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Two decades of interaction between the MacArthur–Wilson model and the complexities of mammalian distributions

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More than two decades after its publication, MacArthur and Wilson's equilibrium model of insular biogeography continues to provide the conceptual foundation for investigating the distribution of species on islands and the composition of insular biotas. During this period, studies of the distributions of mammals among insular habitats have tested, modified, and extended MacArthur and Wilson's simple formalism to enhance greatly our understanding of the complexities of biogeographic patterns and processes. The papers in this symposium summarize many of the past contributions of mammalian biogeographers and introduce important new data and ideas. The diversity of biological characteristics and associated distributional patterns exhibited by mammals has facilitated this endeavour. Some insular mammalian faunas appear to represent approximate equilibria between opposing rates of contemporary colonization and extinction. Other faunas are currently decreasing in diversity because of extinctions, owing either to natural habitat fragmentation that has occurred since the Pleistocene or to human activities within the last few centuries. Still other faunas have been increasing in diversity (at least until recent human impacts) because limiting rates of origination, both colonization and speciation, have been extremely low. The questions and analyses of island biogeography can also be applied to continents with comparable overall results: the distributions of continental faunas reflect the consequences of similar processes of colonization, speciation and extinction. Analyses of insular distributions show unequivocally that probabilities of extinction, colonization and speciation are highly deterministic and vary in predictable ways among different taxa and archipelagos. These findings have important implications for applying the theory and data of insular biogeography to the pressing practical problems of designing natural reserves to preserve native species.

KEY WORDS:—Colonization – conservation – continental biogeography – equilibrium biogeography – extinction – island biogeography – mammals – natural reserves – speciation.

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INTRODUCTION

With the publication of their elegantly simple and intuitively appealing model, which represented insular species richness as a dynamic equilibrium between opposing rates of colonization and extinction, MacArthur & Wilson (1963, 1967) stimulated a resurgence of interest and research in biogeography. Subsequent developments—including the collection and analysis of data on insular distributions, the testing and modification of the MacArthur–Wilson model, the development of alternative, non-equilibrial hypotheses to account for insular distributions, the extension of insular concepts to continental biogeography, the application of the theory and data of insular biogeography to the design and management of natural reserves, and the investigation of other aspects of the ecology, evolution, and genetics of insular populations—have not only revitalized biogeography, they have made the integrated study of insular biotas one of the most conspicuous and successful research programmes in biology during the last two decades. The papers in this symposium attest both to the great increase in understanding of the biology of insular mammals that has resulted, and to the important contributions that studies of insular mammals have made to recent conceptual developments in biogeography.

In my attempt to evaluate and synthesize these diverse contributions, I shall develop several different but interrelated themes. First, the MacArthur–Wilson model has endured, not necessarily as the correct explanation for the vast majority of insular mammal distributions, but as a heuristic construct. It has provided the conceptual and methodological basis for evaluating the differential contributions of colonization, extinction and speciation to the composition of isolated biotas, and for understanding how these processes operate in different kinds of organisms with distinctive biologies and in different kinds of insular habitats with distinctive histories and environments. Secondly, mammals exhibit a wide variety of patterns of insular distribution. These reflect differences among mammalian taxa in dispersal ability, population structure and dynamics, and resource requirements and other niche dimensions, and differences among islands in history, size, habitat and barriers to dispersal. Thirdly, the diversity of these insular patterns does not imply that they are disordered. Although there is often some unexplained, apparently stochastic variation, many of the patterns are highly deterministic, suggesting that they are the consequences of biogeographic processes that operate in regular, predictable ways. Fourthly, mammalian biogeographers have taken advantage of the diversity of insular patterns to develop increasingly complete and rigorous interpretations of how the biological attributes of different mammalian taxa and the histories and environments of different archipelagos have influenced the composition of insular faunas through the processes of colonization, extinction and speciation. Some of these faunas represent an approximate balance between opposing rates of origination and extinction, whereas others are far from equilibrium. Fifthly, I incorporate some recent analyses by Flessa (1975, 1981) and my student, Renee Rusler (unpubl. obs.), to suggest that the concepts and data used by insular biogeographers can also be applied to the distributions of mammals among continents. Results of these analyses suggest that the spectacular large mammalian herbivores and carnivores are particularly susceptible to extinction because they require very large areas of appropriate habitat. Sixthly, the data and theories of insular mammal distributions are sufficiently precise to permit reasonably accurate predictions of the fates of island populations and faunas under alternative scenarios of natural and human-caused environmental change. It should now be possible to assess realistically the prospects for survival of many rare and endangered species and to apply sound scientific principles in the design and management of nature preserves. I shall end by considering some of the current problems and future prospects of contemporary mammalian biogeography.

THE MACARTHUR-WILSON MODEL

It is hard to find a paper on insular biogeography, in this symposium or elsewhere in the current literature, that does not cite the equilibrium model of MacArthur & Wilson (1963, 1967; hereafter abbreviated M–W). The idea that the number of species inhabiting an island represents a dynamic equilibrium between opposing rates of colonization and extinction remains the starting point of most investigations, which usually begin by testing the predictions of the familiar, elegantly simple graphical model showing effects of island size and isolation by distance on rates of extinction and colonization, respectively. The enduring value of the M–W model is not so much that it is right, as that it provides a robust conceptual framework for understanding the patterns of insular distribution and the ecological and evolutionary processes that have produced them.

In fact, I suspect that the model has ultimately proven more valuable when its predictions have been refuted than when they have been supported. Certainly this is true in the case of my own work. It was in trying to figure out why mammals and birds on mountaintops (Brown, 1971, 1978), fishes in lakes (Barbour & Brown, 1974), and arthropods on thistle plants (Brown & Kodric-Brown, 1977) were not distributed as the model predicted that we really began to understand the processes that determined the composition of these insular biotas. These cases are hardly unique. In the last two decades we have gone far beyond MacArthur and Wilson's simple idea to document and explain many of the complexities of insular distributions.

It is an interesting commentary on the role of theory in contemporary biology that so much of this progress can be attributed directly to falsification of the M–W model. That MacArthur and Wilson recognized this role of their theory is eloquently expressed in Crowell's recollection of MacArthur saying that a model is a lie which helps you to see the truth. This point seems to have been lost on the vociferous critics of the M–W model, most notably Sauer (1969) and Gilbert (1980), who have argued that the model is so oversimplified as to be of little value in understanding the real complexities of the distributions of particular kinds of organisms on different archipelagos.

Elsewhere (Brown, 1980; Brown & Gibson, 1983), I have discussed some of the features of the M–W model that have enabled it to remain a conceptual cornerstone of insular biogeography for more than two decades, serving, as Crowell says, as a null hypothesis against which to evaluate the real world. It is worth re-emphasizing these attributes, because many are so well exemplified in the contributions to this symposium. They include the following:

(1) MacArthur and Wilson shifted the emphasis of biogeographic investigation from attempts to reconstruct the histories of particular taxa to an

effort to understand the general processes that determine the diversity and composition of biotas. Under this new perspective, similarities and differences in the distributional patterns of different taxa became the basis for studies (such as Lawlor, 1986) that have used a comparative approach to identify the underlying mechanisms.

(2) The seminal insight—that there is a theoretical equilibrium between opposing origination and extinction processes—provided the basis for a wide variety of analyses and interpretations. Results of these studies revealed that some biotas represent an approximate equilibrium between opposing rates of contemporary colonization and extinction, as the model predicts (Crowell, 1986; Hanski, 1986; Lomolino, 1986). Other biotas, however, can be viewed as still changing in response to historical perturbations, either increasing in diversity owing to very low rates of colonization (Lawlor, 1986) and speciation (Heaney, 1986), or decreasing in richness owing to extinctions (Lawlor, 1986; Morgan & Woods, 1986; Patterson & Atmar 1986).

(3) The model employs variables that are relatively easy to measure. Many of these variables, such as number of species in the taxon of interest, island area, and distance of the island from the nearest mainland, can often be obtained from the literature. Others, such as colonization and extinction rates, require much more effort, but can be measured by long-term monitoring (Crowell, 1986; Hanski, 1986; Lomolino, 1986), perturbation experiments (Crowell, 1986), and careful collection and interpretation of fossils (Morgan & Woods, 1986).

(4) The model makes robust, qualitative predictions about how species richness and turnover rate should vary with island size and isolation. These predictions can be tested rigorously with quantitative data, and they have frequently been falsified unequivocally. Now investigators are not only testing the critical predictions about turnover rates (Crowell, 1986; Hanski, 1986; Lomolino, 1986), they are also extending the theory to make and test new predictions (Lomolino, 1986; Lawlor, 1986).

(5) The basic framework of the model has provided a valuable point of departure for investigating other important issues of biogeography. Examples in the present symposium include the degree of determinism in extinction and colonization rates (Patterson & Atmar, 1986; Hanski, 1986; Lomolino, 1986), the effects of interactions among species (Crowell, 1986; Hanski, 1986), the interpretation of faunal composition and endemism in archipelagos with complex histories (Heaney, 1986; Morgan & Woods, 1986), and the effectiveness of parks in preserving endangered native biotas (Newmark, 1986).

Like Darwin, Wallace, Mayr, Darlington, and Lack before them, MacArthur and Wilson recognized the potential of islands as replicated natural experiments for studying evolution, ecology and biogeography. Their unique and lasting contribution, however, was to show the kinds of patterns that could be documented and the kinds of processes that could be modelled to make biogeography the vigorous, modern, quantitative, hypothesis-testing science that it has become.

PATTERNS OF MAMMALS ON ISLANDS

Biogeography will always remain a discipline comprised largely of taxonomic specialists. There are several reasons for this. The basic data on distributions and phylogenetic affinities of taxa have traditionally been obtained by systematists and described in their literature. A sound knowledge of the phylogenetic affinities of insular forms is essential to frame realistic hypotheses about their geographic origins, pathways of colonization and patterns of evolutionary differentiation. A thorough knowledge of their biology is just as essential for understanding how historical events and ecological interactions have influenced their distribution.

Given the necessity of becoming a taxonomic specialist, mammals are an ideal group for a biogeographer to choose. No other taxon of comparable size has its basic biology so well known, exhibits such a wide variety of morphologies, physiologies and behaviours, and exemplifies such a diversity of distributional patterns and processes. As the papers in this symposium show, mammals provide excellent systems for investigating all kinds of biogeographic problems, from those attempting to reconstruct the history of colonization and speciation (Heaney, 1986) to those trying to understand the ecological dynamics of insular populations (Crowell, 1986; Hanski, 1986; Lomolino, 1986). That the diversity of mammalian form, function and distribution is expressed within the constraints imposed by a common evolutionary history and similar body plan, greatly facilitates comparative studies, such as Lawlor's (1986) tests of alternative hypotheses using comparisons of bats and small terrestrial mammals.

A survey of the papers in this symposium and in the recent literature illustrates the amazing diversity of insular distribution patterns exhibited by mammals. Colonizing abilities differ greatly among the taxa. As might be expected from their capacity for flight, bats are the most widely dispersed insular mammals. They have managed to reach such distant outposts as New Zealand and Hawaii and are well represented on larger, less isolated archipelagos such as the Philippines and West Indies (Darlington, 1957; Koopman, 1968, 1975; Lawlor, 1986; Heaney, 1986; Morgan & Woods, 1986). Other patterns of colonization are not so straightforward. Small mammals, especially rodents and insectivores, are reasonably good colonists, presumably in part because their habits facilitate rafting and other kinds of migration, and in part because there are so many individuals and species that begin to disperse that, just by chance, some manage to make long-distance journeys. Both taxa have managed to cross substantial water gaps, so that rodents inhabit the Galapagos, New Guinea and Australia and both taxa are found on Celebes, Madagascar and the West Indies (Darlington, 1957). But even these small mammals can surprise us. On the one hand, they readily cross 1 km or so of water, especially if they do not hibernate and can cross on ice in winter (Crowell, 1986; Hanski, 1986; Lomolino, 1986; see also Lomolino, 1982, 1984a, b). On the other hand larger water gaps and a few kilometres of unsuitable terrestrial habitat constitute such severe barriers that successful dispersal is extremely infrequent (Brown, 1971, 1978; Patterson, 1980; Lawlor, 1986; Heaney, 1986; Morgan & Woods, 1986). Many larger mammals, such as carnivores and ungulates, can disperse substantial distances by swimming or by travelling over ice or inhospitable land (Crowell, 1986).

Patterns of extinction are becoming increasingly well documented. The occurrence of extinctions no longer must be inferred from indirect distributional evidence, as it usually was in the past. Now, extinctions are increasingly well documented by direct observations of faunal turnover (Crowell, 1986; Hanski, 1986; Lomolino, 1986) and by the discovery of fossils (Morgan & Woods, 1986; see also Grayson, 1981; Thompson & Meade, 1982). Since extinction is typically regarded as a highly stochastic process, it is surprising how deterministic the extinctions of species on archipelagos have been. This is particularly apparent in the faunas of landbridge islands, which have been reduced by extinctions from once diverse continental biotas. The predictability of extinctions is evidenced by the tendencies of most species to be found only on islands above some threshold size (Lomolino, 1986), by the fact that certain insular faunas constitute highly non-random nested subsets of species (Patterson & Atmar, 1986; see also Diamond & May, 1976; Brown & Gibson, 1983), and by the infrequent occurrence of species that would have low population sizes because of attributes of large body size, carnivorous diet, or specialized habitat requirements (Heaney, 1986; see also Brown, 1971, 1978; Patterson, 1984; Heaney, 1984). These patterns of extinction have important implications for conservation and the design of natural reserves (Newmark, 1986), especially as it becomes apparent that some of them are true for spatial scales up to entire continents (see p. 240).

Because mammals, aside from bats, are such poor long-distance dispersers, the relatively few populations that have managed to reach distant islands and to persist there have been isolated from genetic exchange with related populations on other land masses or habitat patches. Such isolation, depending on the time and selective pressures involved, has led to genetic differentiation of insular races, species, and higher taxa. At its most extreme, insular differentiation has resulted in extensive adaptive radiation by the descendants of a single propagule. Mammals require lots of space, however, and such radiations have occurred only on large islands and archipelagos. The best known examples are the spectacular radiations that occurred on continent-sized islands: marsupials on Australia, several groups of both marsupials and placentals on South America (before its connection to North America; see Simpson, 1980), and lemurs on Madagascar. Less well known radiations of solenodontid insectivores in the West Indies (MacFadden, 1980) and of murid rodents in the islands of the Sunda Shelf (Heaney, 1986; see also Musser, 1977; Musser, Heaney & Rabor, 1985) are of particular interest because they involved repeated episodes of inter-island colonization followed by differentiation.

Despite several centuries of collecting and systematic work, the various levels of insular endemism remain incompletely documented and understood. Excellent case studies of patterns of differentiation and endemism within archipelagos (e.g. Lawlor's work in the Gulf of California, and Heaney's and Musser's studies in the Malaysian region) show the importance of basing biogeographic inferences on a sound knowledge of geological and climatic history, but accurate reconstructions of past land forms and climates are still undergoing extensive revision for most regions of the world. Endemic taxa are so numerous and diverse that there has as yet been no major effort to sort through the mass of data in search of general patterns. The kind of comparative approach that Lawlor (1986) has applied to species–area relationships seems to offer considerable promise for the analysis of endemism.

Trends in insular evolution, such as flightlessness, tameness, gigantism and dwarfism have long fascinated island biogeographers. Mammals have contributed most of the data for discussions of insular trends in the evolution of body size. The general pattern seems to be a 'central tendency': that is, small forms (especially rodents and insectivores) typically evolve giant forms on islands, whereas large mammals (carnivores and ungulates) usually evolve dwarfed races. Although it has not been a major topic of this symposium, the basis of these trends has been the subject of much discussion, most recently by Lomolino (1985, and references therein). Loss of flight and degeneration of wings is such a pervasive pattern in the evolution of many groups of insular birds and insects, that I wonder why there have apparently been no flightless bats and why this non-phenomenon has not received more discussion.

No discussion of insular evolution would be complete without an analysis of patterns of genetic differentiation. Most of the recent research on genetics of insular mammalian populations (and of continental ones) has focused on isozymic and karyotypic evolution (Berry, 1986). Epigenetic morphological traits may offer a valuable alternative to direct genic and chromosomal markers for assessing the roles of founder events, immigration, genetic drift, inbreeding and selection in the evolution of insular populations (Hanski, 1986; Berry, 1986). A particular benefit of morphological markers is that they can be assayed on museum specimens and even on fossils, providing invaluable information on the evolutionary history of insular populations, including those that are extinct or so endangered that additional collecting is impossible. The relationship between variation in these kinds of easily scored markers (whether they are genic, chromosomal or epigenetic) and those kinds of genetic changes that cause major, functionally significant modifications of the phenotype remains one of the most challenging problems of population biology. The kinds of advances discussed by Berry (1986) suggest that islands may prove to be excellent systems to investigate these genetic mechanisms, just as they have for studying other features of the evolutionary process.

CONCEPTUAL CONTRIBUTIONS OF MAMMALIAN STUDIES

Ever since Wallace's original work in the Malay Archipelago, many of the seminal contributions to biogeography have come from studies of mammals. And ever since the M–W model provided a theoretical perspective for investigating insular distributions, analyses of the diverse patterns exhibited by mammals on islands have contributed importantly to understanding the processes that determine the composition of insular biotas.

Some of the most significant contributions of mammalian studies have been methodological ones. It is easy to underestimate the importance of methodology. At least in these cases, methodological innovations have led to major conceptual advances and helped to resolve important questions.

Deterministic or random?

A nagging question raised by the M–W model is the extent to which insular distributions are deterministic or stochastic. MacArthur and Wilson themselves were unclear and almost contradictory on this point. On the one hand, the equilibrium model presents a very stochastic view of essentially random colonization and extinction events determining the richness of an insular biota; the names, taxonomic affinities and ecologies of the species are not considered to be important variables. Yet, MacArthur and Wilson clearly recognized that this was an oversimplification, and they studied cases in which differences among species in such attributes as mechanisms of dispersal, demography and competitive ability profoundly influenced the composition of insular biotas (MacArthur & Wilson, 1967; see also Wilson, 1959, 1961; MacArthur, 1972; MacArthur *et al.*, 1972, 1973).

Trying to distinguish between random and deterministic patterns and processes has continued to provide one of the major challenges in understanding insular distributions. A major contribution was made by Simberloff and his associates (e.g. Simberloff, 1978, 1980; Connor & Simberloff, 1978, 1979; Connor & McCoy, 1979), who advocated the development and testing of null or random hypotheses that assume a minimum of deterministic mechanism. Their analyses have tended to support a highly stochastic view of insular biogeography. In contrast, several of the contributions to this symposium (Patterson & Atmar, 1986; Lomolino, 1986; Lawlor, 1986; Crowell, 1986) advocate just the opposite viewpoint: that many of the differences among individual islands and entire archipelagos and among individual species and higher taxa can be explained, and hence predicted, in terms of measurable variation in the attributes of islands and organisms.

Although MacArthur & Wilson (1967) performed some simulations to show how probability of extinction could depend on population size and other demographic variables, extinction has long been regarded as a highly stochastic process. Certainly there is a significant element of chance, both in the fluctuations of any small population and in the environment, that may cause some of the variations. Nevertheless, the *relative* susceptibility to extinction of populations of different species or on different islands may be highly predictable. This is convincingly demonstrated by the analyses of Patterson & Atmar (1986), who have developed statistical techniques for determining whether the species compositions of islands within archipelagos differ from random assemblages. They find that landbridge islands, which are presumed to have biotas derived primarily by extinction from a common set of once widespread, continental species, exhibit non-random, nested subsets of species: i.e. each island with a successively smaller biota tends to have a subset of the species on more species-rich islands. Patterson & Atmar (1986) imply that the extinction process may be just as predictable in other situations, but its effect may be more difficult to detect when colonization as well as extinction has played a major role in determining the composition of the biota.

This latter problem is addressed by Lomolino (1986; see also Hanski, 1986), who has developed elegant techniques for determining the extent to which the occurrence of a species among the islands of an archipelago can be attributed to island size, distance from a source of species, or an interaction between these two variables. Like MacArthur and Wilson, Lomolino assumes that island size influences population size and hence extinction probability, and that distance from source affects colonization probability. Then, by analysing the incidence of each species as a function of these two variables, Lomolino is able to distinguish between species whose distributions are affected primarily by their capacities to immigrate from those whose distributions reflect mostly their ability to maintain viable populations on islands. That these assessments correspond well to our knowledge of the biology of the species supports the assumptions of the M–W model and the validity of Lomolino's analyses.

Equilibrium or non-equilibrium?

The issues addressed by the M–W model remain the fundamental problems of insular biogeography: does the biota of an individual island or an entire archipelago represent an equilibrium between origination and extinction processes, and what are the processes that determine the number, taxonomic relationships and ecological characteristics of the species? Several papers in this symposium address these questions. As mentioned above, the analyses of Patterson & Atmar (1986) and Lomolino (1986) provide valuable insights into the processes of extinction and colonization. Both studies lend additional support to my conclusion (Brown, 1971; see also Findley, 1969; Patterson, 1980, 1984; Grayson, 1981; Thompson & Mead, 1982) that the boreal mammal faunas inhabiting the isolated mountain ranges in the southwestern United States are not in equilibrium, but are relicts, derived by extinctions from a set of species that colonized when appropriate habitat connections existed in the Pleistocene. Lawlor's (1986) analysis supports a similar interpretation for the non-volant mammal faunas of continental islands that were connected to the mainland by landbridges during the Pleistocene.

On the other hand, the studies of Crowell (1986), Hanski (1986) and Lomolino (1986) on real islands in the Gulf of Maine, lakes of Finland, and St. Lawrence River, respectively, indicate that the mammalian faunas of these archipelagos are approximately in equilibrium between opposing rates of colonization and extinction. These studies (see also Crowell, 1973, 1983; Lomolino, 1982, 1984a, b) largely agree, not only in adducing evidence for ongoing colonization (from an inverse relationship between species richness and distance to a source of species and from observations of turnover in species composition over time), but also in the specific mechanisms of colonization (dispersal across ice in winter) and extinction (small population size owing to limited resources, interspecific competition and predation).

Yet another contrast is provided by Lawlor's conclusion that some oceanic islands and archipelagos are not in equilibrium, because colonization rate has been insufficient to achieve an equilibrium with the relatively low extinction rate, especially on large and distant islands. Lawlor's evidence is based primarily on systematic differences in the slopes of species–area curves between bats and non-volant mammals and between oceanic and landbridge islands. Although there is precedence for such comparisons (e.g. MacArthur & Wilson, 1967; Brown, 1971, 1978; Barbour & Brown, 1974), the biological meaning of species–area relationships and the kinds of inferences that can be drawn from differences in slopes have been questioned (Schoener, 1974; Connor & McCoy, 1979; but see Sugihara, 1981). The fact that Lawlor (1986) can make *a priori* predictions that are supported by subsequent analyses of data suggests that species–area relationships can embody important biogeographic information, especially when specific comparative hypotheses are carefully framed and tested so as to control for the effects of extraneous variables.

Another perspective on the problem of equilibrium is provided by Heaney (1980), who emphasizes the importance of speciation as well as colonization in contributing to the origination of insular species. In his paper, Heaney synthesizes a large body of primarily descriptive work (but see Musser, 1977; Musser *et al.*, 1985; Heaney, 1984, 1985) to understand the composition of the mammal faunas of the islands of the Philippines and Sunda Shelf. This region has been the scene of much tectonic and volcanic activity, and it has a complex history of land connections among islands and to the mainland of SE Asia during the Pleistocene. Not surprisingly, the relationships among the non-volant mammals are also complex and reflect the influences of these historical events on the processes of colonization, differentiation, speciation and extinction. Perhaps the most important contribution of Heaney's work is his analysis of patterns of endemism and taxonomic affinity, which permits convincing reconstructions of dispersal (over both landbridges and water gaps) and of differentiation and speciation of isolated populations. The composition of the fauna can be visualized as approaching an equilibrial species richness through repeated episodes of colonization and speciation opposed by episodic extinctions. Perhaps more realistically, the fauna can be viewed as being in a perpetual state of perturbation, because geological and ecological changes occur so rapidly relative to some of the origination and extinction processes that the hypothetical equilibrium is never attained. This sort of general model can probably be applied to other archipelagos (i.e. the West Indies; see below), large islands (i.e. Madagascar and New Guinea), and even to continents.

Heaney's (1986) and Berry's (1986) studies indicate the importance of obtaining a much better understanding of the process of speciation. In particular, when speciation occurs by geographic isolation, it is essential to know whether allopatry resulted from long-distance colonization by a few individuals or from a vicariance event that isolated large populations. Resolution of this question is crucial for resolving the role of founder effects and other evolutionary forces in the speciation process. Berry and Heaney show that for some islands it is possible to identify populations that have been isolated by each mechanism, to estimate the date of separation and to assess the direction and rate of genetic and phenotypic differentiation.

A final insight into the problems of trying to understand the dynamics of insular biotas comes from the synthesis of Morgan & Woods (1986) of the present and past distributions of West Indian mammals. Although they place much more emphasis on the unique evidence provided by an excellent fossil record, Morgan & Woods (1986) develop a general scenario that is remarkably similar to that of Heaney (1986) for the islands of SE Asia. The non-volant mammal fauna of the archipelago reflects a complex history of: colonization across water gaps, interisland connections during periods of low sea level, and ancient landbridges to the mainland; differentiation and speciation of populations isolated on different islands or in different regions within single large islands; and highly episodic extinction. Perhaps the most important and sobering lesson of their work, however, is the enormous number of extinctions that can apparently be attributed to the direct and indirect effects of humans, both aboriginal and modern. So many species have been lost since humans colonized these islands, that the present faunas (especially of the large islands, which once supported diverse species including many well-differentiated endemics) bear little resemblance to their late-Pleistocene antecedents. These findings (see also Crowell, 1986) illustrate the potential pitfalls of assuming that the biota of any island that has ever been settled or otherwise substantially affected by humans reflects 'natural' processes of origination and extinction, let alone some kind of equilibrium! Perhaps we can take some consolation from the fact that some of the general patterns of insular biogeography, such as species–area relationships and Lawlor's contrast between bats and non-volant forms, appear to persist in the West Indian mammals despite this enormous effect of human-caused extinctions.

Continents as islands?

The complexity of patterns and processes exhibited by the mammalian faunas of the SE Asian and West Indian archipelagos raises the question of whether and how the conceptual approach pioneered by MacArthur and Wilson can be applied to continental biogeography. This question has not been addressed comprehensively by any of the contributors to this symposium, but it is relevant here for several reasons. It represents a logical extension of ideas presented in several of the papers, but especially in those of Heaney (1986) and Morgan & Woods (1986). In fact, it offers the logical opportunity to generalize the entire approach of M–W, because from a biogeographic perspective continents are nothing more than very large islands with complex histories of climatic and geological change. Their faunas must reflect equally complex histories of colonization over both land and water, allochthonous and autochthonous differentiation, speciation and radiation, and highly episodic extinction owing to both natural causes and the effects of human beings. Any general theory of biogeography should apply to continents (and oceans) as well as to islands, and the same kinds of quantitative data are available to show patterns and test hypotheses.

Credit for first applying the M–W model to continents must go to my colleague Karl Flessa (1975, 1981), who analysed data on the distribution of mammalian genera from Walker (1968). Flessa's analyses demonstrated patterns of generic richness and affinities that suggested underlying mechanisms of colonization and extinction similar to those predicted by the M–W model. A positive relationship between number of genera and area of continent was closely fitted by a power curve and suggested that increasing extinction rates play a major role in limiting diversity on progressively smaller land masses. Flessa (1975) analysed data for all living mammals except marine forms. My plotting of genera- and species–area relationships for non-volant terrestrial mammals (Fig. 1) shows a similar pattern. Interestingly, as Lawlor predicts, the slope of the species–area relationship for non-volant mammals is very steep (z value$=0.48$) and diversity–area relationships are much steeper for non-volant mammals than for bats (e.g. z values for genera–area curves$=0.39$ and 0.18 for non-volant mammals and bats, respectively).

Flessa (1981) used measures of generic similarity (Jaccard coefficients) to assess colonization and interchange among continents. This analysis, performed for both the non-volant mammals and the entire terrestrial mammal fauna including bats, revealed that in both cases similarity in faunal composition at the generic level was closely and inversely correlated with the overland distance separating the continents. This suggests that there has been and probably still is substantial interchange among continental faunas, and that such colonization occurs primarily over land connections at a rate inversely proportional to the distance that must be travelled by dispersing individuals. Interestingly, Flessa obtained a closer inverse correlation between faunal similarity and overland distance when bats were included than when they were omitted. This does not

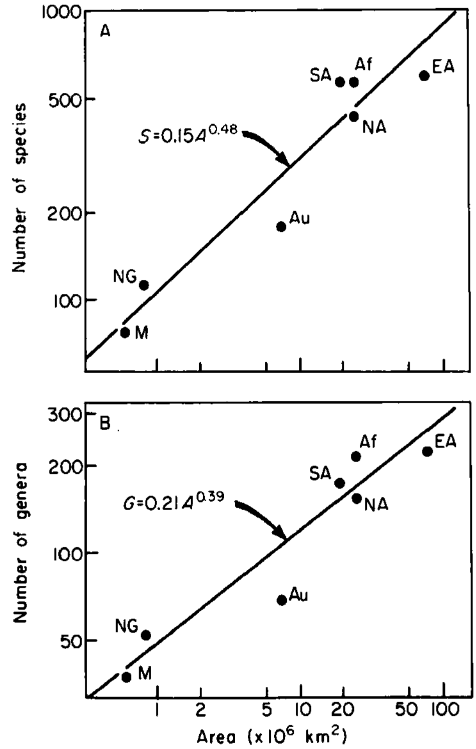

Figure 1. Plots on logarithmic axes of number of species (A) and genera (B) of non-volant terrestrial mammals inhabiting continents and large islands. The regression line and equation are shown. Land masses are identified as follows: New Guinea, NG; Madagascar, M; Australia, Au; South America, SA; North America, NA; Africa, Af; Eurasia, EA. Note the good fit of both regressions and the steep slope of the species–area relationship. (Species data from D. H. Wright, unpubl. obs.; genetic data from Nowak & Paradiso, 1983.)

indicate that bats are unable to colonize across large water gaps, because we know they have done so (e.g. Lawlor's analysis). Rather, it suggests that bats are excellent colonists that disperse over land even better than over water. Although Flessa does not emphasize this point, the overall magnitude of faunal dissimilarity among continents should be related to the degree of endemism, and hence reflect the extent to which the faunas have acted as isolated units, giving rise to distinctive taxa by speciation and evolutionary differentiation. Marshall and colleagues (Marshall *et al.*, 1982, Marshall, 1985) provide an excellent example of how these kinds of analyses and arguments can be applied to a particular case study. They account for the present composition of the South American mammal fauna in terms of colonization from other land masses (both over water gaps and the inter-American landbridge), autochthonous speciation, and extinction.

My student, Renee Rusler (unpubl. obs.), has analysed data obtained principally from Nowak & Paradiso (1983) on the body sizes of non-volant mammals in relation to their distribution among continents. Two patterns are of particular interest here. First, the relative number of large forms in the fauna, measured as the proportion of genera with median body mass exceeding some arbitrary threshold, increases directly with the area of the land mass (Fig. 2).

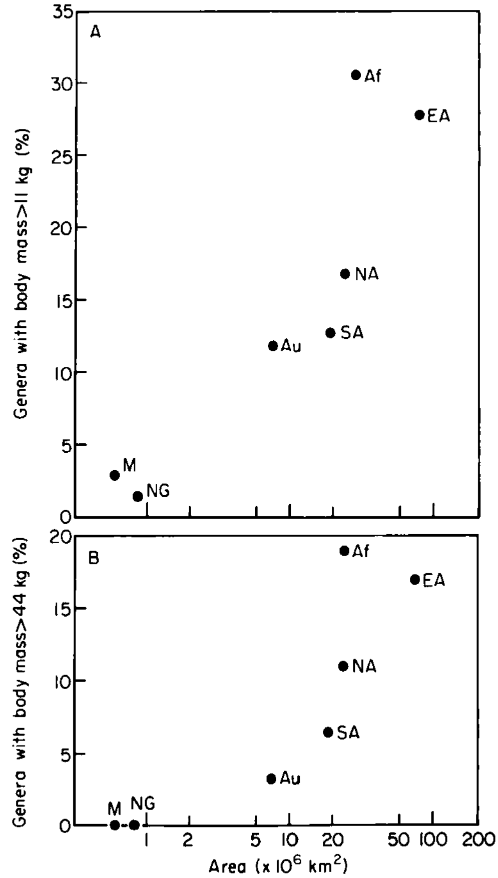

Figure 2. Plots of the percentage of mammalian genera with median body masses greater than two arbitrary values (11 and 44 kg) as a function of area of land mass on a logarithmic scale. Note that the proportion of genera of large body size in the fauna increases consistently with the size of the continent (data and analysis from R. Rusler, unpubl. obs.).

Secondly, the extent to which genera tend to be endemic to single land masses decreases with increasing body size, with the striking exception of the seven heaviest genera, which are without exception endemic to a single large continent (Fig. 3). Taken together, these patterns suggest that probability of extinction varies inversely with body size and hence with population density. Consequently, increasing land areas are required to support progressively larger mammals, and areas as large as the largest continents are necessary to maintain the largest living mammals over the time spans required for differentiation and radiation at the generic level. Since, in the last stages before its extinction, a taxon will tend to be restricted to a single region, we take the endemism of the largest mammals to single continents as evidence of high probabilities of extinction. Thus, this analysis complements that of Patterson & Atmar (1986) in providing independent evidence that variation in probability of extinction between taxa can be highly deterministic and can be attributed to biological variables that affect ecological attributes such as population size.

Taken together, the analyses of Flessa and Rusler suggest that the conceptual framework developed by MacArthur & Wilson (1963, 1967) for islands can

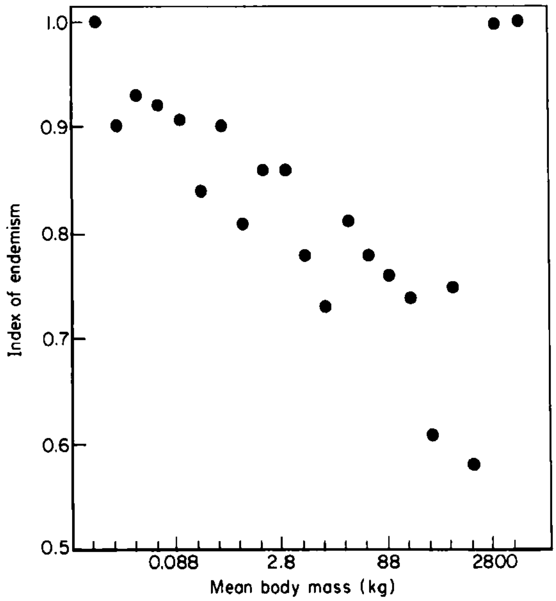

Figure 3. Plot of an index of endemism (1/the average number of continents inhabited) for genera of non-volant terrestrial mammals as a function of body size. Median body masses of genera were lumped into log_2 categories for analysis. Note that endemism decreases regularly with increasing size, except for the very largest genera which are all endemic to single continents (data and analysis from R. Rusler, unpubl. obs).

productively be applied to continents. As in the case of island biogeography, however, considerable modification of the original M–W model is necessary to deal with the complexity of patterns and processes that are exhibited at a continental scale. For example, it should be emphasized that the analyses of both Flessa and Rusler are based on the mammalian genera and species that survived into historical times and are documented in museum collections of contemporary forms. Thus, they do not include the numerous forms known to have disappeared in the late Pleistocene and/or early Holocene. Like the extinction of the West Indian island faunas documented by Morgan & Woods (1986), the demise of these mammals has been attributed in large part to the impact of humans (e.g. Martin & Klein, 1984).

APPLIED BIOGEOGRAPHY AND THE DESIGN OF NATURAL RESERVES

Applications of the M–W model of island biogeography to the design of natural reserves represent some of the first concerted efforts to apply theories of modern population biology to practical problems of ecosystem management. These efforts are now more than a decade old, and they have increased in sophistication with the theoretical and empirical advances of the field. These applications must be intensified if we are to preserve not only individual endangered species, such as the spectacular large mammalian carnivores and herbivores, but also entire habitats and ecosystems that support both human and non-human populations. Is the theory of biogeography and related areas of ecology and evolution up to this formidable task?

I do not think we know the answer to this question, and one could argue that we will know the answer only when it is negative and it is too late. On the other hand, I believe we are making progress rapidly, and that many beneficial results could be obtained by synthesizing and applying the kind of information contained in this symposium.

In particular, one of the important issues that has thus far been the subject of much controversy can now be largely resolved. There has been a long-standing debate about whether or not a single large reserve is preferable to several small ones of the same total area and habitat diversity, i.e. SLOSS: (e.g. Diamond, 1975; Terborgh, 1975; Wilson & Willis, 1975; Diamond & May, 1976; Forman, Galli & Leck, 1976; Galli, Lech & Forman, 1976; Simberloff & Abele, 1976, 1982; Whitcomb *et al.*, 1976; Simberloff, 1978; Kitchener *et al.*, 1980; Higgs, 1981; Reed, 1983; Lynch & Wigham, 1984; Wilcox, 1985). This problem is addressed cogently by Patterson & Atmar (1986). The nestedness expected in the distribution matrix (occurrence of species by islands) provides a rigorous theoretical basis for choosing the appropriate reserve design, but application of the theory requires detailed data on the variation in the environment and the requirements of the species.

In the absence of sufficient data (which is usually the case), the appropriate general model for reserve design is the biota of an archipelago of islands that were once interconnected but now are isolated by virtually absolute barriers. Mammals on isolated desert mountaintops (Brown, 1971, 1978; Patterson, 1980, 1984) or on continental shelf, landbridge islands (Lawlor, 1983, 1986) that have been isolated since the end of the Pleistocene provide excellent examples. Patterson & Atmar's (1986) demonstration that these faunas comprise highly nested subsets of species indicates the deterministic nature of extinction, and shows that species that are near the threshold of their area requirements (see also Lomolino, 1986; and data of R. Rusler presented above) should have a high probability of becoming extinct in all patches if the habitat is fragmented. The tendency of relictual faunas to occur as nested sets, together with their steep-sloped species–area relationships (Lawlor, 1986; see also Brown, 1971, 1978; Lawlor, 1983), means that a single large island preserves substantially more species of mammals than almost any combination of similar, but smaller islands. Such a large preserve will have to include the habitat types required by all species, however, or else it will have to be supplemented by other, presumably smaller, reserves that are designed specifically to preserve particular habitats and species.

From the perspective of conservation, the mammalian diversity supported by existing reserves can be misleading. For example, it is not surprising that Newmark (1986) reports many more species and a much lower slope for the species–area relationship for the mammals currently inhabiting National Parks in the western United States than Lawlor (1986) and I find for post-Pleistocene relictual insular faunas in islands of comparable habitat. This difference can be attributed to the fact many of the species that inhabit the parks also have substantial contiguous populations living outside the reserves, so that the persistence of these species cannot be attributed to the parks serving as the sole refuges. If all of the matrix between the parks were converted into uninhabitable terrain, the parks would be unable to preserve their present mammalian diversity (for an instructive mammalian example see Kitchener *et al.*, 1980). In fact, the diversity of relictual mammals on desert mountain tops would suggest that reserves of less than about 500 km^2 should lose more than half of their species in a few thousand years!

Furthermore, the loss of species would not be random. Species that maintain small populations because of large body size, carnivorous diet, specialized habitat requirements, or other constraints would be differentially lost by extinction from all preserves. In fact, Renee Rusler's analyses suggest that the largest mammalian carnivores and herbivores require continent-sized areas in order to persist, so even the largest reserves in the world will not be sufficient to prevent the inevitable extinction of these species if present trends of human population growth and habitat alteration continue. This raises the disturbing spectre of a future world mammal fauna of drastically reduced diversity, comprised primarily of small herbivorous and insectivorous species that can persist in the reserves, and of commensals and other forms that can live in the drastically man-modified habitats outside the parks. Clearly, to avert such a future we require increasing attention to problems of applied biogeography.

CRITIQUE AND PROSPECT

It would be easy to find some basis for criticizing all of the papers in this collection. Biogeography is such a large, diverse field that none of us can really master all of its many facets. I believe that one of the great strengths of mammalian biogeography during the last two decades has been its ability to produce empirically sound, conceptually important contributions without becoming embroiled in the often bitter, counterproductive ideological disputes that have dominated some parts of the discipline. It is easier to be a critic than a creator; it is easier to find fault with previous work than to evaluate its original contributions. In my role as commentator on this symposium, I have deliberately emphasized the positive. I have tried to synthesize the important data and ideas in the individual papers in order to assess the progress of the last twenty years and to point out the contributions of mammalian biogeographers to these advances.

But some general criticism of the subdiscipline of mammalian biogeography as represented by this symposium and the recent literature is warranted lest we become complacent. There are limitations and deficiencies in our present knowledge and approaches that require attention if mammalian biogeography is to maintain its position of prominence and leadership.

For one thing, we must avoid becoming too parochial and specialized. This symposium abundantly demonstrates that distributional patterns and processes are complex. To understand them accurately and completely requires that one know the geological and climatic history of the regions as well as their current geography and environments, and the past distribution and phylogenetic relationships of the organisms as well as their present ranges and ecological relationships. One must manage to keep abreast of the latest theory and statistical techniques, and still maintain the first-hand field experience with the regions and organisms that is essential to evaluate current ideas in a realistic context. One must know the distributional patterns of other groups in the same region and of the same group in other regions, because the similarities and differences offer valuable clues to the underlying processes. None of us can do all of these things really well, but we must do the best we can, admit our limitations and seek help to overcome them.

I suspect so many of us have chosen to study islands not just because islands are inherently interesting, but because, like Darwin & Wallace and MacArthur & Wilson before us, we believe that islands offer simplified, replicated, model systems for investigating more complex ecological, evolutionary and biogeographic problems. Up to a point, this perspective is justified, but we should question the extent to which islands provide good models for the more complex phenomena that are probably characteristic of continental and oceanic systems. Compare the satisfyingly simple patterns and processes invoked by Crowell (1986), Hanski (1986), and Lomolino (1986) to explain the distributions of a relatively few species on tiny islands, with the much more complex and tentative explanations advanced by Heaney (1986) and Morgan & Woods (1986) to account for the distribution and diversity of the mammalian faunas of the islands of SE Asia and the West Indies. Then imagine the problems of trying to explain the entire biogeography of South American or Eurasian mammals!

It is unfortunate that the kind of 'ecological' biogeography pioneered by MacArthur & Wilson (1963, 1967) and pursued by most of the contributors to this symposium, and the kind of 'historical' or 'vicariance' biogeography pioneered by Croizat (1958) and developed recently by Nelson, Platnick, Rosen and others (e.g. Nelson & Platnick, 1981; Nelson & Rosen, 1981), have developed as alternative, competing research programs. Although it is true that the former emphasizes dispersal and its role in the colonization of small islands, whereas the latter focuses on speciation and its effects on the distribution and diversification of biotas of large archipelagos and continents, the two approaches need not be mutually exclusive. In fact, as the studies of Heaney (1986), and Morgan & Woods (1986) clearly show, an integration of ecological and historical explanations is absolutely essential for understanding any reasonably complex distributional pattern. I predict that some of the greatest advances in biogeography in the next two decades will be made by those who have the breadth of knowledge and the courage to try to understand the distributions of organisms in terms of the influences of both ecological factors and historical events on the dynamics of colonization, speciation and extinction processes.

Perhaps one of the most important lessons of this symposium is that it is extremely difficult to account for the contemporary distribution of mammals on either islands or continents in terms of 'natural' patterns and processes that ignore or deliberately exclude the effects of human beings. Man has been an increasingly important part of the environment of mammals and other organisms for more than a million years. The distributions of all species of living mammals have been influenced by human activities. As shown by the studies of Crowell (1986), Heaney (1986), and Morgan & Woods (1986), it is virtually impossible to separate the effects of humans from 'natural' processes. It makes neither good sense nor good science to try. We must understand the world as it is, with man as an integral part of it. Basic as well as applied biogeographers must come to terms with this reality.

CONCLUSIONS

Two decades after its publication, the equilibrium model of MacArthur & Wilson (1963) continues to have enormous influence on the field of biogeography. This is not because the model itself provides an adequate explanation for the diverse patterns of insular distributions. The model, like most good models, is a deliberately oversimplified characterization of a much more complex reality. Often its assumptions have been shown to be incorrect and its predictions have been falsified. Nevertheless, the model continues to provide the conceptual foundation for an extremely successful research program that is largely responsible for the emergence of biogeography as a vigorous, modern, quantitative, hypothesis-testing science. As exemplified by the contributions to this symposium, the last two decades have seen real progress in understanding the distribution of organisms, especially among islands and other isolated patches of habitat.

This progress has occurred not so much because MacArthur and Wilson gave us the answers, but because they showed us how to ask the questions. The M–W model retains its influence because it still provides a conceptual framework that suggests interesting questions to ask, data sets to assemble, analyses to perform and alternative explanations to evaluate. This conceptual foundation, together with the numerous corrections, modifications, and extensions developed in the last two decades, provides the basis for interpreting the composition of biotas in terms of the interaction between the biological processes of colonization, extinction, and evolutionary differentiation and the historical and ecological settings in which these processes have occurred.

Studies of mammals have made major contributions to this endeavour. Mammals are amazingly diverse and this is reflected in a wide variety of distributional patterns. Bats are almost as vagile as birds, whereas terrestrial mammals are more sedentary than reptiles. Commensal murid rodents are currently colonizing and differentiating rapidly as they follow modern man around the world, whereas elephants have lost ground and diversity as they appear to be following the titanotheres and glyptodonts to extinction. The analysis of such diverse distributional patterns has enabled investigators working on mammals, from A. R. Wallace to G. G. Simpson to M. V. Lomolino, to make some of the most important conceptual contributions to biogeography.

This symposium suggests that the future of mammalian biogeography should be as bright as its past. There has been much progress in explaining the distribution of mammals, but much exciting work remains to be done. For good reason, we have tackled the easier problems first. Like Darwin & Wallace and MacArthur & Wilson, we have focused on islands because they provide small, replicated systems that facilitate analysis. The distributions of species and higher taxa within continents are more complex and for the most part remain to be deciphered. I believe it will require a combination of the approaches of MacArthur & Wilson, the recent promising developments in vicariance biogeography, and still additional conceptual advances of this magnitude before some of these continental distributions are well understood. In the meantime, we cannot delay applying our flawed and incomplete knowledge to the pressing problems of preserving natural ecosystems and their endangered native species, of which our nearest relatives, the mammals, comprise a distressingly large proportion.

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