

Breeding birds on small islands: island biogeography or optimal foraging?

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Summary

1. We test MacArthur and Wilson's theory about the biogeography of communities on isolated habitat patches using bird breeding records from 16 small islands off the coasts of Britain and Ireland.

2. A traditional examination of patterns of species richness on these islands suggests that area and habitat diversity are important predictors, but that isolation and latitude have a negligible impact in this system.

3. Unlike traditional studies, we directly examine the fundamental processes of colonization and local extinction (cessation of breeding), rather than higher-order phenomena such as species richness.

4. We find that many of MacArthur and Wilson's predictions hold: colonization probability is lower on more isolated islands, and extinction probability is lower on larger islands and those with a greater diversity of habitats.

5. We also find an unexpected pattern: extinction probability is much lower on more isolated islands. This is the strongest relationship in these data, and isolation is the best single predictor of colonization and extinction.

6. Our results show that examination of species richness alone is misleading. Isolation has a strong effect on both of the dynamic processes that underlie richness, and in this system, the reductions in both colonization and extinction probability seen on more distant islands have opposing influences on species richness, and largely cancel each other out.

7. We suggest that an appropriate model for this system might be optimal foraging theory, which predicts that organisms will stay longer in a resource patch if the distance to a neighbouring patch is large. If nest sites and food are the resources in this system, then optimal foraging theory predicts the pattern we observe.

8 We advance the hypothesis that there is a class of spatial systems, defined by their scale and by the taxon under consideration, at which decision-making processes are a key driver of the spatiotemporal dynamics. The appropriate theory for such systems will be a hybrid of concepts from biogeography/metapopulation theory and behavioural ecology.

Key-words: colonization, extinction, foraging, species–area, turnover.

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Introduction

In this paper we test many aspects of MacArthur & Wilson's (1963, 1967) equilibrium theory of island biogeography, using data on the breeding populations of terrestrial birds on 16 islands off the coasts of Britain

and Ireland. The species–area effect, wherein larger areas tend to contain more species than smaller areas, was first observed over 80 years ago (Arrhenius 1921). Subsequent studies (e.g. Mayr 1940; Williams 1943; Ripley 1944; Darlington 1957) confirmed it as one of the strongest empirical patterns in ecology. Explanations for the effect are numerous and continually debated. There are basically two kinds. The first invoke sampling and other ‘geometric’ effects (e.g. see Discussions in Rosenzweig 1995 and Storch, Šizling & Gaston 2003). For example, if species are distributed in a uniform, random manner across a landscape, then a subset of that area is unlikely to contain representatives of all the rarer species. The smaller the area sampled, the fewer species it is likely to contain. The effect is enhanced by the presence of species at low density, and it is another long-standing observation that in the majority of studied assemblages of species, most species occur at relatively low density (e.g. Preston 1948). Another example is Williams’ (1964) proposal that larger islands contain a greater diversity of habitats. Lack (1969, 1976) tested this idea for bird species on oceanic islands, concluding that species richness is determined by the islands’ ‘ecological poverty’, a measure of the number of habitats, or perhaps ecological niches, available for colonizing species to exploit.

The second kind of explanation for species–area effects invokes population dynamics. Preston (1962a,b) took a particular sampling model and added to it the concept of a minimum viable population size, in the form of a lower bound on the allowable abundance of species in the model. This implicit acknowledgement of population extinction was quickly followed by MacArthur & Wilson (1963, 1967). They proposed a model to explain the number of species on islands that explicitly invoked both population colonization and extinction. Their novel suggestion was that isolated communities can be understood as a dynamic equilibrium between colonization and extinction processes. In its classic form, the model predicts that the number of species will not only increase with the area of an island (the species–area effect), but also decrease with its distance from a source of colonizing species (the species–distance effect). Another feature of the MacArthur and Wilson model is that it predicts community turnover (i.e. change in composition over time; Diamond 1969; Power 1972; Hunt & Hunt 1974; Lynch & Johnson 1974; Jones & Diamond 1976; Schoener 1983; Russell *et al.* 1995), and further predicts that turnover will decrease with both area and distance. This model and its set of predictions are often collected under the term ‘Island Biogeography Theory’ (IBT).

There is continuing debate over the appropriateness of different island biogeographical models. In our view, the main reason for this is that most of the available data are on the number of species in patches (‘islands’) of different areas. A plot of log (number of species) against log (area) is usually approximately linear, which implies a relationship of the form $S = cA^z$ where c and

z are constants. Unfortunately, most models predict either this form exactly, or one that is very similar over the typically encountered range of data.

A partial solution is provided by common sense. If data are from a homogeneous landscape, then models that invoke discrete, isolated communities are clearly inappropriate. If the data are from discrete islands or habitat patches, it is more difficult to eliminate explanations, because the sampling effect nearly always applies in addition to any other phenomena. But if the data are from discrete islands that host small populations of mobile organisms, then the model of MacArthur and Wilson is an obvious candidate. The data we will present here, on the presence and absence of breeding populations of birds on various islands off the coasts of the United Kingdom and the Republic of Ireland, are of exactly this form.

A second and more powerful solution to the problem of testing competing explanations for biogeographical patterns is to test (1) their assumptions, and (2) the full range of their predictions. This is rarely done, perhaps because the appropriate data are hard to come by. In this paper we will use the remarkable extent and quality of the British and Irish island bird data to directly test MacArthur and Wilson’s model, in terms of both its underlying assumptions about colonization and extinction, and its predictions about species richness and turnover. Our results will show that a number of the relationships proposed by their model are present, but there is another, unexpected relationship that is very strong and that dominates biogeographical patterns. Specifically, we find that extinction probability decreases with increasing isolation from the mainland, and that this is the strongest of all the relationships. It is enough to cause species incidence (and by extension, species richness) to increase not only with area, but also (slightly) with isolation. We suggest that the relative mobility of birds makes colonization and, in some cases, extinction, largely a matter of choice. (As defined here, extinction can be the result of individuals simply choosing not to breed, or leaving.) In such cases, optimal foraging theory, which predicts longer persistence times in isolated patches, might provide a more suitable model.

Methods

THE ISLANDS

Our study locations are 16 offshore islands of the United Kingdom and the Republic of Ireland, shown on Fig. 1, for which biogeographical data are given in Table 1. Our study organisms are terrestrial bird species, including those that make use of small freshwater habitats. So, we exclude ducks, gulls, diving birds and shorebirds, but include grey heron *Ardea cinerea*, bittern *Botaurus stellaris*, kingfisher *Alcedo atthis* and dipper *Cinclus cinclus* (see Appendix for list of all species included in this study).



Fig. 1. Map of the United Kingdom and Republic of Ireland, showing the locations of the islands in this study. Dashed lines indicate the areas from which local species pools for different islands are drawn. These are the mainland coastal regions nearest to the islands in question, and species are included based on their ‘use’ of the area in question (*sensu* Gibbons, Reid & Chapman 1992) during the period for which data on the relevant islands is available. Usage is based in part on the two atlases by Sharrock (1976) and Gibbons *et al.* (1992), and in part on previous research by one of us (Reed 1981a,b). In most cases, the interior limit to the pool region is provided by a topographic feature, such as a range of mountains, which is known to affect the composition of the bird community or to provide a barrier to dispersal. Examples are shown in the figure. Species pools also include long-distance migrants as appropriate, although most are already included in the local pools because the definition of ‘use’ includes stopovers by migrants. Given the limitations of the available data, there is inevitably some subjectivity in assigning species to pools – see Results for an analysis of the impact of different assumptions.

Previous studies have suggested five main factors that affect species richness and community dynamics on islands: area, isolation, habitat complexity, latitude and ‘pool size’ (the number of species with a reasonable chance of reaching the islands). For some of these, the best way to measure the factor is unclear. The most important measure of isolation might be the distance to the nearest ‘mainland’ (Great Britain or Ireland), or it might be the distance to the nearest larger island (especially if the species composition of the islands tends to be nested, whereby species-poor islands have a subset of the species found on more species-rich islands). At least two measures of habitat complexity are commonly used: the number of identifiable habitat types (from a predetermined classification), and the complexity of the most complex habitat type (on an arbitrary scale). We quantified the following measures (notation refers to the headings of Table 1):

- Latitude, Longitude. In decimal degrees. Positive values are North and East, respectively.
- Area (a). Total area above high tide line, in hectares, estimated from 1 : 2500 Ordnance Survey maps and gazetteers.
- Distance to mainland (d_m). Measured as the shortest distance in kilometres from the island shore to the nearest mainland shore (Britain, Northern Ireland or the Republic of Ireland). Some islands are so close to the mainland that they are separated by a narrow channel that fluctuates in width with the tides. In those cases an ‘average’ separation was estimated, based on high and low tide marks and direct observation.
- Distance to nearest larger island (d_n). Measured as the shortest distance in kilometres from the island shore to the nearest landmass in the direction of the mainland that is at least the size of the island in question. If there is no such island, distance to the mainland is used.

Table 1. Biogeographical data for the islands in this study. See text for fuller descriptions

Name	Lat.	Long.	Area	d_m	d_n	H_c	H_r	Pool	P	P_{JMD}
Bardsey	52.77	-4.80	180	3.0	3.0	8	19	4	95	132
Calf of Man	54.05	-4.83	249	53.0*	0.5†	9	18	4	95	132
Cape Clear	51.43	-9.50	639	3.5*	3.5	7	20	3	77	105
Copeland	54.67	-5.52	32	1.5*	1.5	8	11	3	77	132
Fair Isle	59.53	-1.65	765	119.5	40.3‡	5	19	1	96	147
Farne Islands¶	55.62	-1.65	29	2.4	2.4	5	7	7	97	123
Handa	58.37	-5.20	310	0.3	0.3	5	18	2	94	130
Havergate	52.08	1.55	1108	0.2	0.2	6	11	6	97	164
Hilbre	53.38	-3.23	7	0.02	0.02	7	12	4	95	132
Isle of May	56.18	-2.57	49	7.5	7.5	6	11	7	97	123
Isles of Scilly¶	49.92	-6.33	1640	40.5	40.5	11	26	5	103	164
Lundy	51.17	-4.67	452	18.0	18.0	10	21	5	103	164
Scot Head	52.98	0.70	334	0.05	0.05	4	9	6	97	164
Skokholm	51.70	-5.27	97	3.5	3.5	5	15	5	103	164
Skomer	51.75	-5.28	292	0.6	0.6	7	18	5	103	164
Steep Holm	51.35	-3.18	19	5.0	5.0	5	8	5	103	164

Area: measured in ha. d_m : Distance to the mainland, in km. d_n : Distance to the nearest island, in km. H_c : Complexity of most complex habitat type, on a scale of 1–12. H_r : Number of distinct habitat types. Pool: Species pool – see Fig. 1 for locations corresponding to codes. P , P_{JMD} : Number of species in pool, according to different criteria – see text for details. *Nearest mainland is Ireland. †Nearest larger island is the Isle of Man. ‡Nearest larger island is Sanday in the Orkney Islands. ¶These are compact groups of islands that are treated as a single island in this analysis, largely because breeding bird information is frequently aggregated over all the islands.

- Habitat complexity (H_c). The complexity and height of the most complex habitat type on a scale of 1–12, where 1 indicates a barren island; 3, scattered clumps of grass and herbs; 6, scattered shrubs; 9, scattered trees; and 12, a large area of unbroken woodland.
- Habitat richness (H_r). The number of distinct habitat types, tabulated by Reed (1981b) using Fuller's (1974) habitat classification.
- Pool size (P). The number of terrestrial bird species considered to be candidates for breeding on a given island. We used two, nested definitions of candidate species in this study. The first type of pool for an island includes all species found breeding in the nearest adjacent region of the mainland. This definition has been used previously by JMD (Diamond & May 1977). The second type of pool is a subset of the first, in that it we also eliminate species that have never been known to travel over water to any island in the general vicinity of the island in question. This definition has been used previously by TMR (Reed 1981a,b). Figure 1 shows the pool regions, and Table 1 shows the sizes of the pools according to both definitions. All numerical results in this paper are based on definition 2 above, as is the list of pool compositions in the Appendix. Using the first, larger definition has little impact on our results.

In our statistical analysis we log-transform the raw area and distance measures, which range over a few orders of magnitude and have a right-skewed distribution. In addition, both theory and data suggest that the relationships between higher order variables such as species richness with area and isolation are often well-described by a power form, so log-transforming helps to linearize relationships and improves residual distribution. For the other predictor variables there is no need to log-transform on distributional grounds, and

the statistical models we will present fit slightly better without transformation. For simplicity, notation using capitals for area (A) and distance (D_m , D_n) will henceforward refer to the log-transformed variables, even when not explicitly stated.

Particularly if we include the alternative measures, there is a large amount of collinearity between some of the variables. Much of this is expected: (1) only three of the islands are closer to a larger island than to the mainland (for the others, the two distance measures are identical); (2) the two habitat measures are clearly related, as the more habitat types are present, the greater the likely maximum complexity; (3) both habitat measures are expected to be positively related to island area; and (4) the latitudinal gradient of species diversity predicts that pool size will decrease with increasing latitude, as should any measure of habitat diversity. In addition, pairs of variables for which there is no expected causal relationship may show some correlation by chance, a problem that is exacerbated at small sample sizes.

Table 2 shows the correlation matrix of the predictor variables (with the exception of longitude, which is provided to assist in locating the islands, but not used in any analyses). All the expected relationships are present: both habitat measures are positively correlated with each other and with pool size, and negatively with increasing latitude. Habitat diversity is also positively related to area. The two distance measures are also strongly positively correlated. Most likely due to chance, distance is correlated positively with area. Finally, we note the medium-strength, positive association between any measure of habitat diversity and any measure of distance; this relationship will be important in interpreting our results. Our statistical methods will take these correlations into account.

Table 2. Correlation matrix of predictor variables. Correlations for which a relationship is expected are shown in bold

	<i>L</i>	<i>A</i>	<i>D_m</i>	<i>D_n</i>	<i>H_c</i>	<i>H_r</i>
<i>A</i>	0.06					
<i>D_m</i>	0.27	0.42				
<i>D_n</i>	0.14	0.37	0.88			
<i>H_c</i>	-0.31	0.31	0.44	0.36		
<i>H_r</i>	-0.11	0.66	0.50	0.47	0.67	
<i>P</i>	-0.53	-0.32	-0.30	-0.18	-0.10	-0.10

THE INFLUENCES OF POOL SIZE AND RARE SPECIES

There is currently no standard method of assigning species pools in biogeographical studies, and we believe that our method makes intuitive sense. However, in order to evaluate the potential effect of our method on our results, we duplicated our analyses a number of times using alternative pool definitions. In addition to the larger pool lists described above, we performed analyses in which Bardsey was in Pool 5, in which Copeland was part of a large, Irish pool with Cape Clear, and in which Fair Isle had its own, smaller pool of 50 species, drawn largely from species found in the Shetland Isles. We also note that some of the pools include rare species such as hoopoe *Upopa epops*, wryneck *Jynx torquilla* and short-toed lark *Calandrella brachydactyla*. These are included because they were present, albeit in small numbers, in various pool regions during the time periods for which the relevant island data are available. To test whether the inclusion of these rarities has a substantial impact on our results, we also repeated all analyses with them removed.

RECORDS OF BREEDING OF TERRESTRIAL BIRD SPECIES

Our data consist of records of breeding terrestrial species on 16 of the small islands of the United Kingdom and the Republic of Ireland (for other studies of this system see Reed 1981a,b, Pimm *et al.* 1993; Russell *et al.* 1995). Some of these data are in the form of abundances (number of nests or breeding 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 are converted to presence/absence data where necessary. There are four reasons why the data used in this paper are of unusually high quality.

1. Some of these islands have permanent or semipermanent bird observatories, and the others are censused frequently and thoroughly.
2. Most of the islands are small enough that the entire area can be searched many times in a breeding season.
3. Breeding pairs are relatively conspicuous because

the birds return repeatedly to the same location, and because males often exhibit territorial behaviour.

4. Amateur birdwatchers, who collected much of the data here, typically put more effort into finding rarer species. While this tendency can introduce systematic bias into estimates of abundance, it is beneficial when estimating presence or absence.

These data were 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 in the region. We select a subset of 16 islands, including the 13 analysed by Russell *et al.* (1995), because they have long census records.

COLONIZATION AND EXTINCTION AS THE BASIS FOR ISLAND BIOGEOGRAPHIC PATTERNS

According to MacArthur and Wilson's conceptual model, variation in island measures such as species richness is the result of variation in underlying dynamic processes of colonization and extinction, and in the availability of species to colonize the islands (the size of the species pool). We note that some measures, such as species richness, apply only to an entire community, whereas others, such as colonization rate, apply naturally to individual species, but can also be applied to a community as a mean or otherwise aggregated rate. We also note that in this study, presence on an island means breeding presence. Absence of breeding does not necessarily mean absence of individuals. Stracey *et al.* (in prep.) show that many species spend time on these islands without breeding, and examine the relationship between the appearance of a species on an island (the 'immigration' envisioned by MacArthur and Wilson) and the beginning of a breeding population (the 'colonization' of this paper). Here we explain each of the variables as it applies to one island.

Fundamental variables

- Pool size, *P*: See earlier definition.
- Colonization probability, λ_i : The probability that a breeding population on an island, if absent in year *t*, will be present in year *t* + 1. May be applied at the community level by treating all data as if belonging to one species (*sensu* Clark & Rosenzweig 1994).
- Extinction probability, μ_i : The probability that a breeding population on an island, if present in year *t*, will be absent in year *t* + 1. Note that in this case we mean only that the existing individuals disappear. They may or may not be replaced immediately by colonizing individuals (the rescue effect). May also be applied at the community level as per colonization probability.

Derived variables

- Observed extinction probability, δ_i : this is the probability of a breeding presence being followed by

Table 3. Fundamental and higher-order island biogeographic variables. The derivation of higher-order variables from the fundamental variables λ_1 , μ_1 and P is shown, as well as their method of direct calculation. The calculation formulas refer either to a single year or pair of sequential years. Actual estimates would be averages over all years or all pairs of years

Variable	Derivation	Calculation
Pool size, P	—	—
Colonisation probability, λ_1	—	$\frac{C_{t,t+1}}{P - S_t}$
Extinction probability, μ_1	—	$\frac{E_{t,t+1}}{S_t} \left/ \left(1 - \frac{C_{t,t+1}}{P - S_t} \right) \right.$
Observed extinction probability, δ_1	$\mu_1(1 - \lambda_1)$	$\frac{E_{t,t+1}}{S_t}$
Incidence, j	$\frac{\lambda_1}{\lambda_1 + \mu_1(1 - \lambda_1)}$	$\frac{S_t}{P}$
Species richness, S	$\frac{P\lambda_1}{\lambda_1 + \mu_1(1 - \lambda_1)}$	S_t
Per-year island turnover, T_1	$\mu_1(1 - \lambda_1)$	$\frac{C_{t,t+1} + E_{t,t+1}}{S_t + S_{t+1}}$
Per-year pool turnover, τ_1	$\frac{2\lambda_1\mu_1(1 - \lambda_1)}{\lambda_1 + \mu_1(1 - \lambda_1)}$	$\frac{C_{t,t+1} + E_{t,t+1}}{P}$

a breeding absence in the following year. It will only occur if the disappearance of the current set of individuals is not accompanied by a colonization event that replaces them, i.e. $\delta_1 = \mu_1(1 - \lambda_1)$.

- Incidence, j : the probability that a breeding population of a species is present in any given year. A community-level measure can be calculated from data as S/P , where S is the species richness (see below). In terms of probabilities, $j = \lambda_1/(\lambda_1 + \delta_1)$.

- Species richness, S : the number of species on the island in any given year. From the data, this is a simple summation of the observed species. S is expected to vary stochastically from year to year, but in a community at dynamic equilibrium, this variation will be around a constant value. It is also the mean incidence multiplied by the number of species in the pool: $S = Pj = P\lambda_1/(\lambda_1 + \delta_1)$. (Note: we tested the assumption that the islands in this dataset are at approximate equilibrium by testing for trends in $\ln S$ over time. The strongest trend was for Cape Clear, with a 4.8% increase in species richness per year, but this is over just 6 years, and cannot be considered a long-term trend. Four of the other islands had trends of 1–2% per year, and the remainder less than that.)

- Per-year ‘island’ turnover, T_1 : sensu Russell *et al.* (1995), the number of species that either colonize or disappear from one year to the next, scaled to the number of species present in both years. Calculated from community-level data as $(C_{t,t+1} + E_{t,t+1})/(S_t + S_{t+1})$, where $C_{t,t+1}$ and $E_{t,t+1}$ are the number of colonization and observed extinction events, respectively, from one year to the next. Russell *et al.* (1995) showed that at equilibrium, this form of turnover is equal to the observed extinction probability: $T_1 = \delta_1$.

- Per-year ‘pool’ turnover, τ_1 : the number of species that either colonize or disappear from one year to the

next, scaled to the number of species in the pool. Calculated from community level data as $(C_{t,t+1} + E_{t,t+1})/P$. The number of colonizations in the numerator is the number of species not present, multiplied by the probability of colonization. The number of species not present is $(1 - j)P = \delta_1 P/(\lambda_1 + \delta_1)$, so we have $C_{t,t+1} = \lambda_1 \delta_1 P/(\lambda_1 + \delta_1)$. The number of extinctions in the numerator is the number of species present, multiplied by the probability of extinction: $E_{t,t+1} = \delta_1 \lambda_1 P/(\lambda_1 + \delta_1)$ (equal, at equilibrium, to the number of colonizations). Adding these and dividing everything by P gives us $\tau_1 = 2\lambda_1 \delta_1/(\lambda_1 + \delta_1)$.

Table 3 summarizes the derivations and calculation formulas.

ESTIMATING COLONIZATION AND EXTINCTION PROBABILITIES

The most direct way to test MacArthur and Wilson’s theory is to examine the fundamental processes of colonization and extinction – the other, higher-order variables will follow from these patterns. We need therefore to estimate colonization and extinction rates. One way is given by the calculation formulas derived previously. Note, however, that these require censuses in consecutive years, which may be difficult to obtain. Colin Clark and Michael Rosenzweig (Clark & Rosenzweig 1994; Rosenzweig & Clarke 1994) provide another method, as follows. The time series of presences and absences for one species on one island can be modelled as a discrete-time Markov process, where the transition from absent to present over one year is colonization, and the transition from present to absent is called observed extinction. There are four possible transitions, yielding the following probability matrix:

		$t + 1$	
		A	P
t	A	$1 - \lambda_1$	λ_1
	P	δ_1	$1 - \delta_1$

where A is absence, P is presence, and t is time. We can allow for gaps in runs of data (and so maximize the information obtained)

because the probability of colonization and extinction events over intervals longer than one year can be expressed in terms of the probabilities for one year (Diamond & May 1977):

$$\lambda_n = \frac{\lambda_1(1 - (1 - \lambda_1 - \delta_1)^n)}{\lambda_1 + \delta_1} \quad \text{eqn 1}$$

$$\delta_n = \frac{\delta_1(1 - (1 - \lambda_1 - \delta_1)^n)}{\lambda_1 + \delta_1} \quad \text{eqn 2}$$

where $n = 1, 2, \dots$ is the length of the interval between censuses. We can then express the probability of any time series, even one with gaps, in terms of just λ_1 and δ_1 . For the time series

{1980,P}, {1981,P}, {1984,A}, {1985,A}, {1990,A},
{1992,P}, {1993,P},

the probability model is

$$(1 - \delta_1)\delta_3(1 - \lambda_1)(1 - \lambda_5)\lambda_2(1 - \delta_1).$$

So, by substituting eqns 1 and 2 for any λ_n and δ_n terms where $n > 1$, an entire time series can be expressed in terms of just two 1-year event probabilities, λ_1 and δ_1 . And by the further substitution $\delta_1 = \mu_1(1 - \lambda_1)$, we can express an entire time series in terms of the two fundamental probabilities λ_1 and μ_1 .

We can estimate the parameters λ_1 and μ_1 for a species using the method of maximum likelihood. The product of the terms in the probability model is the probability of obtaining the data, given the model, i.e. the likelihood of the model. Maximum likelihood estimators (MLEs) for λ_1 and μ_1 are easily found by a numerical search over the two-dimensional parameter space $0 \leq \lambda_1 \leq 1, 0 \leq \mu_1 \leq 1$. The MLEs for the example data are $\hat{\lambda}_1 = 0.19$ and $\hat{\mu}_1 = 0.35$.

The data requirements for meaningful results are stringent. A good estimate of colonization probability can only be obtained if a species was absent in many years (giving many opportunities for potential colonization), and of extinction probability only if a species is present in many years. The difficulty is obvious; most species are either mostly present or mostly absent. Even in a long time series of records, there are typically few opportunities to observe one of the kinds of events. This means that the estimate for one of the parameters is likely to be highly uncertain. Worse, there is bias; the most accurate estimates tend to be the lowest (for example, for there to be lots of opportunities to observe colonizations, a species must be absent much of the time, which implies a low colonization rate). Imposing some minimum cut-off on the number of ‘opportunities to observe’ will tend to eliminate the higher values.

The best-case scenario is that colonization and extinction rates are similar, so that a species is present about 50% of the time. Even then, if those rates are (both) low then the time series will be characterized by long periods of presence followed by long periods of absence. For example, suppose that the ‘true’ values for yearly colonization and extinction of a species on an island are $\lambda_1 = 0.1$ and $\mu_1 = 0.2$ (so $\delta = 0.2 \times (1 - 0.1) = 0.18$). These values are entirely plausible for data such as will be presented here. The average period of presence following a colonization will be $c. 5.5$ years (the expected value of the geometric distribution with parameter δ_1), and the average period of absence following an observed extinction will be 10 years. Even if we had 20 years of continuous data for this species, it is quite likely to be mostly absent or mostly present during that time, and the estimate of either λ_1 or μ_1 will be highly biased.

The general rule is: a time series should be long enough to contain repeated examples of both presence and absence. Unfortunately, simple simulations show that even for the long, high-quality time series of data available for birds on British and Irish islands (in some cases over 50 years), it is not possible to obtain reliable estimates of colonization and extinction probabilities for most species.

Clark and Rosenzweig proposed that even when the length of the census period is too short for species-level estimates of either parameter, the method may be usefully used at the community level. In this scheme, data for all species at a site are combined, and maximum likelihood estimates obtained for a single pair of λ_1 and μ_1 . The combined data usually have enough ‘opportunities to observe’ that the estimates of both quantities are quite precise. While the interpretation of such single estimates is unclear, they may be used for comparative purposes, because MacArthur and Wilson’s theory makes predictions about overall colonization and extinction rates.

Finally, we note that because colonization probability is estimated as a function of pool size (i.e. potential colonists), when applying this approach to communities we must add zero counts for all the species in the pool, even those that have never been seen on the island (and thus may not be included in the raw data matrix).

Table 4 shows the calculated and estimated biogeographical variables for all islands, including all species. The correlations between the derived variables and their calculated alternatives are quite good: $r = 0.83$ for $\{\hat{S}, \bar{S}\}$, $r = 0.93$ for $\{\hat{T}_1, \bar{T}_1\}$, and $r = 0.66$ for $\{\hat{\tau}_1, \bar{\tau}_1\}$.

STATISTICAL METHODS

We wish to test for relationships between yearly colonization and extinction probability (λ_1 and μ_1), and the biogeographical variables latitude (L), area (A), distance to the mainland (D_m), distance to the nearest island (D_n), habitat complexity (H_c) and habitat richness (H_r), with area and distance measures log-transformed as described previously. Pool size is automatically included because the estimated colonization

Table 4. Biogeographical parameter estimates for the islands in this study, using all species. The fundamental estimates are probabilities, estimated using the likelihood method of Clark & Rosenzweig (1994). The derived estimates are of higher-order variables, and are obtained by combining the fundamental estimates according to the formulas of Table 3. The calculated estimates are obtained directly from the data, also as specified in Table 3

Island	Fundamental		Derived				Calculated		
	λ_1	μ_1	δ_1, T_1	j	S	τ_1	S	T_1	τ_1
Bardsey	0.0125	0.041	0.041	0.235	22.3	0.019	21.8	0.053	0.023
Calf of Man	0.0195	0.075	0.073	0.210	19.9	0.031	19.7	0.089	0.037
Cape Clear	0.0122	0.028	0.027	0.309	23.8	0.017	28.5	0.046	0.032
Copeland	0.0142	0.150	0.147	0.110	8.4	0.032	9.4	0.137	0.035
Fair Isle	0.0039	0.027	0.027	0.125	12.0	0.007	11.5	0.061	0.015
Inner Farnes	0.0071	0.168	0.167	0.041	4.0	0.014	3.3	0.199	0.013
Handa	0.0083	0.060	0.059	0.124	11.7	0.015	11.8	0.094	0.023
Havergate	0.0149	0.149	0.147	0.092	8.9	0.027	8.6	0.160	0.028
Hilbre	0.0062	0.149	0.148	0.040	3.8	0.012	6.1	0.135	0.017
Isle of May	0.0041	0.050	0.050	0.076	7.3	0.008	7.0	0.080	0.011
Isles of Scilly	0.0120	0.049	0.049	0.197	20.3	0.019	24.1	0.061	0.028
Lundy	0.0158	0.060	0.059	0.211	21.7	0.025	17.7	0.110	0.037
Scolt Head	0.0080	0.137	0.135	0.055	5.4	0.015	5.6	0.136	0.017
Skokholm	0.0068	0.060	0.060	0.103	10.6	0.012	9.5	0.064	0.013
Skomer	0.0118	0.061	0.060	0.164	16.9	0.020	21.7	0.104	0.047
Steep Holm	0.0064	0.062	0.062	0.094	9.6	0.012	9.2	0.083	0.016

probabilities are based on the whole set of species in the pool. Probabilities are bounded in the range 0–1, so we perform multivariate linear regression using logit-transformed versions of the dependent variables $\lambda'_1 = \ln[\lambda_1/(1 - \lambda_1)]$ and $\mu'_1 = \ln[\mu_1/(1 - \mu_1)]$. Even so, we encounter two of the most common problems in statistical analyses of ecological data. We have already seen that there is considerable collinearity among the predictor variables. We also have an overabundance of predictors (in our case, six) relative to the sample size of the data ($n = 16$): there are $2^6 = 64$ possible models (assuming we consider only one form for each variable). Coping with this largesse comes down to a question of model choice.

Traditional multivariate hypothesis-testing methods, such as stepwise regression, have a number of flaws (see Freedman 1983 and Burnham & Anderson 1998). Instead, we use information-based statistics, the most well-known of which is Akaike's Information Criterion, or AIC (Akaike 1973). For a set of alternative models $k = 1, 2, \dots, 2^q$,

$$\text{AIC}(k) = -2 \log L(\hat{\theta}_k) + 2m(k) \quad \text{eqn 3}$$

where $\hat{\theta}_k$ is the maximum likelihood estimate of the parameter vector θ_k , $L(\hat{\theta}_k)$ is the value of the likelihood function at that point, and $m(k)$ is the number of independent parameters in model k . The left-hand term is a measure of fit (or more precisely, lack of fit), based on likelihood, and the right-hand term is a penalty for model complexity. Smaller values are better, in the sense of being more parsimonious. Applying AIC is straightforward: one simply evaluates it for every model in the candidate set (which need not be nested). The one with the smallest value is the best (given AIC's quantification of parsimony).

Since 1973 there have been numerous developments and refinements of Akaike's original idea, all of which make the penalty term more sophisticated. AIC uses just one piece of information: the number of free parameters in the model. This is a very simple view of what constitutes model complexity. Other undesirable qualities that models can have include interdependencies among the variables, highly variable parameter variances, and interdependencies among the residuals (if there is more than one dependent variable). All of these can be thought of as unwanted complexity, and information theory provides the tools to quantify them, and so calculate a penalty term that takes them all into account.

In this paper, we use the criterion ICOMP(IFIM) developed by Bozdogan (1990, 2000), which penalizes the complexity of the inverse Fisher information matrix (\hat{F}^{-1}) of the statistical model.

In particular, we use the correlational form ICOMP(IFIM)-R (Bozdogan 2000; henceforward ICI_R), which penalizes the 'size' of a model, collinearity among predictors, and collinearity among residuals, but does not penalize inequality in the variances of the parameter estimates. In mathematical notation,

$$\text{ICI}_R = -2 \log L(\hat{\theta}_k) + 2C_1(\hat{F}_R^{-1}) \quad \text{eqn 4}$$

where $\hat{F}_R^{-1} = D_{\hat{F}^{-1}}^{-1/2} \hat{F}^{-1} D_{\hat{F}^{-1}}^{-1/2}$ and $D_{\hat{F}^{-1}}$ is a matrix containing just the diagonal elements of \hat{F}^{-1} . Russell and Bozdogan (unpublished) give more details of this statistic, in general and as it applies specifically to multivariate regression, as well as a fuller explanation of the rationale behind it and its variants.

Measures such as AIC and ICI_R allow for a variety of helpful presentations of the model-choosing results. All information-based statistics, being modifications of log-likelihood values, are measures of the relative

plausibility of different models, given the data. The best model is not necessarily the true model (assuming the true model is even in the candidate set – a different problem). A standard way to quantify uncertainty about the true model is to quantify the relative performance of the models according to the information-based statistic of choice. This is done with the statistic $P_i = e^{-0.5\delta_i}$ where $\delta_i = c_i - \min c_i$ and c_i is the information-based statistic (in our case, ICI_R) for the i th model. $P_i = 1$ for the best model, and decreases for less parsimonious models. We can define a ‘confidence set’ of models as those whose performance is better than some arbitrary (but consistently applied) fraction of the performance of the best model. Here, we use 0.1 as our cut-off.

A second use of the relative performance measure is in examining the importance of individual parameters. We convert the relative plausibility measures into model weights by dividing each one by the sum of all of them: $w_i = P_i / \sum P_i$. A simple measure of the importance of a parameter is obtained by summing the w_i for every model in which that parameter appears (Burnham & Anderson 1998, p. 140). A third use is in generating parameter estimates: Burnham & Anderson (1998) define the model-averaged estimate of a parameter as the weighted average of the estimates for that parameter in every model in which it occurs, where the weights are given by the w_i .

We can also calculate importance values for pairs, triples, etc., of variables in the same way. Pair values are useful for assessing when two variables are redundant (in which case they will not appear together in the better models, and so will have a low pair importance score), and when they are complementary (they do tend to appear together).

Autocorrelation

An assumption of our analyses is that the islands represent independent observations of colonization and extinction processes. This might not be the case if, for example, years of high and low extinction probability are common across islands (perhaps because of environmental drivers such as minimum winter temperature), and is more likely to be true for islands that are close together and therefore share a species pool. To test for autocorrelation, we quantified year to year colonization rates for each island, and then correlated these across island pairs for all pairs within each pool, plus a set of comparisons of Bardsey with each of the Pool 5 islands. (Reliable year-to-year estimates of extinction rates are not available for most islands in most years, making comparison across islands almost impossible.) Each of the 24 comparisons had a different sample size, determined by the number of consecutive year-pairs of data the two islands have in common, and so each correlation coefficient was tested separately using a t -test with $\alpha = 0.05$. At this level, three pairs showed significant correlations: Handa and Fair Isle, Bardsey and Skomer, and Bardsey and Steep Holm. The probability of getting three or more significant

Table 5. Best models for simultaneously predicting colonization and extinction probability with different numbers of parameters, according to ICI_R . m is the number of free parameters in the model, where $m = pq + p(p + 1)/2$ and $p = 2$. AIC values are shown for comparison

Model components	q	$2m$	r^2	$-2 \ln L$	AIC	ICI_R
	1	10	0.000	51.2	61.2	51.3
H_r	2	14	0.348	32.3	46.3	39.2
$H_c H_r$	3	18	0.556	24.0	42.0	31.6
$D_n H_c H_r$	4	22	0.700	13.9	35.9	21.1
$A D_n H_c H_r$	5	26	0.768	6.1	32.1	15.2*
$A D_m D_n H_c H_r$	6	30	0.775	5.1	35.1	16.8
$L A D_m D_n H_c H_r$	7	34	0.795	2.0	36.0	22.4

*The best model overall is the one with the smallest value of ICI_R , i.e. $\{A, D_n, H_c, H_r\}$.

Table 6. Confidence set of models for simultaneously predicting colonization and extinction probability, according to ICI_R . The confidence set contains three out of the 64 possible models. Latitude does not appear in any models from the confidence set

Model components	r^2	ICI_R	P	w
$A D_n H_c H_r$	0.768	15.2	1	0.548
$A D_m D_n H_c H_r$	0.775	16.8	0.453	0.248
$A D_m H_c H_r$	0.743	18.6	0.188	0.103

results out of 24 by chance is 0.12; combining this with the fact that some close pairs showed very little correlation (e.g. Skomer and Skokholm, $\rho = 0.55$), we conclude that autocorrelation is not an important factor and do not consider it in our analyses.

Results

FUNDAMENTAL VARIABLES

The best model (i.e. the most parsimonious, as measured by ICI_R) for simultaneously predicting colonization and extinction includes every predictor variable except latitude and distance to the mainland (Table 5). There are three models in the confidence set (Table 6), meaning that two other models are sufficiently close to the best model in their ICI_R scores that we consider them to be plausible alternatives. All three models are similar in composition, and between them they indicate that area, both measures of habitat diversity (richness and complexity) and at least one measure of isolation are important predictors.

A crude measure of the relative importance of the individual predictor variables is the order in which they appear in models of increasing complexity (Table 5): H_r appears first, H_c second, and so on. The parameter importance values, both for single variables (Table 7) and pairs of variables (Table 8), provide a more refined ranking. Both habitat variables are equally and maximally important, followed closely by area and distance to the nearest island, with distance to the mainland being

Table 7. Importance and weighted average parameter estimates of the fundamental biogeographical parameters. $\hat{\beta}\lambda'_i$ and $\hat{\beta}\mu'_i$ are the parameter estimates for logit-transformed colonization and extinction probability, respectively

Parameter	Importance	$\hat{\beta}\lambda'_i$	$\hat{\beta}\mu'_i$
H_c	1.00	0.219 ± 0.097*	0.200 ± 0.102*
H_r	1.00	-0.039 ± 0.049	-0.121 ± 0.050*
A	0.95	0.168 ± 0.119*	0.092 ± 0.126
D_n	0.88	-0.093 ± 0.089*	-0.118 ± 0.100*
D_m	0.40	0.006 ± 0.131	-0.076 ± 0.124
L	0.04	-0.032 ± 0.059	0.027 ± 0.063

*Indicates that the confidence interval for the weighted average estimate does not include zero.

somewhat important and latitude not important at all. The very high pair importance values for all combinations of habitat variables and area indicate, surprisingly, almost no redundancy among these three measures.

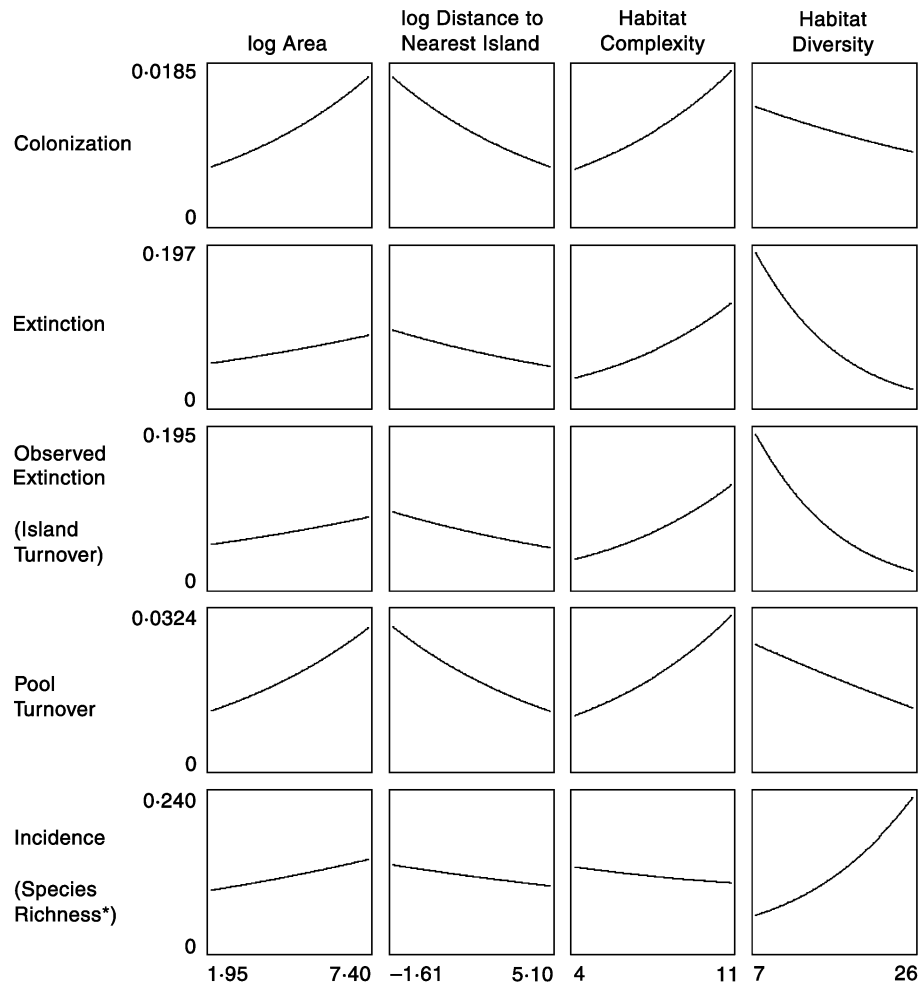
The model-averaged estimates with their associated confidence intervals (Table 7) are one way to examine which dependent variables (colonization or extinction

Table 8. Importance values of pairs of predictor variables. A low pair importance value, especially in conjunction with high individual importance values for at least one of the pair, suggests redundancy. Pairs in which the variables are believed to measure similar aspects of the environment are given in boldface. Clearly, the two distance measures are redundant, whereas the area and habitat measures are not

	L	A	D_m	D_n	H_c
A	0.046				
D_m	0.023	0.373			
D_n	0.042	0.837	0.277		
H_c	0.049	0.947	0.395	0.881	
H_r	0.049	0.946	0.395	0.881	0.999

probability) each predictor variable has a significant effect on. For example, area is a better predictor of colonization probability than of extinction probability (its confidence interval for predicting colonization does not include zero – more on this result later).

The directions and shapes of the relationships between selected predictors and both fundamental and higher-order IBT variables are shown in Fig. 2 (based

**Fig. 2.** The relationships between selected island biogeographical predictors and fundamental and higher-order community variables, based on the 'best' model as chosen by ICI_R. The curve for each predictor variable was obtained by holding the other predictor variables constant at their mid-points. *Species richness is not shown separately because it is incidence multiplied by pool size.

on the estimates from the 'best' model). The relative amounts of the y -axis spanned by the curves in a given row of Fig. 2 are rough measures of the relative strengths of the respective predictor variables in predicting that dependent variable – their effect sizes. These measures are functions of the ranges of the predictor variables in our data, and so should be interpreted carefully, as in the following example: the total range of areas in our data appears to have a similar effect on the magnitude of colonization probability as the total range of distances in our data.

EXPECTED RESULTS

The following relationships observed in our data are those we expect, based on more generally observed patterns and on theory:

1. Colonization decreases with distance from the nearest island (Fig. 2, row 1). This is a foundation of MacArthur and Wilson's model. Distance to the nearest island is a superior predictor than distance to the mainland: consider their importance values of 0.88 and 0.40, respectively (Table 7), or the fact that the best model, including only distance to the nearest island, is over five times as plausible as the third best model, including only distance to the mainland (Table 6). Unexpectedly, the parameter-averaged estimates also suggest that colonization probability increases with distance to the mainland, but this is a consequence of the fact that in the best model in which distance to the mainland occurs, it does so in combination with distance to the nearest island. As a result, D_m is relegated to explaining residual variation in colonization probability. In models in which D_m occurs alone, its sign is negative as expected. Finally, we note that the relationship between colonization and D_n , while expected, is not strong, at least not compared with the following.
2. Colonization probability (Fig. 2, row 1) is higher for larger islands – the target effect (Lomolino 1990) – and those with greater habitat complexity. Both of these relationships are as influential in our dataset as the more traditional relationship between colonization and distance (Table 7). This is most likely because the range of distances is quite small, given the relative mobility of birds (see Introduction).
3. Colonization probability shows no significant relationship with latitude. At first, this appears to contradict numerous studies that have demonstrated higher species-averaged dispersal of temperate-zone birds than of tropical birds, and of northern-temperate compared with mediterranean-temperate birds (Diamond 1971). However, the weakness of the effect in our data is to be expected. First, the range of latitudes encompassed by these islands, all of which are northern-temperate, is relatively small. Second, and perhaps more significantly, those latitudinal effects will apply to the species pools that supply small islands, just as they apply to the islands themselves. So, much variation in species richness on islands may be attributed to variation

in pool richness. In our study, pool sizes (and therefore any latitudinal effects on them) are already factored into estimates of colonization probability, so in our regression models latitude is reduced to explaining variation in per species colonization and extinction probabilities, which it does less well than any other variable.

UNEXPECTED RESULTS

Some of our results are surprising. We list them here, but leave detailed examination to the Discussion.

1. Habitat complexity and habitat richness seem to be highly and equally important, occurring together in the top 12 models (not shown). This suggests very strongly that they are measuring fundamentally different aspects of habitat availability for these bird communities, an inference that is strengthened by the observation that they have opposite relationships with both colonization and extinction probability (Fig. 2). Greater habitat complexity predicts both a higher colonization probability and a higher extinction probability, whereas greater habitat richness predicts lower colonization and extinction probability. Complexity is the dominant influence on colonization, whereas richness is the dominant influence on extinction.
2. The surprise of the nonredundancy of the two habitat measures is enhanced by the fact that area is almost as important in addition, appearing in seven of the top 12 models alongside both habitat measures. This suggests that area captures a further aspect of population demography that is not included in either of the habitat measures. An obvious candidate would be population size, but note the next observation.
3. Extinction probability (Fig. 2, row 2) is higher on islands with greater area and habitat complexity.
4. Extinction probability is lower on islands that are more distant (no matter which distance measure is used).
The last two patterns in this list are highly unusual, and we will return to them in our Discussion.

HIGHER-ORDER VARIABLES

Results for the more commonly measured higher-order variables are easily obtained by converting the predictions about the logit-transformed probabilities back to regular probabilities, and then applying the formulas of Table 3. These relationships are also shown in Fig. 2.

1. Observed extinction (and also therefore island turnover; Fig. 2, row 3) shows similar relationships as population extinction. Any differences between the two measures of extinction reflect the influence of colonization – the rescue effect.
2. Pool turnover (Fig. 2, row 4) shows the same patterns as island turnover, except that area and habitat complexity are relatively more important, and habitat diversity relatively less important. The relationships of island and pool turnover to biogeographical variables are not expected to be much different from each other unless there is huge variation in pool size.

3. Finally, incidence (Fig. 2, row 5) increases with area, which is expected and also with distance, which is opposite to theory. In both cases the relationship is weak. The relationship between incidence and area is analogous to the traditional species–area relationship, but comparing our results with those of more traditional species–area studies is difficult, for two reasons. First, our use of distinct pools for different islands adds noise to the relationship. If all islands shared a common pool, then the exponent of the species–area relationship (assuming a conventional power form) would be the same as the exponent of the incidence–area relationship, because number of species would simply be incidence multiplied by the constant pool size. Using different pools adds considerable variability. Second, we include two measures of habitat in our set of candidate predictors, and each varies positively with area. Most traditional examinations of species–area relationships measure only area, assuming that it encapsulates variation in habitat diversity (among other things). To examine the parameter estimates for area in a model that includes one or more habitat variables may lead to incorrect conclusions, especially if, as in this case, the habitat variable is a stronger predictor than area. Most likely, the area relationship would seem weak. To confirm that our model makes predictions about species–area relationships that are in line with previous ‘area-only’ studies, we simply calculated estimates of incidence from a model that included L , A , D_m and D_n , but no habitat measures. We then regressed log incidence against the same variables. The estimate of the slope parameter for A was 0.21, in line with established patterns. Finally, we multiplied our estimates of incidence by the appropriate pool sizes and performed the regression again. This time, the estimate of the parameter for A was 0.19.

Interestingly, in these regressions richness always increases with the dominant distance variable, with a value in the range 0.13–0.14. This is the same unexpected result from our preliminary regressions where we used raw species richness as a dependent variable and only area and distance as predictors (see Introduction), except that the effect of distance is stronger when the larger set of variables are considered.

POOLS AND RARITIES

None of the analyses with adjusted pool definitions changed our results – even the more unexpected ones – substantially. This is not surprising, given that most of the adjustments change pool sizes, and therefore estimated colonization rates, by a few per cent at most.

Discussion

In many ways, these data validate MacArthur and Wilson’s ideas. Most obviously, the idea of a dynamic balance between colonization and extinction is obviously right for these islands, and many of their pre-

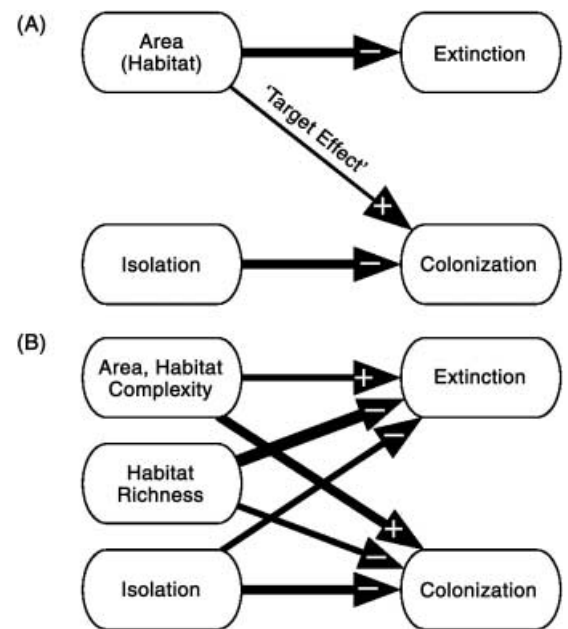


Fig. 3. Traditional (A) and modified (B) versions of MacArthur and Wilson’s theory of island biogeography. Plus and minus signs indicate whether the dynamic variable on the right is positively or negatively associated with the biogeographical variable on the left. The thickness of the line represents the relative strength of the relationship. The modified version includes a variety of additional effects, including a decrease in extinction probability on more isolated islands that may be explained by incorporating foraging theory into the theory.

dictions are borne out. Figure 3A shows the expected relationships. In our study, colonization does indeed decrease for more distant islands and, to an even greater extent, increase for larger islands. Extinction does not, however, decrease on larger islands, but rather on islands with greater habitat richness. Once this is taken into account, extinction appears to increase with area, and with habitat complexity also.

The apparent increase of extinction probability with area (weakly) and habitat complexity (strongly) has a number of possible explanations. One is sampling; we may just be looking at an unusual subset of islands. Another relates to the nature of complex habitats; it may be that the more complex habitats tend to be present with relatively small or patchy distributions, such that any characteristic species they support are vulnerable to local extinction (Pimm, Jones & Diamond 1988). We also cannot exclude the possibility of interaction with humans, in that habitat complexity may be related to human activities (plantations, gardens, etc.) in which case the complex habitat is likely to be not only small, but also nonindigenous and frequently disturbed.

Extinction-causing predators such as rats and foxes might also be associated with human presence, or with islands that are very close to the mainland (Hilbre, Scolt Head), but there are no records of foxes on these islands, and rat populations are controlled on most of them. The other main nest predators are gulls, and

while these are also controlled on some islands, they are also not expected to show a positive relationship with distance.

Related to disturbance is the more general idea that more complex habitats may be more variable from year to year. This would simultaneously explain the strong positive relationship of habitat complexity to both extinction and colonization. Looking at the data, we find that the four islands with greatest habitat complexity host 18 species that are not found on the other islands. Of these, 14 species have bred only occasionally (typically once) on those islands. These include many migratory species (e.g. blackcap, lesser whitethroat, nightjar, whinchat), some of which also breed only rarely in their respective mainland pools (e.g. black redstart on Calf of Man). We note that all of these islands are medium to large in size, three are also relatively distant from the mainland, and all of them function as attractive stopover sites for many migratory species (Stracey *et al.* in prep.). We suggest that this constant immigration leads to occasionally successful, but rarely repeated, attempts at breeding even when conditions on the island are far from ideal.

Another striking feature of our results is that populations on distant islands are less likely to go extinct than those on near islands (Fig. 3B). We discuss two potential explanations. One invokes colonization. From theory, previous studies and our data, we know that colonization decreases with distance. Perhaps individuals that do colonize distant islands find themselves with fewer competitors in the form of members of other species, because fewer individuals of these species can or do make the journey. However, the number of species on an island is also a function of extinction, and this decreases with distance (the effect we are trying to explain), so that incidence, and by extension species richness, actually increases (albeit weakly) with distance. Reduced species richness cannot therefore be an explanation.

The second potential explanation invokes that fact that, compared with other taxa, birds are both highly mobile and capable of sophisticated decision-making. The various theories of island biogeography tend to see extinction as a passive process; extinction is expected to be higher on small islands because of the stochastic demographic and genetic difficulties encountered by the small populations that live on them. (For species incapable of directed flight, or of swimming long distances, colonization will be a largely passive process as well, depending on air and water currents.)

However, if most birds are good enough fliers that they can choose to stay on or leave an island, a more appropriate model for birds might be one that addresses the decision-making process. Such a model, of decision-making on a patchy landscape, already exists, in the form of optimal foraging theory (OFT). OFT assumes that individuals make decisions about when to move on from a resource patch to search for another, and that these decisions form a strategy that

optimizes the overall rate of acquisition of the resource. Some of the predictions of OFT are strikingly similar to those of IBT. For example, if larger patches contain the same amount of a given resource as smaller patches, but distributed at a lower density, individuals should stay longer in larger patches. (This mirrors Lack's (1969, 1976) explanation of the species–area effect, in which larger areas contain a greater variety of habitats.) However, OFT differs from IBT in that it predicts that when the distance between patches is large, it is optimal for an individual to spend longer in each patch. If the search time for a new patch is long, a higher overall rate of resource acquisition will occur if individuals deplete the resources within each patch to a lower level before moving on. When other patches are distant, leaving one too soon means an organism spends a lot of time in the resource-free interpatch matrix. In the current study, the 'resources' are nesting sites and food, and what is assumed to be optimized is the successful fledging of offspring. A bird that has invested a lot of energy reaching a distant island, and that would have to invest at least as much to leave it again and try elsewhere, may be more inclined to stay and attempt breeding than if it were just a short hop back to the mainland, or on to another island.

If birds really are making foraging-type decisions about whether to attempt breeding on an island, then OFT predicts exactly the pattern we observe in our data. We further note that our distinction between the likely dynamics of mobile, intelligent organisms, vs. those whose initiation and method of dispersal are more passive, should apply equally to metapopulation theory, which is, after all, the species-level analogue of MacArthur and Wilson's ideas.

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Appendix I

LIST OF SPECIES AND SPECIES POOLS

Species used in these analyses, and their membership in seven regional 'pools'. See Fig. 1 for map of pool locations. Common and scientific names are from Gibbons *et al.* (1992)

Common name	Scientific name	Pool						
		1	2	3	4	5	6	7
Honey buzzard	<i>Pernis apivorus</i>						Y	
Red kite	<i>Milvus milvus</i>					Y		
Whitetailed eagle	<i>Haliaeetus albicilla</i>	Y	Y					
Marsh harrier	<i>Circus aeruginosus</i>						Y	
Hen harrier	<i>Circus cyaneus</i>	Y	Y	Y	Y			Y
Montague's harrier	<i>Circus pygargus</i>			Y	Y	Y	Y	
Goshawk	<i>Accipiter gentilis</i>				Y	Y		Y
Sparrowhawk	<i>Accipiter nisus</i>	Y	Y	Y	Y	Y	Y	Y
Buzzard	<i>Buteo buteo</i>	Y	Y	Y	Y	Y	Y	Y
Golden eagle	<i>Aquila chrysaetos</i>	Y	Y		Y			
Osprey	<i>Pandion haliaetus</i>	Y	Y					
Kestrel	<i>Falco tinnunculus</i>	Y	Y	Y	Y	Y	Y	Y
Merlin	<i>Falco columbarius</i>	Y	Y	Y	Y	Y		Y
Hobby	<i>Falco subbuteo</i>					Y	Y	
Peregrine	<i>Falco peregrinus</i>	Y	Y	Y	Y	Y		Y
Red grouse	<i>Lagopus lagopus</i>	Y	Y	Y	Y	Y		Y
Ptarmigan	<i>Lagopus mutus</i>	Y	Y					
Black grouse	<i>Tetrao tetrix</i>	Y	Y					Y
Capercaillie	<i>Tetrao urogallus</i>	Y	Y					Y
Redlegged partridge	<i>Alectoris rufa</i>					Y	Y	Y
Grey partridge	<i>Perdix perdix</i>	Y	Y	Y	Y	Y	Y	Y
Quail	<i>Coturnix coturnix</i>	Y	Y	Y	Y	Y	Y	Y
Pheasant	<i>Phasianus colchicus</i>	Y	Y	Y	Y	Y	Y	Y
Rock dove (feral pigeon)	<i>Columba livia</i>	Y	Y	Y	Y	Y	Y	Y
Stock dove	<i>Columba oenas</i>	Y	Y	Y	Y	Y	Y	Y
Woodpigeon	<i>Columba palumbus</i>	Y	Y	Y	Y	Y	Y	Y
Collared dove	<i>Streptopelia decaocto</i>	Y	Y	Y	Y	Y	Y	Y
Turtle dove	<i>Streptopelia turtur</i>	Y	Y	Y	Y	Y		Y
Cuckoo	<i>Cuculus canorus</i>	Y	Y	Y	Y	Y	Y	Y
Barn owl	<i>Tyto alba</i>	Y	Y	Y	Y	Y	Y	Y
Snowy owl	<i>Nyctea scandiaca</i>	Y						
Little owl	<i>Athene noctua</i>				Y	Y	Y	Y
Tawny owl	<i>Strix aluco</i>	Y	Y		Y	Y	Y	Y
Longeared owl	<i>Asio otus</i>	Y	Y	Y	Y	Y	Y	Y
Shorteared owl	<i>Asio flammeus</i>	Y	Y		Y	Y	Y	Y
Nightjar	<i>Caprimulgus europaeus</i>	Y	Y	Y	Y	Y	Y	Y
Swift	<i>Apus apus</i>	Y	Y	Y	Y	Y	Y	Y
Kingfisher	<i>Alcedo atthis</i>	Y	Y	Y	Y	Y	Y	Y
Hoopoe	<i>Upupa epops</i>					Y		
Wryneck	<i>Jynx torquilla</i>						Y	
Green woodpecker	<i>Picus viridis</i>				Y	Y	Y	Y
Great spotted woodpecker	<i>Dendrocopos major</i>	Y	Y		Y	Y	Y	Y
Lesser spotted woodpecker	<i>Dendrocopos minor</i>				Y	Y	Y	
Short-toed lark	<i>Calandrella brachydactyla</i>					Y	Y	
Skylark	<i>Alauda arvensis</i>	Y	Y	Y	Y	Y	Y	Y
Sand martin	<i>Riparia riparia</i>	Y	Y	Y	Y	Y	Y	Y
Swallow	<i>Hirundo rustica</i>	Y	Y	Y	Y	Y	Y	Y
House martin	<i>Delichon urbica</i>	Y	Y	Y	Y	Y	Y	Y
Tree pipit	<i>Anthus trivialis</i>	Y	Y	Y	Y	Y	Y	Y
Meadow pipit	<i>Anthus pratensis</i>	Y	Y	Y	Y	Y	Y	Y
Rock pipit	<i>Anthus petrosus</i>	Y	Y	Y	Y	Y	Y	Y
Yellow wagtail	<i>Motacilla flava</i>				Y	Y	Y	Y
Grey wagtail	<i>Motacilla cinerea</i>	Y	Y	Y	Y	Y	Y	Y
Pied/white wagtail	<i>Motacilla alba</i>	Y	Y	Y	Y	Y	Y	Y
Dipper	<i>Cinclus cinclus</i>	Y	Y	Y	Y	Y		Y
Wren	<i>Troglodytes troglodytes</i>	Y	Y	Y	Y	Y	Y	Y
Duncock	<i>Prunella modularis</i>	Y	Y	Y	Y	Y	Y	Y
Robin	<i>Erithacus rubecula</i>	Y	Y	Y	Y	Y	Y	Y
Nightingale	<i>Luscinia megarhynchos</i>					Y	Y	
Black redstart	<i>Phoenicurus ochruros</i>						Y	

Common name	Scientific name	Pool						
		1	2	3	4	5	6	7
Redstart	<i>Phoenicurus phoenicurus</i>	Y	Y	Y	Y	Y	Y	Y
Whinchat	<i>Saxicola rubetra</i>	Y	Y	Y	Y	Y	Y	Y
Stonechat	<i>Saxicola torquata</i>	Y	Y	Y	Y	Y	Y	Y
Wheatear	<i>Oenanthe oenanthe</i>	Y	Y	Y	Y	Y	Y	Y
Ring Ouzel	<i>Turdus torquatus</i>	Y	Y	Y	Y	Y		Y
Blackbird	<i>Turdus merula</i>	Y	Y	Y	Y	Y	Y	Y
Fieldfare	<i>Turdus pilaris</i>	Y	Y					Y
Song thrush	<i>Turdus philomelos</i>	Y	Y	Y	Y	Y	Y	Y
Redwing	<i>Turdus iliacus</i>	Y	Y					Y
Mistle thrush	<i>Turdus viscivorus</i>	Y	Y	Y	Y	Y	Y	Y
Grasshopper warbler	<i>Locustella naevia</i>	Y	Y	Y	Y	Y	Y	Y
Savi's warbler	<i>Locustella luscinioides</i>						Y	
Sedge warbler	<i>Acrocephalus schoenobaenus</i>	Y	Y	Y	Y	Y	Y	Y
Marsh warbler	<i>Acrocephalus palustris</i>					Y	Y	
Reed warbler	<i>Acrocephalus scirpaceus</i>	Y	Y		Y	Y	Y	
Dartford warbler	<i>Sylvia undata</i>					Y		
Lesser whitethroat	<i>Sylvia curruca</i>	Y	Y		Y	Y	Y	Y
Whitethroat	<i>Sylvia communis</i>	Y	Y	Y	Y	Y	Y	Y
Garden warbler	<i>Sylvia borin</i>	Y	Y	Y	Y	Y	Y	Y
Blackcap	<i>Sylvia atricapilla</i>	Y	Y	Y	Y	Y	Y	Y
Wood warbler	<i>Phylloscopus sibilatrix</i>	Y	Y		Y	Y	Y	Y
Chiffchaff	<i>Phylloscopus collybita</i>	Y	Y	Y	Y	Y	Y	Y
Willow warbler	<i>Phylloscopus trochilus</i>	Y	Y	Y	Y	Y	Y	Y
Goldcrest	<i>Regulus regulus</i>	Y	Y	Y	Y	Y	Y	Y
Firecrest	<i>Regulus ignicapillus</i>						Y	
Spotted flycatcher	<i>Muscicapa striata</i>	Y	Y	Y	Y	Y	Y	Y
Pied flycatcher	<i>Ficedula hypoleuca</i>	Y	Y		Y	Y		Y
Bearded tit	<i>Panurus biarmicus</i>						Y	
Longtailed tit	<i>Aegithalos caudatus</i>	Y	Y	Y	Y	Y	Y	Y
Marsh tit	<i>Parus palustris</i>				Y	Y	Y	Y
Willow tit	<i>Parus montanus</i>	Y	Y		Y	Y	Y	Y
Crested tit	<i>Parus cristatus</i>	Y	Y					
Coal tit	<i>Parus ater</i>	Y	Y	Y	Y	Y	Y	Y
Blue tit	<i>Parus caeruleus</i>	Y	Y	Y	Y	Y	Y	Y
Great tit	<i>Parus major</i>	Y	Y	Y	Y	Y	Y	Y
Nuthatch	<i>Sitta europaea</i>				Y	Y	Y	Y
Treecreeper	<i>Certhia familiaris</i>	Y	Y	Y	Y	Y	Y	Y
Redbacked shrike	<i>Lanius collurio</i>	Y	Y			Y	Y	Y
Jay	<i>Garrulus glandarius</i>			Y	Y	Y	Y	Y
Magpie	<i>Pica pica</i>	Y	Y	Y	Y	Y	Y	Y
Chough	<i>Pyrrhocorax pyrrhocorax</i>	Y	Y	Y	Y	Y		
Jackdaw	<i>Corvus monedula</i>	Y	Y	Y	Y	Y	Y	Y
Rook	<i>Corvus frugilegus</i>	Y	Y	Y	Y	Y	Y	Y
Carrion/hooded crow	<i>Corvus corone</i>	Y	Y	Y	Y	Y	Y	Y
Raven	<i>Corvus corax</i>	Y	Y	Y	Y	Y		Y
Starling	<i>Sturnus vulgaris</i>	Y	Y	Y	Y	Y	Y	Y
House sparrow	<i>Passer domesticus</i>	Y	Y	Y	Y	Y	Y	Y
Tree sparrow	<i>Passer montanus</i>	Y	Y	Y	Y	Y	Y	Y
Chaffinch	<i>Fringilla coelebs</i>	Y	Y	Y	Y	Y	Y	Y
Greenfinch	<i>Carduelis chloris</i>	Y	Y	Y	Y	Y	Y	Y
Goldfinch	<i>Carduelis carduelis</i>	Y	Y	Y	Y	Y	Y	Y
Siskin	<i>Carduelis spinus</i>	Y	Y	Y	Y	Y	Y	Y
Linnet	<i>Carduelis cannabina</i>	Y	Y	Y	Y	Y	Y	Y
Twite	<i>Carduelis flavirostris</i>	Y	Y	Y	Y	Y	Y	Y
Common crossbill	<i>Loxia curvirostra</i>	Y	Y		Y	Y	Y	Y
Bullfinch	<i>Pyrrhula pyrrhula</i>	Y	Y	Y	Y	Y	Y	Y
Hawfinch	<i>Coccothraustes coccothraustes</i>				Y	Y	Y	Y
Snow bunting	<i>Plectrophenax nivalis</i>	Y	Y					
Yellowhammer	<i>Emberiza citrinella</i>	Y	Y	Y	Y	Y	Y	Y
Cirl bunting	<i>Emberiza cirlus</i>					Y	Y	Y
Reed bunting	<i>Emberiza schoeniclus</i>	Y	Y	Y	Y	Y	Y	Y
Corn bunting	<i>Miliaria calandra</i>	Y	Y	Y	Y	Y	Y	Y
Total species		96	95	77	95	103	97	96