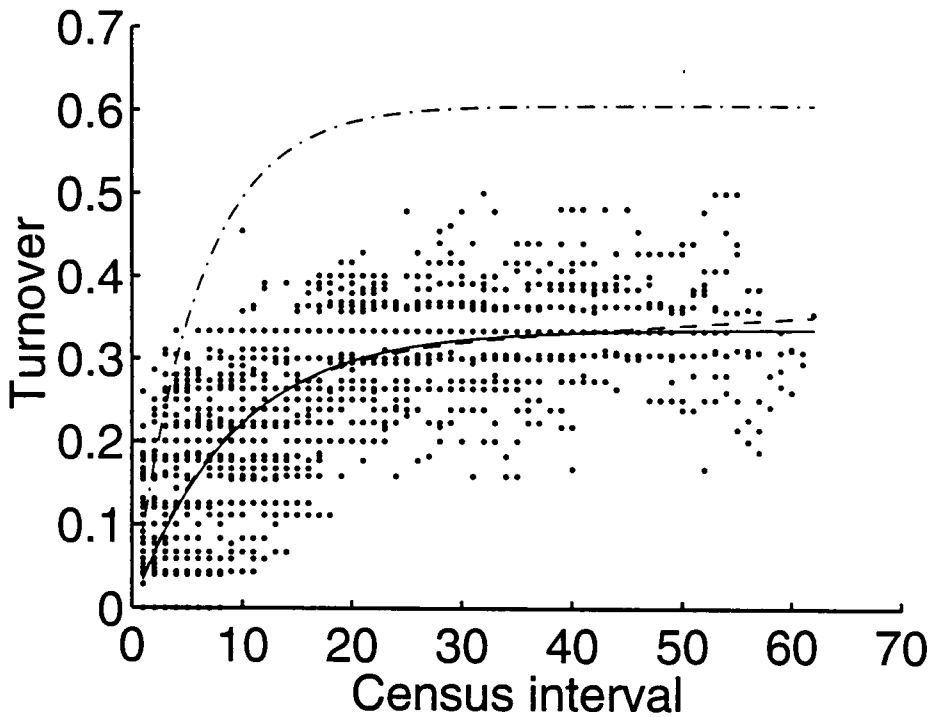
where again, δ_n is given by equation 2.

Over the period for which data are available, Skokholm shows a 4.8% decrease in species number per decade ($\beta = 0.0048$). I calculate turnover for the Skokholm data of Figure 1 using all possible pairwise combinations of censuses. I fit both the models use a non-linear fitting algorithm, except that in this case the model is a regression so I minimize the sum of squares of the residuals. Figure 5 shows the observed turnover on Skokholm, the least-squares fit of the equilibrium model (solid line) and of the non-equilibrium model (dashed line). In addition, I show the turnover predictions based on the estimates of λ_1 and δ_1 obtained from the maximum likelihood approach of the previous section (dot-dash line)

THE RELATIVE MERITS OF THE MODELS

The turnover models, especially the non-equilibrium model, provide a good fit to the data for Skokholm except at the shortest intervals, where they underestimates (see Russell *et al.* 1995 for other examples of the fit of this model). The estimates of λ_1 and δ_1 obtained by the community-level maximum likelihood approach make good predictions *only* at the shortest intervals. The reason probably lies in the fact the turnover models are fitted to the data as shown—to every pair-wise combination of years—whereas the maximum likelihood models are only fitted to sequential pair-wise combinations (see equation 8). Which model is better

Figure 5. The predictions of three models about turnover on the island of Skokholm. Solid line—equilibrium turnover model, dashed line—non-equilibrium turnover model, dash-dot line—maximum likelihood model.


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Turnover
0
10
20
30
40
50
60
70
Census interval

depends upon the questions we want to ask. But in either case there is a caveat. The results of the species-by-species approach suggest that distributions of appearance and disappearance probabilities are highly skewed. In this case 'average' values for a community may not be useful statistics. They may, however, allow us to compare communities.

MARKOV EXPANSIONS FOR NON-REPEATABLE EVENTS

What if our data are from scales where appearances are originations and disappearances are global extinctions? Since, as table 1 suggests, there are two processes, any model should have two probabilities, just like the models above. The probabilities will not the same, however. There is still a probability that a species (or other taxon) will disappear. But instead of a probability of recolonization, there is a probability that a taxon will split into two. Gilinsky and Good (1991; see also Gilinsky—chapter 8) show that these probabilties can be used to predict changes in the total number of taxa (rather than turnover). Since an increase is assumed to be the result of branching evolution of one of the taxa already present, both appearances and disappearances are a function of the number of taxa present. If p_0 is the probability of a taxon going extinct over a given interval, and p_2 is the probability of a taxon splitting into two, then the probability of going from S_0 to S_1 entities over that same interval is the coefficient of the x^{S_1} term in the expanded form of the following expression

$$\left(p_0 + p_1 x + p_2 x^2\right)^{S_0} \tag{12}$$

where $p_1 = 1 - p_0 - p_2$. As in the other Markov expansions, this expression can be usd backwards. By fitting it to an observed diversity path, whose overall likelihood is equal to the product of the probabilities of each transition, we can obtain maximum likelihood estimates of p_0 and p_2.

IDENTIFYING "LAZARUS" SPECIES: A CASE STUDY IN CROSS-SCALE MODELING

The preceding sections suggest that some models, developed for particular entities and scales, might be applied in different contexts. In this section I will present one example where a model developed in ecology may be usefully applied to paleontological data. These data consist of records of 102 species of foraminifera from a west-central Florida stratigraphic core (McKinney and Frederick 1992; McKinney and Allmon 1995). The core samples are from 1032 to 915 feet in depth, spanning the late Eocene and early Oligocene (Priabonian and Rupelian stages, a period of a few million years). The exact ages of the samples are unavailable, so there are two ways of treating the time component of these data. We can assume equal spacing, in which case we assign the time-step value of one to the first (deepest) sample, two to the second, and so on. Or, we can assume that the depth of the samples is proportional to their age, in which case we assign to each sample a measure of depth in whatever units we like. In this case I assume equal spacing, as if the samples were in consecutive 'years'

One of the many problems encountered by paleontologists is that of 'Lazarus' taxa: taxa which disappear from the fossil record for an extended period of time,

only to reappear unexpectedly and show that they were not globally extinct at all (Jablonski 1986). The reappearance of a taxon after any period of time indicates that the absence was either a local extinction (in the area sampled by the core) or a sampling artifact. If we are simply interested in whether the taxon was extant *somewhere*, we can ignore this distinction and interpolate between two appearances in the fossil record. Absences are still a problem, however, at the beginning and end of a stratigraphic sequence. If the taxon disappears before the end, and does not reappear, is it truly extinct or not? Would it be found in this end period if our sample was larger? Would it reappear if our record was longer? If the taxon is absent from the earliest part of the sequence, did it originate before or during the time covered by the sample? The shorter the record available, the worse the problem becomes.

Marshall (1994) has addressed this problem for continuous samples, using the distribution of gaps within the record to generate confidence intervals for gaps at the beginning or end. Unfortunately his method is not appropriate for discrete samples such as the foraminifera counts in the example datatset used here. The maximum likelihood model of Clark and Rosenzweig does, however, provide a method for evaluating apparent extinctions. By estimating per time unit probabilities of disappearance and appearance based on discrete samples, we can quantify the likelihood of an apparent extinction. Consider the foraminiferan species *Reussella moodyensis*, which has the following fossil sequence

P A A P P A A P A P A A A A A P A A A A A A A A A

(where A = absence and P = presence). We would like to know if the species has truly become extinct at the end of this record, or if this might be due to inadequate sampling. The simplest procedure is to obtain the maximum likelihood estimators for that part of the sequence that is bounded by presences:

P A A P P A A P A P A A A A A P,

since in this region, we know that absences are not true extinctions. $\lambda_1 = 0.333$, $\delta_1 = 0.667$, using the stage-based approach. We can then estimate the likelihood of the final sequence of ten absences as $(1 - 0.333)^9 = 0.026$.

The smaller this likelihood, the more likely it is that the species has really become extinct. We might choose to define truly extinct species as those for which this likelihood is below a certain threshold (say, 0.05). We would then suspect the others—those for which the likelihood is above the threshold—of being Lazarus species. Of the 102 foraminiferan species in our example dataset, 60 are not present in the final (most recent) sample. Six of these (including *R. moodyensis*) have a likelihood for their final sequence of absences of less than 0.05, and we may choose to regard them as truly extinct. The remaining 54 species would probably be found at some point after their last recorded disappearances if more samples were analyzed or if the data extended to more recent times (i.e., if the absence is due to local extinction from the area sampled by the core).

Similarly, fifty-eight foraminiferan species are not present in the first (oldest) sample. Of these, ten show initial sequences of absence with probabilities of less

than 0.05. We might conclude that only these species originated during this period, and that the rest were just locally extinct.

This approach could also be used to identify "Elvis taxa" (Erwin and Droser 1993). These are fossils which appear to represent the reemergence of a taxon that was presumed to be extinct, i.e., they appear to be Lazarus taxa. They are, however, different taxa which bear a strong similarity to the extinct form, perhaps because of convergent evolution as they evolved to fill its vacant niche. Using the same procedure as for Lazarus taxa, we can quantify the likelihood that a reemergence is indeed the original taxon (as opposed to an 'impersonator'). Again, we estimate the likelihood of the period of absence before the supposed 'return' of the taxon in question. If the likelihood is below a certain threshold, we can consider it probably extinct and investigate the new form more closely as a possible Elvis taxon.

If long datasets are available, we might be able to calibrate the thresholds by comparing predictions made from a short subset of the data with what the longer timeseries reveals about the existence of Lazarus and Elvis taxa.

THE FUTURE OF TURNOVER

At the beginning of this chapter I suggested that turnover is an underutilized phenomenon; that it has the potential allow comparisons of biological dynamics across time and space, and at different scales. This can only happen if there are standards in measurement and terminology. We need not fix upon just one kind

of index or one kind of model. Rather, we should be explicit about *pairwise* vs. *cumulative* turnover, and about *intracensus* vs. *intercensus* turnover.

Later I suggested that for communities at the combined extremes of the spatial and temporal scales, just two processes are important. These processes are different, but in each case there is one 'appearance' and one 'disappearance' process. This suggests that any mechanistic models developed to model change at these extremes should look rather similar. Differences will be related to those between colonization and origination, and between local and global extinction. Indeed, sometimes little distinction between these is made (Harrison, Chapter 2). Schopf and Ivany (Chapter 9) find evidence for such similarity of extremes in their review of empirical patterns in paleobiology. I can envisage a set of related models, tailored for different circumstances but which allow estimation of the same parameters (probably λ_1 and δ_1). We couldthen make even wider comparisons.

Another cross-scale link that needs to be made is that between the species-by-species approach and the community-level approach. We need to know just how a community-level phenomenon like turnover is a function of species-level probabilities of appearance and disappearance. I suspect that the next generation of cross-scale models will invoke these distributions, rather than average values

Finally, the link between two parameter models of a) colonization and local extinction, and b) origination and global extinction. needs investigating. Could the paleontological model presented by Gilinsky and Good predict turnover?

Could the maximum likelihood approach of Clark and Rosenzweig predict changes in the number of species? Could there be an expression which combines the probabilities of repeatable and non-repeatable events?

ECOLOGY AS A 'NULL MODEL' FOR PALEONTOLOGY

Our understanding of ecological turnover can inform our understanding of paleontological turnover. For example, the nonlinear model of ecological turnover presented in equation 12 predicts that the turnover of breeding species on small islands will approach its maximum, unity, after 1000–10 000 years (Russell *et al.* 1995). If our island data were in the form of fossils, spread over intervals of millions of years, then we would expect to see a turnover of unity even for the shortest available interval, and certainly for the longest. We should be amazed that we find any of the same species in rock samples separated by 'geological' intervals of time—ecological theory provides a 'null model' for the fossil record. That we do find the same species is partly explained the sampling bias of the fossil record discussed earlier—we tend to see only the most abundant, widespread and hence persistent species. Again, ecological theory provides an expectation of paleontological patterns. It makes sense to try to first interpret paleontological data using ecological principles. Only when we find a pattern that ecological theory does not predict need we search for alternative explanations.

TURNOVER EVERYWHERE

At the beginning of this chapter, I suggested that we can study turnover at any level in the hierarchy of life. The same basic processes—appearances and disappearances—are the foundation of any dynamic set of objects. In principle, we could measure the spatial or temporal turnover of populations across a species' range, of cells in the body of an individual, proteins in a cell membrane, carbon dioxide molecules in the sea, or ozone molecules in the upper atmosphere. Who knows what similarities might emerge? Patterns and theories of turnover are fundamental to our understanding of the natural world.

ACKNOWLEDGMENTS

A number of individuals receive my heartfelt thanks. Kevin Schopf, Stuart Pimm, James Drake, John Gittleman and an anonymous reviewer provided useful comments on an earlier draft of this paper. Michael McKinney invited me to contribute to this book, and has been an inexhaustible fund of ideas and references. The research was funded in part by the the Pew Foundation, through a grant to Stuart Pimm.

REFERENCES

Bambach, R. K. and J. J. Sepkoski, Jr. (1992) Historical evolutionary information in the traditional Linnean hierarchy. *Proceedings of the Fifth North American Paleontological Convention, Paleontological Society Special Publication* **6**:16–21.

Block, W. M., L. A. Brennan and R. J. Gutiérrez (1986) The use of guilds and guild-indicator species for assessing habitat suitability. *Wildlife 2000: Modeling Habitat Relationships Of Terrestrial Vertebrates* (eds. Verner, J., M. L. Morrison and C. J. Ralph) pp. 109–113. University of Wisconsin Press, Madison, WI.

Brett, C. E. and G. C. Baird (1995) Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. *New Approaches To Studying Speciation In The Fossil Record* (eds. Erwin, D and R. Anstey) pp. 285–315. Columbia University Press, New York, NY.

Brown, J. H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.

Clark, C. W. and M. L. Rosenzweig (1994) Extinction and colonization processes: parameter estimates from sporadic surveys. *American Naturalist* **143**: 583–596.

Clements, F. E. (1916) Plant succession: an analysis of the development of vegetation. *Carnegie Institute Publication* **242**. Carnegie Institute, Washington, DC.

Clements, F. E. (1936) Nature and structure of the climax. *Ecology* **24**: 252–284.

Cody, M. L. (1975) Towards a theory of continental species diversity. *Ecology And Evolution Of Communities* (eds. Cody, M. L. and J. M. Diamond) pp. 214–257. Belknap Press (Harvard University Press), Cambridge, MA.

Cowles, H. C. (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* **27**: 95–117, 167–202, 281–308, 361–391.

Cuvier, G. (1812) *Recherches sur les ossemens fossiles des quadrupèdes*, etc. Déterville, Paris.

Diamond, J. M. (1969) Avifaunal equilibria and species turnover rates in the channel islands of California. *Proceedings of the National Academy of Sciences of the USA* **64**: 57–63.

Diamond, J. M. (1971) Comparison of faunal equilibrium turnover rates on a tropical and a temperate island. *Proceedings of the National Academy of Sciences of the USA* **68**: 2742–2745.

Diamond, J. M. (1984a) "Normal" extinctions of isolated populations. *Quaternary Extinctions: a prehistoric revolution* (eds., Martin, P. S. and R. G. Klein) pp. 824–862. University of Arizona Press, Tucson, AZ.

Diamond, J. M. (1984b) Historic extinctions: a rosetta stone for understanding prehistoric extinctions. *Extinctions* (ed. Niteki, M. H.) pp. 191–246. University of Chicago Press, Chicago, IL.

Diamond, J.M. and R. M. May (1977) Species turnover rates on islands: dependance on census interval. *Science* **197**: 226–270.

Drake, J. A. (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* **137**: 1–26.

Erwin, D. H. and M. L. Droser (1993) Elvis taxa. *Palaios* **8**: 623–624.

Fry, M. E., R. J. Risser, H. A. Stubbs and J. P. Leighton (1986) Species selection for habitat evaluation procedures. *Wildlife 2000: Modeling Habitat Relationships Of Terrestrial Vertebrates* (eds. Verner, J., M. L. Morrison and C. J. Ralph) pp. 105–108. University of Wisconsin Press, Madison, WI.

Gaston, K. J. (1994) *Rarity*. Chapman & Hall, London.

Gilinsky, N. and I. J. Good (1991) Probabilities of origination, persistence, and extinction of families in marine invertebrate life. *Paleobiology* **17**: 145–166.

Gingerich, P. D. (1983) Rates of evolution: effects of time and temporal scaling. *Science* **222**: 159–161.

Gleason, H. (1926) The individualistic concept of the the plant association. *Bulletin of the Torry Botanical Club* **53**: 1–20.

Goodman, D. (1987) The demography of chance extinction. *Viable Populations For Conservation* (ed. Soulé, M. E.) pp. 11–34. Cambridge University Press, Cambridge.

Gould, S. J. (1980) Is a new and general theory of evolution emerging? *Paleobiology* **6**: 119–130.

Gould, S. J. (1981) Palaeontology plus ecology as palaeobiology. *Theoretical Ecology: Principles And Applications* (ed. May, R. M.) pp. 145–162. Sinauer, Sunderland.

Gould, S. J. and N. Eldredge (1977) Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* **3**: 115–151.

Harrison, S. (1994) Metapopulations and conservation. *Large Scale Ecology And Conservation Biology* (eds. Edwards, P., R. M. May and N. R. Webb) pp. 111–128. Blackwell, London.

Hunt, G. L. and M. W. Hunt (1974) Trophic levels and turnover rates: the avifauna of Santa Barbara Island, California. *Condor* **76**: 363–369.

Jablonski, D. (1986) Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* **231**: 129–133.

Jablonski, D. (1995) Extinctions in the fossil record. *Extinction Rates* (eds. Lawton, J. H. and R. M. May) pp. 25–44. Oxford University Press, Oxford.

Jackson, J. B. C. (1988) Does ecology matter? (Book review). *Paleobiology* **14**: 307–312.

Jones, H. L. and J. M. Diamond (1976) Short-time-base studies of turnover in breeding bird populations on the Californian channel islands. *Condor* **78**: 526–529.

Kremen, C. (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**: 203–217.

Levins, R. (1970) Extinction. *Lectures on Mathematics in the Life Sciences* **2**: 75–107.

Luh, H.-K. and S. L. Pimm (1993) The assembly of ecological communities: a minimalist approach. *Journal of Animal Ecology* **62**: 749–765.

Lynch, J. F. and N. K. Johnson (1974) Turnover and equilibria in insular avifaunas, with special reference to the California channel Islands. *Condor* **76**: 370–384.

MacArthur, R. H. and E. O. Wilson (1963) An equilibrium theory of insular zoogeography. *Evolution* **17**: 373–387.

MacArthur, R. H. and E. O. Wilson (1967) *The Theory Of Island Biogeography*. Princeton University Press, Princeton, NJ.

Marshall, C. R. (1994) Confidence intervals on stratigraphic ranges: partial relaxation of the assumption of randomly distributed fossil horizons. *Paleobiology* **20**: 459–469.

Maurer, B. A. (1994) *Geographical Population Analysis: Tools For The Analysis Of Biodiversity*. Blackwell Scientific, Oxford.

Mayr, E. (1982) *The Growth Of Biological Thought*. Belknap Press (Harvard University Press), Cambridge, MA.

McGhee, G. R. (1988) The Late Devonian extinction event: evidence for abrupt ecosystem collapse. *Paleobiology* **14**: 250–257.

McKinney, M. L. (1989) Periodic mass extinctions: product of biosphere growth dynamics? *Historical Biology* **2**: 273–287.

McKinney, M. L. (In press) The biology of fossil abundance. *Revista Española de Paleontología.*

McKinney, M. L. and D. Frederick (1992) Extinction and population dynamics: new methods and evidence from Paleogene foraminifera. *Geology* **20**: 343–346.

McKinney, M. L. and W. D. Allmon (1995) Metapopulations and disturbance: from patch dynamics to biodiversity dynamics. *New Approaches To Studying Speciation In The Fossil Record* (eds. Erwin, D. and R. Anstey) pp. 123–183. Columbia University Press, New York, NY.

Oliver, W. A., Jr. (1990) Extinctions and migrations of Devonian rugose corals in the Eastern Americas Realm. *Lethaia* **23**: 167–178.

Oliver, W. A., Jr. and A. E. H. Pedder (1994) Crises in the Devonian history of the rugose corals. *Paleobiology* **20**: 178–190.

Peterson, C. H. (1983) The pervasive biological explanation. (Book review.) *Paleobiology* **9**: 429–436.

Pimm, S. L., J. M. Diamond, T. M. Reed, G. J. Russell and J. M. Verner (1993) Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences of the USA* **90**: 10871–10875.

Pimm, S. L., J. L. Gittleman, G. J. Russell and T. M. Brooks (1995) The future of biodiversity. *Science* **269**: 347–350.

Raup, D. M. (1994) The role of extinction in evolution. *Proceedings of the National Academy of Sciences of the USA* **91**: 6758–6763.

Reed, T. M. (1980) Turnover frequency in island birds. *Journal of Biogeography* **7**: 329–335.

Rosenzweig, M. L. and C. W. Clark (1994) Island extinction rates from regular censuses. *Conservation Biology* **8**: 491–494.

Roth, P. H. (1987) Mesozoic calcareous nanofossil evolution: relation to paleoceanographic events. *Paleoceanography* **2**: 601–611.

Russell, G. J., J. M. Diamond, S. L. Pimm and T. M. Reed (1995) Centuries of turnover: community dynamics at three timescales. *Journal of Animal Ecology* **64**: 628–641.

Russell, M. P. and D. R. Lindberg (1988) Real and random patterns associated with molluscan spatial and temporal distributions. *Paleobiology* **14**: 322–330.

Schindel, D. E. (1982) Resolution analysis: a new approach to gaps in the fossil record. *Paleobiology* **8**: 340–353.

Schoener, T.W. (1983) Rate of species turnover decreases from lower to higher organisms: a review of the data. *Oikos* **41**: 372–377.

Schoener, T. W. and D. A. Spiller (1987) High population persistence in a system with high turnover. *Nature* **330**: 474–477.

Schopf, T. J. M. (1978) Fossilization potential of an intertidal fauna: Friday Harbor, Washington. *Paleobiology* **4**: 261–270.

Sepkoski, J. J. Jr. (1981) A factor analytic description of the Phanerzoic marine fossil record. *Paleobiology* **7**: 36–53.

Sepkoski, J. J. Jr. (1984) A kinetic model of Phanerzoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* **10**: 246–267.

Sepkoski, J. J. Jr. (1987) Environmental trends in extinction during the Paleozoic. *Science* **235**: 64–66.

Sepkoski, J. J. Jr. (1991a) Population biology models in macroevolution. *Analytical Paleobiology* (ed. Gilinsky, N. L.) pp. 136–155. Paleontological Society, Knoxville, TN.

Sepkoski, J. J. Jr. (1991b) Diversity in the Phanerzoic oceans: a partisan review. *Proceedings of ICSEB IV: The Unity Of Evolutionary Biology* (ed. Dudley, E. C.) pp. 72–94. Dioscorides Press, Portland, OR.

Sepkoski, J. J. Jr. (1992) Phylogenetic and ecologic patterns in the Phanerzoic history of marine biodiversity. *Systematics, Ecology, And The Biodiversity Crisis* (ed. Eldredge, N.) pp. 77–100. Columbia University Press, New York, NY.

Sepkoski, J. J. (1994) Limits to randomness in paleobiologic models: the case of Phanerzoic species diversity. *Acta Paleontologica Polonica* **38**: 175–198.

Sibley, C. G. and B. L. Monroe, Jr. (1990) *Distribution and Taxonomy of Birds of the World*. Yale University Press, Newhaven, CI.

Sibley, C. G. and B. L. Monroe, Jr. (1993) *A Supplement to Distribution and Taxonomy of Birds of the World*. Yale University Press, Newhaven, CI.

Simberloff, D. S. (1969) Experimental zoogeography of islands. A model of insular colonization. *Ecology* **50**: 296–314.

Simberloff, D. S. (1974) Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics* **5**: 161–182.

Simberloff, D. S. and E. O. Wilson (1969) Experimental zoogeography of islands. The colonization of empty islands. *Bird Study* **16**: 193–209.

Simpson, G. G. (1944) *Tempo And Mode In Evolution*. Columbia University Press, New York, NY.

Soulé, D. F. and G. S. Kleppel (1988) *Marine Organisms As Indicators*. Springer-Verlag, New York, NY.

Soulé, M. E. (1980) Threshold for survival: maintaining fitness and evolutionary potential. *Conservation Biology: An Evolutionary-Ecological Perspective* (eds. Soule, M. E. and B. A. Wilcox) pp. 151–169. Sinauer, Sunderland, MA.

Stanley, S. M. (1979) *Macroevolution: Pattern And Process*. W. H. Freeman, San Francisco, CA.

Terborgh, J. and J. Faaborg (1973) Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk* **90**: 759–779.

Thomas, W. A., G. Goldstein and W. H. Wilcox (1973) *Biological Indicators Of Environmental Quality*. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

Watt, A. S. (1947) Pattern and process in the plant community. *Journal of Ecology* **35**: 1–22.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**: 279–338.

Whittaker, R. H. (1970) *Communities and Ecosystems*. Macmillan, London

Williamson, M. H. (1983) The land-bird community of Skokholm: ordination and turnover. *Oikos* **41**: 378–384.

World Conservation Monitoring Centre (1992) *Global Biodiversity: Status Of The Earth's Living Resources*. Chapman & Hall, London.

PART FIVE

DECREASED TAXONOMIC SELECTIVITY IN THE FUTURE EXTINCTION CRISIS

This chapter has been submitted to *The American Naturalist* as: Russell, G. J., T. M. Brooks, M. L. McKinney and C. G. Anderson. Decreased taxonomic selectivity in the future extinction crisis.

ABSTRACT

We compare the distribution of observed bird and mammal species extinctions with the distribution we would expect if these extinctions occurred at random. We find three differences. First, actual bird and mammal species extinctions are concentrated within certain genera (selectivity by genus). Second, actual bird and mammal species extinctions are more likely to occur in species-poor genera and less likely to occur in species-rich genera (selectivity by genus size). Third, actual bird and mammal species extinctions have caused a greater overall number of genus extinctions than a random distribution predicts (a consequence of selectivity). We extend the analyses to include threatened bird and mammal species, using data from IUCN 'Red Lists'. For threatened mammals, we find the same kind of selectivity described above. Threatened birds, however, show less selectivity by genus size and only a slight increase in the overall number of genus extinctions. This suggests a change in the causes of bird extinctions.

INTRODUCTION

Recent estimates suggest that our planet is losing species at an unprecedented rate (Myers 1979; Lovejoy 1980; Raven 1988; Wilson 1988; Reid 1992; see Pimm et al. 1995 for a review). Surprisingly, there are no estimates of the consequent loss of higher taxa such as genera or families. Exactly how many genera or families we are losing depends upon taxonomic 'selectivity'—the observation that species extinctions are common within some higher taxa, and rare within others.

Analyses of selectivity are commonplace for extinctions in the fossil record (McKinney 1995). For the first time, we examine the selectivity of some historical and likely future extinctions. Specifically, we analyze the selectivity within genera of bird and mammal extinctions.

We obtain data on recently extinct and threatened species from current IUCN 'Red Lists' (Groombridge 1993; Collar et al. 1994) and from a recent report (World Conservation Monitoring Center 1992). These data vary greatly in quality, reflecting a disproportionate number of studies on large, showy taxa such as butterflies, birds and mammals (Smith et al. 1993). Nevertheless, Red Lists are the only sources that apply criteria for threatened status consistently across entire groups. The quality of the lists is improving rapidly as these criteria are made more precise (Collar et al. 1994). Restricting ourselves to the best of these data, we consider only mammals and birds—about 50% of mammal species and almost all bird species have been assessed for inclusion in the Red Lists (Groombridge 1993).

The current IUCN categories for extinct and endangered mammal species are (Groombridge 1993):

Extinct—taxa not definitely located in the wild during the past 50 years.

Endangered—taxa in danger of extinction and whose survival is unlikely if causal factors keep operating.

Vulnerable—taxa believed likely to move into the endangered category in the near future if the causal factors keep operating.

Rare—taxa with small world populations that are not at present endangered or vulnerable, but are at risk.

These categories will be updated in the next edition of the Red List for mammals, and will be similar to those currently used for birds. The current IUCN categories for extinct and endangered bird species are (Collar *et al.* 1994):

Extinct—no reasonable doubt that the last individual of the species has died.

Critical—probability of extinction in the wild is expected to be at least 50% in 5 years.

Endangered—probability of extinction in the wild is expected to be at least 20% in 20 years.

Vulnerable—probability of extinction in the wild is expected to be at least 10% in 100 years.

To assess the impact of species extinctions on genera, we combine the above data with recent taxonomies. We classify mammal species according to the taxonomy presented by Wilson and Reeder (1993), which lists 4638 species in 1136 genera. (We obtained these numbers by directly counting the described species and genera, since the compendium's own summary statistics contain some inaccuracies). We do not include 20 species, including five complete genera, that

are listed as being extinct prior to c.1600 (for comparison with birds, where historical extinctions are considered to be those since 1600) and one species that is currently considered to be a domesticated form (*Bos taurus*). Thus our mammal dataset consists of 4617 species in 1131 genera. We classify bird species according to the taxonomy presented by Sibley and Monroe (1990, 1993) which lists 9770 species in 2070 genera. In this taxonomy, all relationships above the genus level are based on molecular comparisons (Sibley and Ahlquist 1990)—the first time that such methods have been applied consistently across a major group.

Both these taxonomies are also the standard references for the Red Lists. Nevertheless, sometimes a species' Red List classification differs from its 'authoritative' classification (see Groombridge 1993 for a discussion of why this is so). For example, the IUCN Red List for mammals identifies *Oryzomys victus* as extinct, but Wilson and Reeder (who include recently extinct species in their taxonomy) list this species as *Oligoryzomys victus*. In such cases, we follow the authority's taxonomy.

RAREFACTION—A MODEL OF RANDOM EXTINCTION

Suppose that a certain number of objects are organized into categories. Different categories may contain different numbers of objects. Rarefaction is the process of sampling these objects without replacement and at random, ignoring their membership in a category. If we sample all the objects, we will obviously include all the categories, but if we sample less than all the objects, it is possible that some of the categories will not be represented. This will be especially likely if we

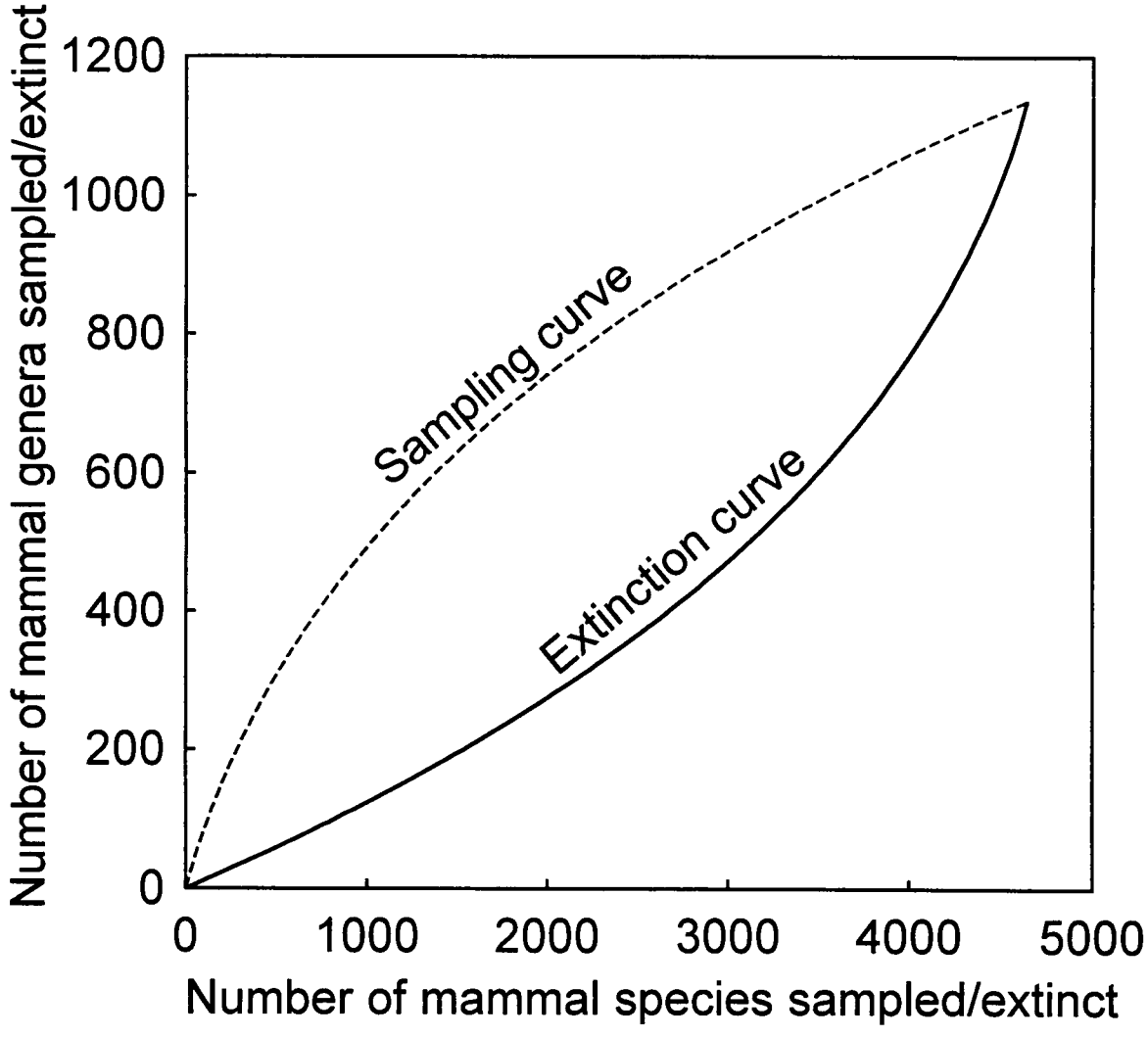
sample only a few objects, and unavoidable if we sample fewer objects than there are categories. For any distribution of objects in categories, there is a unique relationship between the number of objects sampled at random and the average number of categories that will be included. This relationship is called a sampling rarefaction curve, and it may be obtained from an analytical expression (Simberloff 1972; Heck et al. 1975), or by numerical simulation. The curve is convex with an inital slope of one; if we sample just one object, we will include one category, but as more objects are included in the sample, there is an increasing probability that some categories will be represented more than once. The exact shape of the curve depends in a complex manner upon the distribution of objects in categories.

Rarefaction was first used in ecology, to allow comparison of different samples of individuals taken from the same community (Sanders 1968). Different sample sizes will include different numbers of species, so if we wish to compare the number of species in a community at, say, time x and time y, we need to compare equal sample sizes. One approach would be to physically sample exactly the same number of individuals each time, but this might be difficult, or we might be analyzing data that were collected for another purpose. We can still make the comparison—we simply take the larger sample and sample from *it* at random until we have the same number of individuals as in the smaller sample. If we wish to compare many samples, we can use random sampling to reduce all of them to the size of the smallest.

There is another kind of rarefaction curve. Sampling is without replacement, so if a category has all its objects included in a sample, it disappears from the original distribution. Instead of asking how many categories are included in the sample, we could ask how many categories have disappeared from the original distribution. This provides a model of random extinction. If the categories are species, the objects are individuals and sampling an individual represents its death, then we are asking which species no longer have any individuals. So for any distribution of objects in categories, there is not only a sampling rarefaction curve, but also an extinction rarefaction curve. The extinction curve is concave—at first, including an object in a sample is unlikely to leave its original category empty, but as more and more objects are sampled, more and more categories will have had all their objects sampled (and so be 'extinct'). In fact, for a given distribution of objects in categories, the extinction rarefaction curve is the same shape as the sampling curve, except that it is rotated through 180°. Figure 1 shows the sampling and extinction rarefaction curves for the distribution of mammal species in genera.

Paleontologists use extinction rarefaction in a 'reverse' manner, to get information about species (which are not well represented in the fossil record) from data on higher taxonomic levels (which are better represented). For example, during the end-Permian mass extinction, 40% of all families vanished. By assuming that the distribution of species within families at the end of the Permian was the same shape as the distribution today, we can estimate that ~95% of all species must have become extinct at that time (Raup 1979). Of course,

Figure 1. Extinction and sampling rarefaction curves for all mammal species. The sampling curve shows the expected number of genera included in a given random sample of species. The extinction curve shows the expected number of genus extinctions for a given number of randomly distributed species extinctions.


Number of mammal genera sampled/extinct
1200
1000
800
600
400
200
0
Sampling curve
Extinction curve
0
1000
2000
3000
4000
5000
Number of mammal species sampled/extinct

this also assumes that those species extinctions were random, when the evidence suggests that they were not (McKinney 1995). Different patterns of non-random extinction form the subject of our next section.

SELECTIVITY—PATTERNS OF *NON*-RANDOM EXTINCTION

If sampling is non-random—if objects in some categories are more likely to be sampled than objects in others—then that (by definition) is selectivity. In this paper we investigate the selectivity of bird and mammal species extinctions within genera. For each group we ask the following questions:

1) Are extinct or threatened species more common in some genera, and more rare in others, than we expect? (Is there selectivity by genus?)

2) If there is selectivity by genus, can we identify any predictable differences between high-extinction or high-threat genera and low-extinction or low-threat genera? (Is there selectivity by genus *size*?)

3) Is the total number of extinct or threatened genera greater or less than we expect?

As a model of random extinction, rarefaction provides the 'expected' values against which we test field data. The details of obtaining the expected values, and of testing the field data against them, are the subject of the next sections. Throughout, we shall use extinct mammal species as an example.

TESTING FOR SELECTIVITY

Suppose that our data consist of a list of G genera: for each genus g we know S_g, the number of species, and E_g, the number of extinctions. If there is no selectivity, all species will have the same probability of extinction. This probability, which we call e^*, we calculate as the total number of extinctions divided by the total number of species: $e^* = E_T/S_T = \sum E_g / \sum S_g$. For mammals over the last 400 years, $G = 1131$, $S_T = 4617$ and $E_T = 64$, so $e^* = 64/4617 \approx 0.014$.

After calculating e^*, we obtain an estimate of the expected *number* of extinctions from each genus if there is no selectivity: $\hat{E}_g = e^* S_g$. For a one-species mammal genus $\hat{E}_g = 0.014$, for a two-species genus $\hat{E}_g = 0.028$, and so on. To test for selectivity, we compare E_g, the observed number of extinctions, with $\hat{E}_g$. This is quite straightforward because $\hat{E}_g$ represents the mean of a binomial distribution. The probability of observing E_g extinctions from a genus containing S_g species where each species has an extinction probability of e^* is given by the general binomial formula

$$\Pr(E_g) = \frac{S_g!}{E_g!(S_g - E_g)!} e^{*E_g} (1 - e^*)^{(S_g - E_g)} \qquad (1)$$

If we observe more than the expected number of extinctions, we can test the significance of the observation. First we calculate the probability of obtaining *at least* the observed number (this represents the area under the right-hand tail of the distribution from three extinctions upwards). For example, the expected

number of extinctions from the 58-species mammal genus *Pteropus* (Pteropodidae—fruit bats) is $0.014 \times 58 \approx 0.8$. In fact there have been three extinctions from this genus of 'flying foxes'. The sum of the probabilities of obtaining three, four, . . . , fifty-seven or fifty-eight extinctions is 0.048.

If we observe less than the expected number of extinctions, the procedure is the same except that we calculate the area under the left-hand tail of the distribution. If we had observed zero extinctions from the genus *Pteropus*, we would simply calculate the probability of observing zero extinctions, which is 0.445.

Since the observed number of extinctions may be more *or* less than the expected number, we require a two-tailed test of significance. To obtain the probability of observing a number of extinctions that deviates as much or more *in either direction* from the expected number, we multiply the probabilities in the previous example by two. So for the observation of three extinctions $p = 0.096$, and for the hypothetical observation of zero extinctions, $p = 0.89$. The value of p at which we assign significance is, of course, arbitrary.

The above approach tells us which genera exhibit significantly more or less extinctions than expected. We might want, however, to classify the overall dataset as showing or not showing selectivity. The obvious approach is to use a chi-square test (or the related G test), but the rule of thumb in such tests is that the 'expected' value in any category should be greater than five (Sokal and Rohlf 1995). We have already shown that for mammals the expected number of extinctions from a one-species genus is only 0.014—we would only expect five

extinctions from a genus containing 360 species! This kind of overall test at the genus level is not possible. There are, however, alternatives.

One possibility is to combine genera into broader classes. There are many ways to accomplish this lumping: we could, for example, combine genera into higher taxonomic levels (such as families). In this paper we lump genera into size classes: we combine all one-species genera, all two-species genera and so on. Any kind of statistical test will now be addressing not selectivity by genus, but selectivity by genus *size*. We will show presently that this kind of selectivity is particularly important.

No matter how we lump genera in classes, the test for significance is the same as above. There are 525 one-species mammal genera, so the number of species in this size class is $525 \times 1 = 525$. There are 198 two-species mammal genera, so the number of species in this size class is $198 \times 2 = 396$. We analyze each size class just as we analyzed each genus above. The expected number of species extinctions from all one-species genera (in the absence of selectivity) is $525 \times 0.014 = 7.28$. The observed number is 12. The sum of the probabilities of observing 12, 13, . . . , 525 extinctions is 0.0655. Again assuming a two-tailed test, $p = 0.131$.

Another kind of overall test looks at the number of extinct *genera*. The probability that a genus will become extinct, ε_g, is the probability that all of its species will become extinct, which is given by e^{*S_g}. The expected number of genus extinctions from all mammals is $\sum \varepsilon_g = \sum e^{*S_g} = 7.32$. The observed number is 16.

Unfortunately, the distribution of probabilities for the observed number of genus extinctions is not easily obtained analytically. It is, however, easily obtained by numerical simulation. For mammals, we simply 'kill' 64 species at random, and count the number of genera which become exinct. Repeating this simulation 1000 times gives us a distribution for the expected number of genus extinctions. If (as with mammals) we observe more than this number, we calculate the significance of the observation as the proportion of simulations in which the number of extinctions is equal to or greater than the observed number, multiplied by two (for a two-tailed test). If we observe less than the expected number, we calculate the proportion of simulations in which the number of extinctions is equal to or less than the observed number (also multiplied by two). For extinct mammals, none out of 1000 simulations included 16 or more genus extinctions, so in this case $p < 0.002$ (and might be much less—we would only know by performing an even greater number of simulations).

SELECTIVITY IN THREATENED GENERA

We would also like to know if there will be selectivity in future extinctions. One method is to look at threatened species. Currently, 449 mammal and 1107 bird species are listed by the International Union for the Conservation of Nature (IUCN) in one of three categories of threat. The categories are different for birds and mammals, but in both cases they represent a decreasing scale of extinction probability. For each category, we analyse the selectivity as if all species in that category became extinct, using the same methods as above. We make one

additional assumption: that all of the species in categories of more severe threat are already extinct. Thus we start with a dataset from which we have already removed all species that are extinct or more threatened.

RESULTS

EXTINCT AND THREATENED MAMMALS

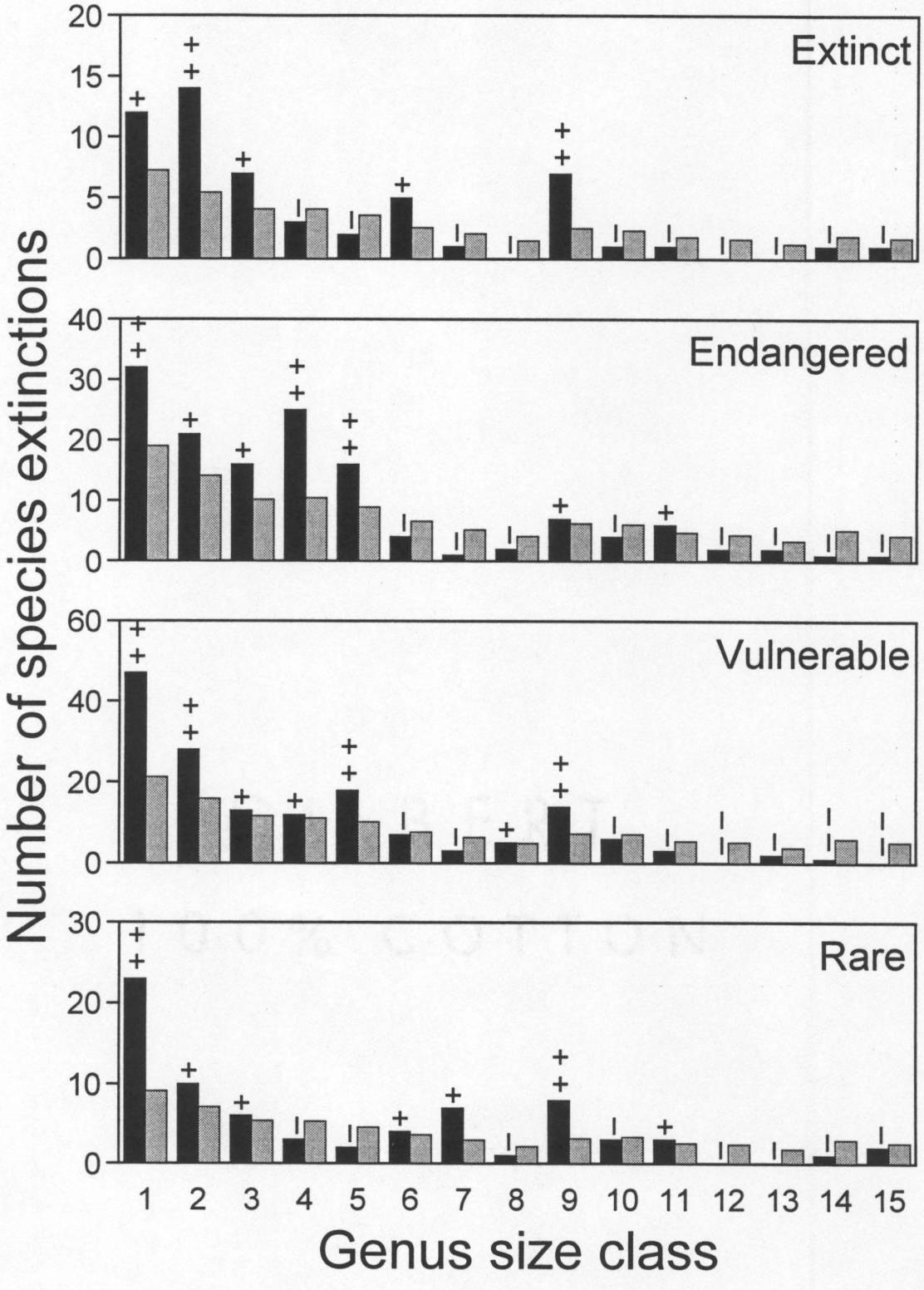
Table 1 summarises some of the results of our analyses of selectivity for mammals. For extinct and rare mammal species, 51% and 44% respectively of genera that contain extinctions contain significantly more or less extinctions than expected. For endangered and vulnerable mammal species the proportions are 19% and 17%. We conclude that there is a large degree of selectivity by genus in historical mammals, and some selectivity by genus in likely future extinctions. In every category, there are significantly more observed (or predicted) genus extinctions than we expect ($p < 0.002$ in every case).

Figure 2 compares the distribution of observed and expected numbers of species extinctions by size class for mammal genera with up to 15 species. Classes where there are more observed than expected extinctions are shown with a '+', classes where there are less observed than expected with a '–'. Values that are significant at $p < 0.05$ are indicated by '+ +' and '– –' respectively. It is clear that in every category, genera with more than the predicted number of extinctions tend to be found towards the left of the distribution—species extinctions are found more often than expected in genera with few species. So while the degree of selectivity

Table 1. Summary of the numerical results of an analysis of extinction selectivity for mammals.

	Extinct	Endangered	Vulnerable	Rare
Number of species remaining after removal of those that are extinct or more threatened	4617	4553	4386	4193
Number of species in this category	64	167	193	89
Number of genera remaining after removal of species that are extinct or more threatened	1131	1115	1077	1015
Number of genera containing extinctions	45	114	137	73
Number of genera containing significantly more extinctions than expected ($p < 0.05$)	23	21	22	32
Number of genera containing significantly less extinctions than expected ($p < 0.05$)	0	1	1	0
Proportion of genera containing extinctions that contain significantly more or less extinctions than expected	0.51	0.19	0.17	0.44
Expected number of additional genus extinctions	7.317	19.36	22.98	10.16
Observed number of additional genus extinctions	16	38	62	28
Significance of the observed number	$p < 0.002$	$p < 0.002$	$p < 0.002$	$p < 0.002$

Figure 2. The distribution of species extinctions within different size classes of mammal genera. The top graph is for historical extinctions. The other graphs assume that all the species in the designated category of threat become extinct (see text).


Extinct
Endangered
Vulnerable
Rare
Number of species extinctions
Genus size class
0
5
10
15
20
30
40
60
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

by genus varies among categories, there is always selectivity by genus size. Table 2 summarizes our findings for mammals.

EXTINCT AND THREATENED BIRDS

Table 3 summarizes some of the results of our analyses of selectivity for birds. For extinct bird species, 52% of genera that contain extinctions contain significantly more or less extinctions than expected. For critical, endangered and vulnerable bird species the proportions are 24%, 24% and 12%. We conclude that there is a large degree of selectivity by genus in historical bird extinctions, and a lesser degree in likely future bird extinctions. In the extinct category there are far more genus extinctions than expected. In all the categories of threat there are also more genus extinctions than expected, but the significance in the critical and endangered categories is borderline.

Figure 3 compares the distribution of observed and expected numbers of species extinctions by size class for bird genera with up to 15 species. Significance is indicated the same way as in Figure 2. In the extinct category, genera with more than the predicted number of extinctions are clearly found towards the left of the distribution. In the vulnerable category the same pattern is weak but discernible. In the other categories there is no pattern. Overall, there is less selectivity by genus size for threatened birds than for extinct birds. Table 4 summarizes our findings for birds.

Table 2. Summary of the observed selectivity in historical and likely future extinctions of mammal species.

	Extinct mammals	Endangered mammals	Vulnerable mammals	Rare mammals
Selectivity by genus?	Yes	Some	Some	Yes
Selectivity by genus size?	Yes	Yes	Yes	Yes
Significantly more genus extinctions?	Yes	Yes	Yes	Yes

Table 3. Summary of the numerical results of an analysis of extinction selectivity for birds.

	Extinct	Critical	Endangered	Vulnerable
Number of species remaining after removal of those that are extinct or more threatened	9770	9652	9484	9249
Number of species in this category	118	168	235	704
Number of genera remaining after removal of species that are extinct or more threatened	2070	2039	2017	1988
Number of genera containing extinctions	92	132	181	409
Number of genera containing significantly more extinctions than expected ($p < 0.05$)	52	32	45	48
Number of genera containing significantly less extinctions than expected ($p < 0.05$)	0	0	0	0
Proportion of genera containing extinctions that contain significantly more or less extinctions than expected	0.57	0.24	0.25	0.12
Expected number of additional genus extinctions	10.47	14.88	21.01	64.79
Observed number of additional genus extinctions	31	22	29	84
Significance of the observed number	$p < 0.002$	$p = 0.048$	$p = 0.068$	$p = 0.010$

Figure 3. The distribution of species extinctions within different size classes of bird genera. The top graph is for historical extinctions. The other graphs assume that all the species in the designated category of threat become extinct (see text).

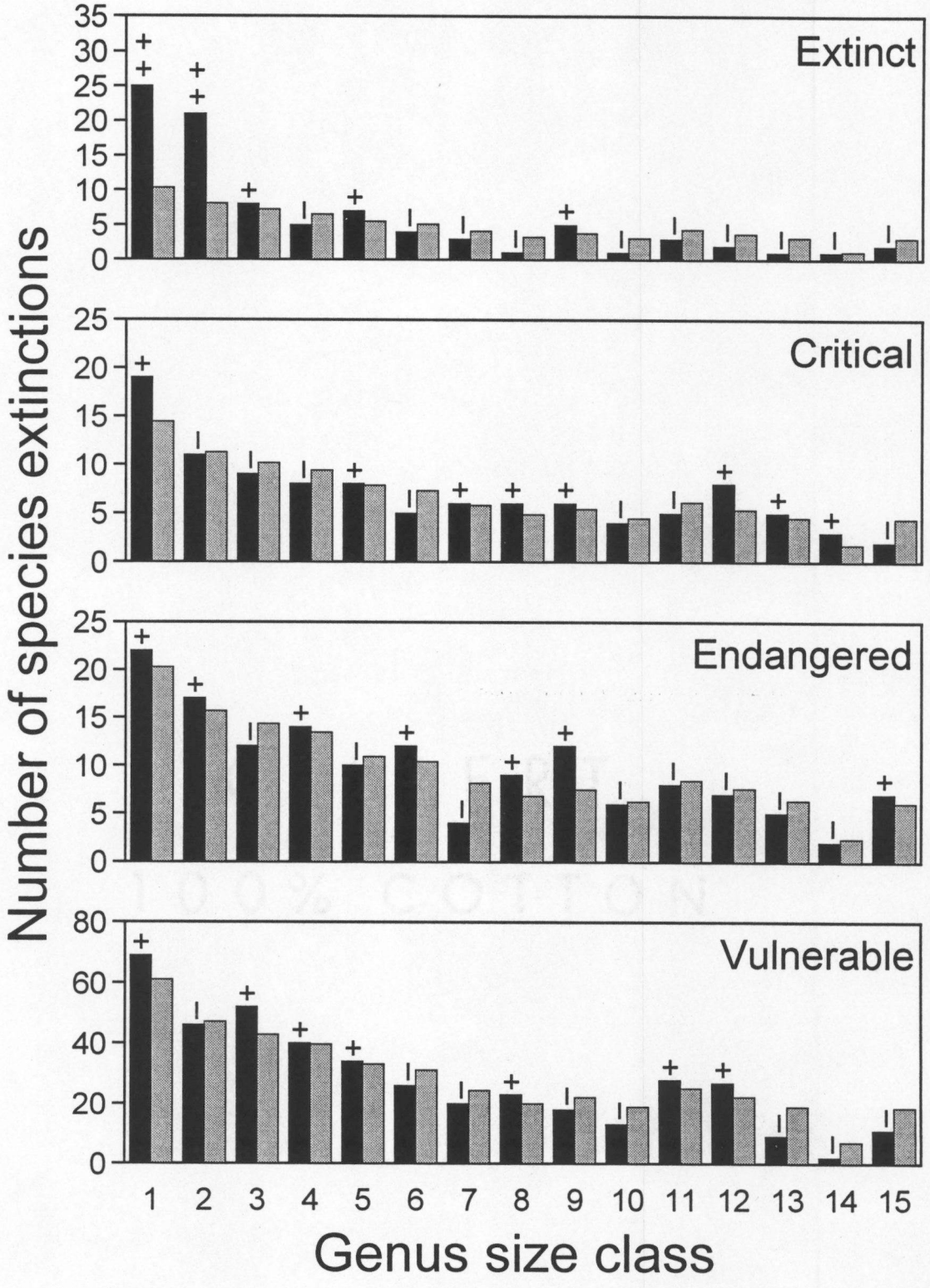

Extinct
Critical
Endangered
Vulnerable
Number of species extinctions
Genus size class
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

Table 4. Summary of the observed selectivity in historical and likely future extinctions of bird species.

	Extinct birds	Critical birds	Endangered birds	Vulnerable birds
Selectivity by genus?	Yes	Some	Some	Some
Selectivity by genus size?	Yes	No	No	Some
Significantly more genus extinctions?	Yes	Borderline	Borderline	Yes

PREDICTING FUTURE BIRD EXTINCTIONS

The categories of threat for birds are quantitative. Rather than performing our analyses on all the species in each category of threat, we can actually predict the number of bird extinctions at any given point in the future (Mace 1994). For a probability of extinction of x% in y years, the number of extinctions expected after z years for a category containing S species is

$$S\left(1-\left(1-\frac{x}{100}\right)^{\frac{z}{y}}\right) \qquad (2)$$

(This is a low estimate, since it is based on species which are threatened now and ignores future additions to the Red Lists.)

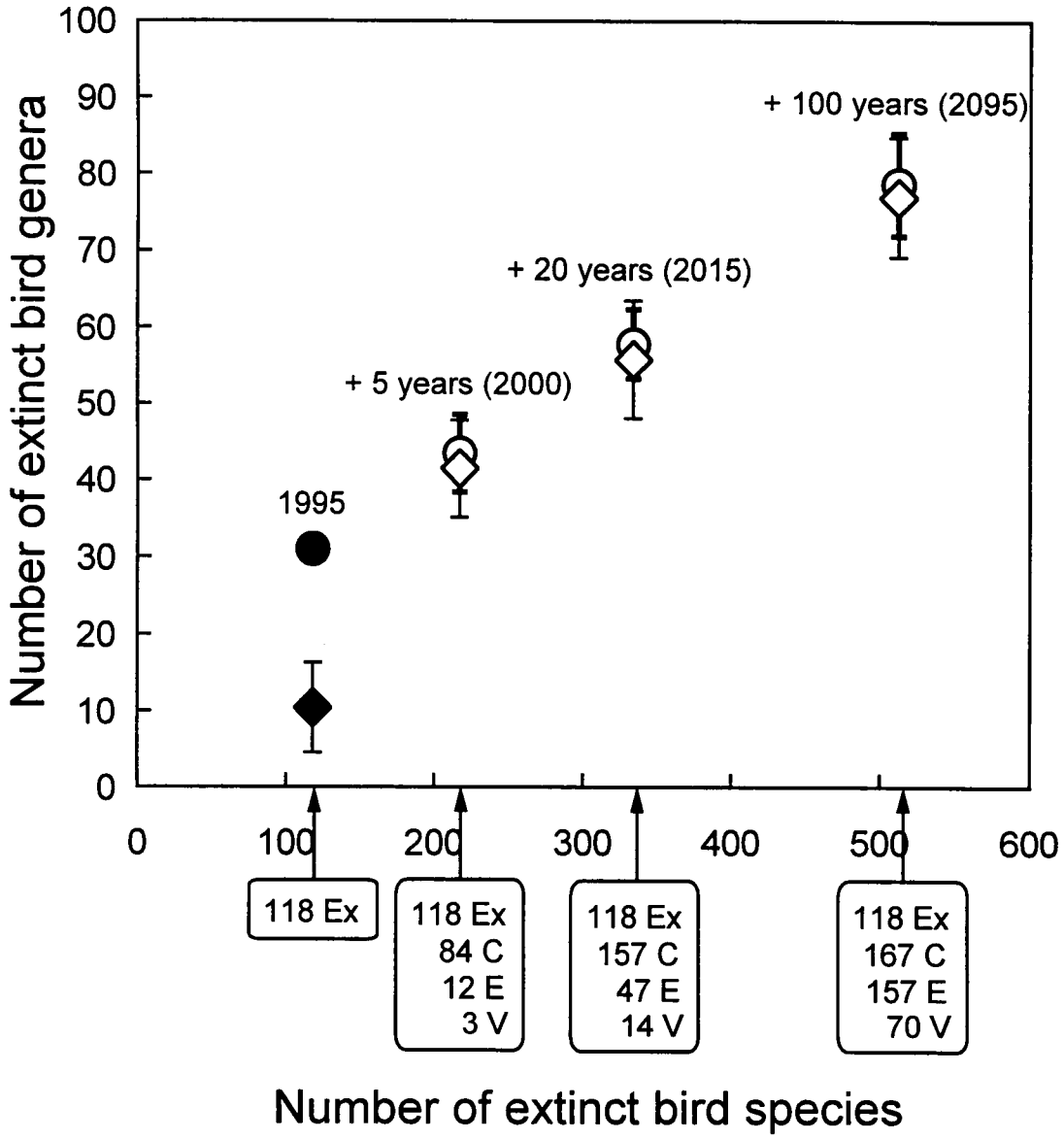
We performed another analysis of the bird data where we compared the overall number of expected genus extinctions under two scenarios: a) where predicted extinctions are random across all species, and b) where predicted extinctions are random within the set of species in a given category. We call these the 'all random' and the 'random within category' simulations respectively. For example five years into the future, according to equation 2, we expect 84 of the 168 critical species, 12 of the 235 endangered species and 3 of the 704 vulnerable species to be extinct, for a total of 99 species. Taking the 118 species and 31 genera known to be extinct, and assigning extinct status to an additional 99 species at random, we predict that 10.4 ± 6.4 additional genera will now be extinct, for a total of 41.4 ± 6.4 (the all random simulations). If we take the same 118 species and 31

genera and assign extinct status to 84 species at random within the set of all critical species, to 12 species at random within the set of all endangered species, and to 3 species at random within the set of all vulnerable species, we get an additional 12.4 ± 5.0 genera for a total of 43.4 ± 5.0 (the random within category simulations). This is not significantly different from the all random simulations.

Figure 4 (open points) shows these results, along with identical comparisons for 20 and 100 years into the future (when successively more species from each category are expected to be extinct, as given by equation 2 and shown at the bottom of the figure). Unlike historical extinctions (shown in Figure 4 as closed points), there are no significant differences between the all-random simulations and the within-category simulations. Whereas when we killed all the species in each category we observed a greater than expected number of additonal genus extinctions, when we kill just a random subset, the pattern disappears. Predicted future extinctions are distributed as we would expect if extinctions were random.

How can reconcile these results? The answer lies in the fact that for our first analyses, we removed all extinct or more threatened species before examining each category. The number of genus extinctions from that category will depend upon the distribution of remaining species within genera. For example, if genera that contain endangered species also tend to contain critical species, then, by the time we analyze the endangered category this genera will have been already reduced in size, and will therefore be more likely to disappear entirely. In the second analysis, of *predicted* extinctions, this 'cumulative' effect is reduced because not all species in each category are killed.

Figure 4. The actual number of extinct bird genera (solid circle) is higher than an expected value based on randomizing the distribution of extinct species (solid diamond). But simulated extinctions of bird species at three points in the future according to current threat categories (open circles) show no difference from a randomized expectation (open diamonds). Error bars show 95% confidence intervals for the simulations. The x-axis shows the number of contributing species from each threat category at each point in time (rounded down to the nearest integer).


Number of extinct bird genera
100
90
80
70
60
50
40
30
20
10
0
+ 100 years (2095)
+ 20 years (2015)
+ 5 years (2000)
1995
0
100
200
300
400
500
600
118 Ex
118 Ex
84 C
12 E
3 V
118 Ex
157 C
47 E
14 V
118 Ex
167 C
157 E
70 V
Number of extinct bird species

SELECTIVITY BY GENUS SIZE AND THE NUMBER OF GENUS EXTINCTIONS

Our three types of result are linked, because the overall number of genus extinctions depends both upon the degree of selectivity by genus, and upon the nature of any selectivity by genus size.

If there is no selectivity, the extinction probability for each species is e^*. Suppose that there is selectivity in a particular dataset, such that half the species have an extinction probability of $e^* + x$, and the other half have an extinction probability of $e^* - x$. The overall number of species extinctions will remain the same. Now consider two genera from this dataset that contain the same number of species ($S_1 = S_2 = S$). For one genus, the probability of extinction is $e^* + x$, and so ε_g, the probability of genus extinction, is $(e^* + x)^S$. For the other genus, the probability of its extinction is $(e^* - x)^S$. It is easy to show numerically that the increase in genus extinction probability for the first species, from e^{*S} to $(e^* + x)^S$, will be greater than the decrease in extinction probability for the second species, from e^{*S} to $(e^* - x)^S$. The overall expected number of genus extinctions in this example will therefore increase. If the distribution of $e^* + x$ genera and $e^* - x$ genera is random, then the overall expected number of genus extinctions from the whole dataset will also increase. Indeed, the result holds true for any set of genus-specific species extinction probabilities as long as the distribution of these probabilities among genera is random. So if there is selectivity by genus, we expect the number of overall genus extinctions to increase.

Even in the absence of selectivity, a small genus is more likely to become extinct than a large genus simply because of the number of species it contains. For this very reason, almost all genus extinctions in our data are of small genera. Now suppose that there is selectivity. If small genera contain species with a higher than average extinction probability, the increase in the number of small genera becoming extinct will be large. But if large genera correspondingly contain species with a lower than average probability, the decrease in the number of large genera becoming extinct will be negligable (since very few would become extinct anyway). So if there is selective extinction of species in small genera, we expect the number of genus extinctions to increase. Using the same argument, if there is selective extinction of species in large genera, the increase in the number of large genera becoming extinct will be small, but the decrease in the number of small genera becoming extinct will be large. The number of genus extinctions will decrease.

The data for mammals show both selectivity by genus and selective extinction of species in small genera (Table 2). In these cases the effects are reinforcing and we expect a large increase in the overall number of genus extinctions. Our data confirm our expectation. The data for birds show some selectivity by genus but only a limited tendency towards the extinction of small genera in future extinctions (Table 4). So this time we expect a small increase in the overall number of genus extinctions and again, our data confirm our expectation.

DISCUSSION

Disproportionate loss of higher taxa is not a new phenomenon—geological data suggest that prehistoric species extinctions of all magnitudes were concentrated within species-poor genera (McKinney 1995). To place our results in context, we first distinguish between two distinct types of selectivity.

CONTINGENT SELECTIVITY

Islands and archipelagos are often homes to endemic genera. In a typical scenario, an island or island group is colonized by one species. Isolated from its ancestral population, this species evolves, and if the island or island group contains a variety of habitats the species may also radiate. However many species eventually appear, all are now sufficiently different from their mainland relatives to be classified in a separate genus. There are many examples. In mammals, *Mesocapromys* (Capromyidae) is a genus of Hutia found only on Cuba. In birds, *Hemignathus* and *Paroreomyza* (Drepanididae) are genera of Honeycreepers endemic to parts of the Hawaiian archipelago. Carson (1987) provides a detailed overview of this effect.

Imagine two hypothetical islands. Each is in the Caribbean, and each is home to an endemic genus of mammal (perhaps rather like the Hutias). Under normal circumstances, the species in each genus have similar extinction probabilities. But, the Caribbean is subject to hurricanes. If a hurricane passes over either of the islands, all the species on that island will have, at least temporarily, a higher

probability of extinction. Now it may be that neither island is more likely than the other to be hit by a hurricane. And it may be that neither genus is better or worse than the other at surviving a hurricane. Nevertheless, the extinction probabilities of all the species in each genus are linked—they rise and fall together depending upon whether their island is in the path of a hurricane.

We call this effect *contingent* selectivity. It has nothing to do with the vulnerability of particular species to extinction. Rather, species in a genus share an extinction mechanism, usually by accident of geography. Of course, the mechanism need not be a hurricane. It might be a volcano on an island. For *Mesocapromys* Hutias, their 'hurricane' is habitat destruction. Habitat destruction has a negative effect on all Hutias, but on Cuba the destruction is particularly severe and so the entire genus *Mesocapromys* is in the front line.

PHYLOGENETIC SELECTIVITY

For real species, probability of extinction is influenced both by their environment and by their specific characteristics or 'traits' (such as rarity or body size: Gaston 1994). Some of these traits will be heritable, and species in the same genus are likely to share heritable traits. We therefore expect real species extinctions to be common in genera whose species share traits that increase their likelihood of extinction, and to be scarce in genera whose species share traits that make them more likely to survive.

Unlike with contingent selectivity, we are proposing that species in a genus might share traits which make *each species* more prone to extinction. In our hypothetical hurricane example, species in one of the genera might have inherited a trait from their common ancestor that allows them to survive hurricanes (perhaps the ability to burrow). If both islands are affected by the same hurricane, there will be no contingent selectivity. Nevertheless, species in the genus whose members share a burrowing trait will be less prone to extinction than species in the other genus. We call this *phylogenetic* selectivity. Human causes of extinction can be phylogenetically selective. Of 16 species in the genus *Gazella* (Cervidae) one is extinct and nine are threatened, largely because Gazelle species share characteristics that make them tempting food for humans.

If hurricanes affect just one island at a time *and* species in two genera differ in their ability to burrow, then there will be both contingent *and* phylogenetic selectivity. We distinguish them to try to understand the origin of selectivity by genus size. Contingent selectivity will tend to affect genera that are endemic to a small area, because it requires that the same extinction mechanism affect the entire genus. The more restricted the area occupied by the genus, the more likely that its species' extinctions will be contingent. In general, genera with highly restricted distributions tend to contain few species, simply because a small area is unlikely to contain the environmental heterogeneity necessary for speciation. So contingent selectivity is most likely to affect small genera. Phylogenetic selectivity describes the influence of heritable traits on extinction probability, and there is no reason to expect a correlation with genus size.

THE NATURAL HISTORY OF EXTINCTIONS

Historical data on both birds and mammals show selective extinction of species-poor genera. The natural history of these extinctions provides an explanation. Most were of island endemics (King 1985)—the extinct Dodo, *Raphus cucullaris* (Raphidae), is a famous example. We have seen that small, isolated island populations tend to evolve rapidly into distinct forms which are then placed in new higher taxa that often contain only one or a few species. Another example is the Solomon Island Crowned-pigeon, *Microgoura meeki* (Columbidae), considered different from its cousins in the genus *Goura* and the victim of introduced cats and dogs. There is a large element of contingent selectivity in such extinctions—if a multi-species genus disappears, it is partly because the species are all found in a small, isolated area (recall the example of the Cuban Hutias). At the same time there is some phylogenetic selectivity. The genus *Raphus* is extinct not just because the Dodo was its only representative, but because Dodos were flightless and unafraid—traits which had evolved because of their isolation on a predator-free island. But it is the contingent selectivity which gives small genera an unusually high probability of extinction and causes a larger-than-expected overall number of genus extinctions.

Our data suggest that future mammal extinctions will exhibit the same pattern, presumably for the same reasons. They also suggest, however, that future bird extinctions will show a marked reduction in selectivity by genus size (and perhaps its elimination altogether). There are three possible explanations. Firstly, mechanisms that target species-poor genera (such as introductions of exotic

species to islands) might be decreasing. While this is an encouraging interpretation, evidence for continuing introductions (King 1985) rules it out. Secondly, so many species-poor genera might already be lost that this kind of selectivity is no longer possible. This less encouraging interpretation must be true to some extent, since all of the 31 genera already lost were mono-specific, that is, species-poor. However, 832 monospecific genera remain. Furthermore, previously species-rich genera that have lost most, but not all of their species will add to this number. So already-lost genera cannot be the primary cause of reduced selectivity. The remaining possibility is that in the future, introduced species will joined by another extinction mechanism—one that does not discriminate between large and small genera.

For most bird species recently listed as threatened, the source of threat is large-scale habitat destruction (Bibby 1994; Collar et al. 1994). Habitat destruction is therefore the main candidate for a new, non-selective cause of future bird extinctions. For example, of eleven Hornbills in the genus *Aceros*, spread over much of Asia, seven are threatened by habitat destruction (Collar et al. 1994.) Habitat loss may even be focused on *mainland* centres of endemism (ICBP 1992; Balmford and Long 1994)—it is responsible for the threatened status of 60 bird species from the Endemic Bird Areas (EBA's) of Brazil's Atlantic forests (Brooks and Balmford 1996).

Since no species, not matter how robust, can withstand complete removal of its habitat, habitat destruction cannot be phylogenetically selective. Rather, it is contingently selective, as the Cuban Hutias demonstrate. Earlier, we argued that

contingent selectivity is most likely to affect localized, and therefore species-poor genera. But the kind of habitat destruction occurring now is different—it is becoming more widespread and diffuse. A good example is provided by the patterns of deforestation that follow human expansion into the Amazon region. The more widespread the destruction, the less that its contingent nature will be restricted to small, endemic genera. Increasingly, large, widespread genera (such as the Hornbills) are finding all of their species threatened. The Red List for birds is evidence not only of an increase in habitat destruction, but of a change in its nature.

It remains to ask why likely future extinctions of mammals show no similar decrease in the selectivity by genus size. Is it that mammals are less affected than birds by habitat destruction? Again, examples like the Hutias suggest otherwise. We suspect that the difference may be traced to a bias in the mammal data that is less prevalent in the bird data. All Red List data display 'selectivity of study'. Researchers tend to focus their efforts on species within a particular genus. It requires a certain amount of study before a species can be listed as threatened, so intensively studied genera are more likely to contain listed species. It might simply be the case that mammal researchers have tended to study small mammal genera the most intensively—they provide a manageable unit and tend to be found in a small area. Selectivity of study in birds is much less because the enormous number of amateur bird-watchers around the globe mean that even large, widespread genera are studied closely.

Since selectivity of study would look very much like selectivity of species-poor genera, we reserve judgement on the mammals. Publication of the next Red List for mammals, with new species listed and new criteria similar to those currently used for birds, will give us a better idea of whether mammals truly differ from birds in term of extinction patterns. Until then, conservation strategies must address a disproportionate loss of small genera (ICBP 1992, Vane-Wright et al. 1991), *and* the emergence of widespread, diffuse habitat destruction as an extinction mechanism from which no genus is safe.

ACKNOWLEDGMENTS

We thank J. H. Brown, E. Funazaki, J. L. Gittleman, B. A. Maurer, K. C. Norris, S. L. Pimm and B. Rashleigh for advice and comments. GJR and TMB were supported in part by the Pew Foundation Program for Scholars in Conservation and the Environment (through S. L. Pimm). MLM was supported by National Science Foundation grant EAR–9316417.

REFERENCES

Atkinson, I. (1989) Introduced animals and extinctions. *Conservation for the Twenty-First Century* (eds. Western, D. and M. Pearl), pp. 54–69. Oxford University Press, New York, NY.

Balmford, A. and A. Long (1994) Avian endemism and forest loss. *Nature* **372**:623–624.

Bibby, C. J. (1994) Recent past and future extinctions in birds. *Philosophical Transactions of the Royal Society of London B* **344**:35–40.

Brooks, T., and A. Balmford (1996) Atlantic forest extinctions. *Nature* **380**:115.

Carson, H. L. (1987) Colonization and speciation. *Colonization, Succession and Stability* (eds. Gray, A. J, M. J. Crawley and P. J. Edwards) pp. 187–206. Blackwell Scientific, Oxford.

Collar, N. J., M. J. Crosby and A. J. Stattersfield (1994) *Birds to Watch 2: The World List of Threatened Birds*. BirdLife International, Cambridge.

Heck, K. L., Jr., G. van Belle and D. Simberloff (1975) Explicit calculation of the rarefaction diversity measurement. *Ecology* **56**:1459–1461.

Gaston, K. J. (1994) *Rarity*. Chapman and Hall, London.

Groombridge, B., ed. (1993). *1994 IUCN Red List of Threatened Animals*. IUCN, Gland.

ICBP (1992) *Putting Biodiversity on the Map: Priority Areas for Global Conservation*. International Council for Bird Preservation, Cambridge.

King, W. B. (1985) Island birds: will the future repeat the past? *Conservation of Island Birds* (ed. Moors, E. J.) pp. 3–15. International Council for Bird Preservation Technical Publication No. 3, Cambridge.

Lovejoy, T. E. (1980) *The Global 2000 Report to the President, vol. 2*. Council on Environmental Quality, Washington DC.

Mace, G. M. (1994) Classifying threatened species: means and ends. *Philosophical Transactions of the Royal Society of London B* **344**:91–97.

May, R. M. (1990) Taxonomy as destiny. *Nature* **347**:129–130.

McKinney, M. L. (1995) Extinction selectivity among lower taxa: gradational patterns and rarefaction error in extinction estimates. *Paleobiology* **21**:300–313.

Myers, N. (1979) *The Sinking Ark: A New Look at the Problem of Disappearing Species*. Pergamon Press, Oxford.

Pimm, S. L., G. J. Russell, J. L. Gittleman and T. M. Brooks (1995) The future of biodiversity. *Science* **269**:347–350.

Raup, D. M. (1979) Size of the Permo-Triassic bottleneck and its evolutionary implications. *Science* **206**:217–218.

Raven, P. H. (1988) Our diminishing tropical forests. *Biodiversity* (eds. Wilson, E. O. and F. M. Peter) pp. 119–122. National Academy Press, Washington, DC.

Reid, M. V. (1992) How many species will there be? *Tropical Deforestation and Species Extinction* (eds. Whitmore, T. C. and J. A. Sayer) pp. 55–73. Chapman & Hall, London.

Sanders, H. L. (1968) Marine benthic diversity: a comparative study. *American Naturalist* **102**:243–282.

Sibley, C. G. and A. E. Ahlquist (1990) *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, Newhaven, CI.

Sibley, C. G. and B. L. Monroe, Jr. (1990) *Distribution and Taxonomy of Birds of the World*. Yale University Press, Newhaven, CI.

Sibley, C. G. and B. L. Monroe, Jr. (1993) *A Supplement to Distribution and Taxonomy of Birds of the World*. Yale University Press, Newhaven, CI.

Simberloff, D. (1972) Properties of the rarefaction diversity measurement. *American Naturalist* **106**:414–418.

Sokal, R. R. and F. J. Rohlf (1995) *Biometry* (3rd. ed.). W. H. Freeman, New York.

Smith, F. D. M., R. M. May, R. Pellew, T. H. Johnson and K. S. Walter (1993) Estimating extinction rates. *Nature* **364**:494–496.

Stattersfield, A. J., M. J. Crosby, A. J. Long and D. C. Wege. In press. *A Global Directory of Endemic Birds Areas*. BirdLife International, Cambridge.

Vane-Wright, R. I., C. J. Humphries and E. H. Williams (1991) What to protect?—systematics and the agony of choice. *Biological Conservation* **55**:235–254.

Wilson, D. E., and D. M. Reeder, eds. 1993. *Mammal Species of the World, a Taxonomic and Geographic Reference* (2nd. ed.). Smithsonian Institution Press, Washington, D.C.

Wilson, E. O. (1988) The current state of biological diversity. Biodiversity (eds. Wilson, E. O. and F. M. Peter) pp. 3–18. National Academy Press, Washington, DC.

World Conservation Monitoring Centre (1992) *Global Biodiversity: Status of the Earth's Living Resources*. Chapman and Hall, London.

VITA

Gareth Russell was born in Reigate (Surrey, England) on 31st. July, 1970. He spent his years of primary education in Birmingham and Manchester, eventually moving to Buckinghamshire where he spent his secondary education at the Royal Grammar School, High Wycombe. In 1988 he completed his studies and departed for Australia on an eleven-month sojourn before beginning university.

From 1989 to 1992, Gareth was an undergraduate at New College, Oxford. He applied to Oxford because of its respected undergraduate courses in biology, and to New College because of his desire to be tutored by Richard Dawkins, who was (and at the time of writing still is) a member of the College. Gareth spent three years soaking up the academic atmosphere and certain amount of biological knowledge, graduating with an 'upper second class honours' Bachelor of Arts degree in 1992.

During his time at Oxford, Gareth's main interest shifted from evolutionary biology to ecology. He attributes this to the 'less developed' state of ecological research, and its concomitant potential for new discoveries and theoretical development. Gareth's particular interest was in community ecology, and after graduation he proceeded immediately to the (then) Department of Zoology at the University of Tennesse to study for a Ph.D. under the instruction of Stuart Pimm. As well as the research described in this dissertation, Gareth spend time doing fieldwork in the cloud forests of Maui and in Everglades National Park.

At the time of submission of this dissertation, Gareth is waiting to take up a two-year post-doctoral position that is based at the National Center for Ecological Analysis and Synthesis in Santa Barbara, but which involves spending four months per year at the Centre for Population Biology in Silwood Park, England. Over the next few years he hopes to combine theoretical models of extinction and colonization with the development of a long-term program of field research based in the islands of Chile.

Gareth is a member of the Ecological Society of America.