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MAMMALS ON MOUNTAINTOPS: NONEQUILIBRIUM INSULAR BIOGEOGRAPHY

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INTRODUCTION

MacArthur and Wilson (1963, 1967) have provided a theoretical model to account for variation in the diversity of species on islands. This model, which attributes the number of species on an island to an equilibrium between rates of recurrent extinction and colonization, appears to account for the distribution of most kinds of animals and plants on oceanic islands. However, in addition to these islands, there are many other kinds of analogous habitats. Obvious examples are caves, desert oases, sphagnum bogs, and the boreal habitats of temperate and tropical mountaintops. It is of interest to ask whether the variables which determine the number of species on oceanic islands have similar effects on the biotas of other isolated habitats. For example, it has recently been shown that aquatic arthropods in caves (Culver 1970) and Andean birds in isolated paramo habitats (Vuilleumier 1970) are distributed as predicted by the equilibrium model of MacArthur and Wilson.

The boreal mammals of the Great Basin of North America provide excellent material for testing the generality of the equilibrium model. Almost all of Nevada and adjacent areas of Utah and California are covered by a vast sea of sagebrush desert, interrupted at irregular intervals by isolated mountain ranges. The cool, mesic habitats characteristic of the higher elevations in these ranges contain an assemblage of mammalian species derived from the boreal faunas of the major mountain ranges to the east (Rocky Mountains) and west (Sierra Nevada). Thanks largely to the work of Hall (1946), Durrant (1952), and Grinnell (1933), mammalian distributions within the Great Basin are documented quite thoroughly. I have used the work of these authors and data accumulated during 3 summers of my own field work in the Great Basin to produce the following analysis.

I shall show that the diversity and distribution of small mammals on the montane islands cannot be explained in terms of an equilibrium between colonization and extinction. Boreal mammals reached all of the islands during the Pleistocene; since then there have been extinctions but no colonizations.

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METHODS

The Montane Islands

Because mountains do not have discrete boundaries, islands were defined by operational criteria applied to topographic maps (U.S. Geological Survey maps of the states; scale 1:500,000). A mountain range was considered an island if it contained at least one peak higher than 10,000 feet and was isolated from all other highland areas by a valley at least 5 miles across below an elevation 7,500 feet. This altitude corresponds approximately to the lower border of montane piñon-juniper woodland. Application of the above criteria defined 17 islands (fig. 1; table 1) which lie in a sea, the Great Basin, between two mainlands, the Sierra Nevada to the west and the central mountains of Utah (a part of the Rocky Mountains) to the east. The sizes (areas) of the islands and the distances between islands and between islands and mainlands have been determined from the topographic maps.

The Boreal Mammals

As with the montane islands, the mammals restricted in range to the higher altitudes must be defined somewhat arbitrarily. I have selected those

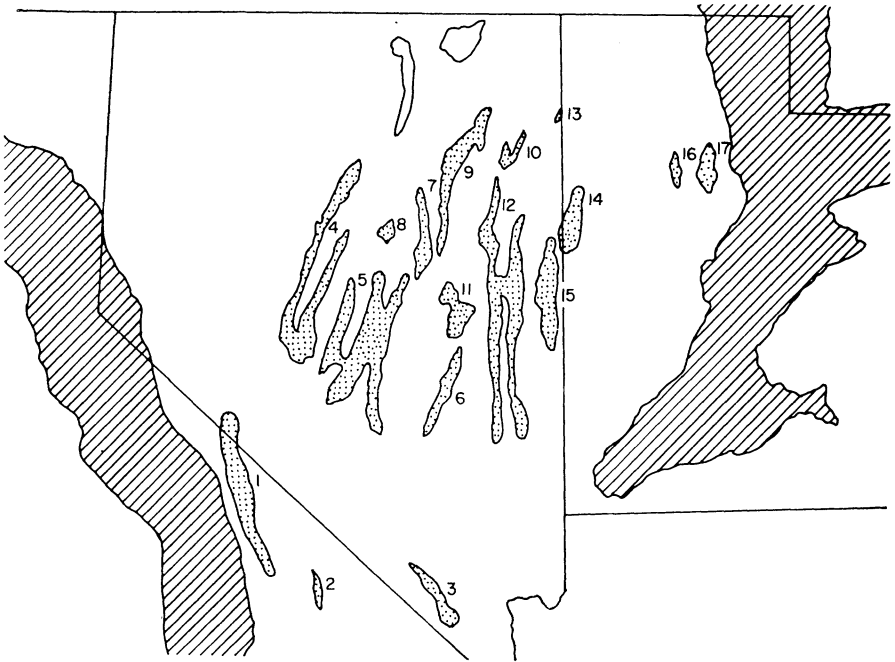


FIG. 1.—The Great Basin, with the montane islands lying between the Sierra Nevada (left) and Rocky Mountains (right). The shaded islands were used for the present analysis and are identified in table 1. The two unshaded islands were not used because they lie on the northern perimeter of the Great Basin and their faunas are poorly known.

TABLE 1
CHARACTERISTICS OF THE MOUNTAIN RANGES CONSIDERED AS ISLANDS

Mountain Range	Area above 7,500 Feet (Sq Miles)	Highest Peak (Ft)	Highest Pass* (Ft)	Nearest Island† (Miles)	Nearest Mainland (Miles)	Boreal Mammal Species (N)
1. White-Inyo	738	14,242	7,000	82	10	9
2. Panamint	47	11,045	5,500	19	52	1
3. Spring	125	11,918	3,500	108	125	3
4. Toiyabe	684	11,353	6,000	...	110	12
5. Toquima-Monitor	1,178	11,949	7,000	9	114	9
6. Grant	150	11,298	7,000	17	138	3
7. Diamond	159	10,614	7,000	7	190	4
8. Roberts Creek ...	52	10,133	7,000	22	216	4
9. Ruby	364	11,387	6,000	...	173	12
10. Spruce	49	10,262	6,500	12	156	3
11. White Pine	262	11,188	7,000	43	150	6
12. Schell Creek-Egan	1,020	11,883	7,000	11	114	7
13. Pilot	12	10,704	5,000	33	114	2
14. Deep Creek	223	12,101	7,000	9	104	6
15. Snake	417	13,063	7,000	76	89	8
16. Stansbury	56	11,031	6,000	4	39	3
17. Oquirrh	82	10,704	5,500	88	19	5

* Elevation of the highest pass separating the island from the mainland or from another island with more species.

† Distance to the nearest island with more species. No distance is given for the Toiyabe and Ruby Mountains because no other islands have more species.

species that occur only at high elevations in the Rockies and Sierra Nevada and are unlikely to be found below 7,500 feet at the latitudes of the Great Basin. I have excluded large carnivores and ungulates from the analysis because their distributions were drastically altered by human activity before accurate records were kept. I have also ignored the bats because their distributions are very poorly known and because their dispersal by flight introduces a completely new variable that could only complicate the present discussion. After these omissions, there remain 15 species of mammals (table 2) which occur in the Sierra Nevada and Rocky Mountains and on at least one of the montane islands of the Great Basin. All of these species occur in piñon-juniper, meadow, or riparian habitats. A striking feature of the mammalian faunas of the isolated peaks is the absence of those species which are restricted to dense forests of yellow pine, spruce, and fir in the Sierra Nevada and Rocky Mountains. None of these species, which include *Martes americana*, *Aplodontia rufa*, *Eutamias speciosus*, *Tamiasciurus hudsonicus*, *T. douglasi*, *Glaucomys sabrinus*, *Clethrionomys gapperi*, and *Lepus americanus*, are found on any of the isolated mountain ranges of the Great Basin, even though some of the large islands have large areas of apparently suitable habitat. However, the well-developed coniferous forests on the large islands have a good sample of the avian species characteristic of these habitats on the mainlands.

Records of occurrence are taken from the literature (Hall 1946; Hall and Kelson 1959; Durrant 1952; Durrant, Lee, and Hansen 1955; Grinnell 1933) and from my own observations which concentrated on the small mountain ranges. Undoubtedly, there are a few errors of omission that will

TABLE 2
CHARACTERISTICS AND DISTRIBUTION IN THE GREAT BASIN OF THE FIFTEEN SPECIES OF BOREAL MAMMALS CONSIDERED

SPECIES	BODY WEIGHT (g)	HABITAT AND DIET	ISLANDS INHABITED															TOTAL NO. ISLANDS INHABITED		
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		16	17
<i>Sorex vagrans</i> *	6.7	Carnivore	X	X	X	X	6
<i>Sorex palustris</i>	14	Carnivore	X	X	6
<i>Mustela erminea</i>	58	Carnivore	X	X	3
<i>Marmota flaviventris</i>	3,000	General herbivore	X	X	X	X	X	9
<i>Spermophilus lateralis</i> ..	147	General herbivore	X	..	X	X	X	..	X	X	X	X	X	X	X	X	X	X	..	13
<i>Spermophilus beldingi</i> ..	382	Meadow herbivore	X	3
<i>Eutamias umbrinus</i> † ..	57	General herbivore	X	..	X	X	X	X	X	X	X	X	X	X	X	X	X	X	..	14
<i>Thomomys talpoides</i>	102	Deep soil herbivore	X	X	8
<i>Microtus longicaudus</i> ..	47	General herbivore	X	X	12
<i>Neotoma cinerea</i>	317	General herbivore	X	X	X	X	14
<i>Zapus princeps</i>	38	Riparian herbivore	X	4
<i>Ochotona princeps</i>	121	Talus herbivore	X	X	4
<i>Lepus townsendi</i>	2,500	Meadow herbivore	1

* On island 17 the species is *Sorex obscurus*, a Rocky Mountain form, which forms a superspecies with *S. vagrans*.

† On island 3 the species is *Eutamias palmeri*, an endemic, which forms a superspecies with *E. umbrinus*.

be revealed by more intensive collecting, but these should not affect the present analysis significantly.

RESULTS AND DISCUSSION

Island Area and Extinction

The number of mammalian species inhabiting a montane island is closely correlated with the area of the island (fig. 2). When both variables are plotted logarithmically, the data are well described ($r = .82$) by a straight line with a slope (z) of .43. Four comparable areas on the mainland (Sierra Nevada) have more species and the species-area curve has much less slope ($z = .12$). These areas can be considered as "saturated" with suitable species. These relationships are similar to those described for various groups of animals and plants on oceanic islands and continental mainlands (MacArthur and Wilson 1967; Johnson, Mason, and Raven 1968) and for birds on tropical montane islands in South America (Vuilleumier 1970), except that the z value describing the data for mammals on montane islands is

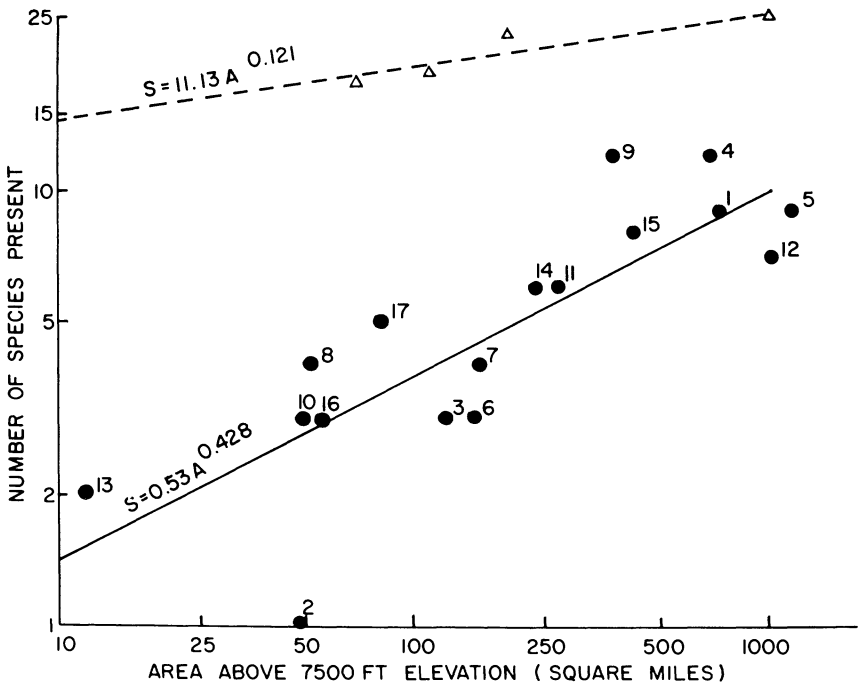


FIG. 2.—Double logarithmic plot of number of species of boreal mammals against area for the 17 montane islands (circles) listed in table 1. The solid line indicates the relationship between number of species (S) and area (A) fitted by least-squares regression. The dashed line represents the "saturation values" based on four areas (triangles) in the Sierra Nevada; data are from Hall (1946) and Grinnell (1933).

considerably higher than most of the values (.24-.34) previously obtained for insular biotas.

Local areas acquire species by immigration and lose them by extinction. In the absence of historical perturbations and speciation, the number of species inhabiting an area will represent an equilibrium between the opposing rates of extinction and immigration. The biotas of most continental areas and oceanic islands (including islands on the continental shelf) approximate such an equilibrium condition (Preston 1962*a*, 1962*b*; MacArthur and Wilson 1963, 1967; Diamond 1969; Simberloff and Wilson 1969). Rates of extinction are dependent largely on population size and, in the absence of recurrent colonization, should be similar for comparable areas of islands or mainlands; to the extent that the absence of competitors results in greater population densities on islands, extinction rates should be slightly lower for islands than for comparable areas on mainlands. Islands, because of their isolation, have much lower rates of immigration (colonization) than local areas of comparable size within relatively homogeneous habitat on mainlands. The net result is that the slope of the species-area curve should be related to the degree of isolation of the islands concerned—the lower the rate of colonization, the higher the z value. The fact that the z value obtained in the present study is higher than the range observed for the biotas of oceanic islands (MacArthur and Wilson 1967) indicates that boreal mammals have an exceptionally low rate of immigration to isolated mountains.

The population size (and, hence, probability of extinction on an island) for a species is greatly affected by three variables—body size, trophic level, and habitat specialization. These variables affect the distribution of mammalian species on montane islands in the manner we would expect from considerations of their effects on population size: small mammals are found on more islands than large ones, herbivores are better represented than carnivores, and herbivores that can live in most montane habitats inhabit more islands than herbivores which can live only in restricted habitats (fig. 3). Those species which occur on only a few islands usually are found only on large islands (see tables 1 and 2). Thus, at least for mammals on montane islands, insular area not only affects the number of species but also can be used to predict quite reliably some ecological attributes of those species which are present.

Distance from the Mainland, Climatic Change, and Colonization

It is frequently observed that the number of species on an island is related to the proximity of the island to the nearest mainland as well as to the size of the island. This suggests that the probability of colonization of an island by new species from the mainland is proportional to the distance involved and that recurrent colonization of islands occurs at a rate sufficient to offset partially the extinction of species. Using this sort of reason-

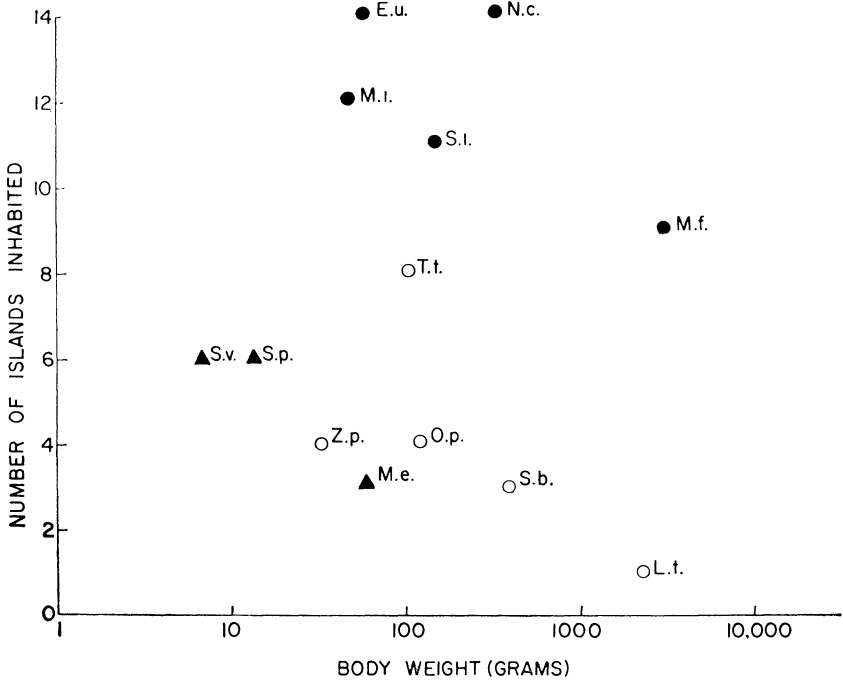


FIG. 3.—Frequency of occurrence on the montane islands of species of boreal mammals plotted against their body weight; shaded circles represent herbivores which are found in most habitats, unshaded circles indicate herbivores with specialized habitat requirements, triangles denote carnivores. The abbreviations are of species names which can be identified by reference to table 2.

ing, MacArthur and Wilson (1963) have proposed a model which represents the number of species on an island as a dynamic equilibrium between rates of colonization and extinction. The effect of recurrent colonization on species diversity is usually assessed by expressing the number of species on an island as a percentage of the number present in an area of the same size on the mainland and plotting this percentage saturation against the distance to the nearest mainland. When this is done for the montane mammals of the Great Basin, no relationship ($r = .005$) is observed (fig. 4). This is in marked contrast to the inverse correlation predicted by the equilibrium model and observed for various groups of organisms on oceanic islands (MacArthur and Wilson 1967) and for birds on montane islands (Vuilleumier 1970).

Before concluding that recurrent colonization has not been a significant factor in determining the diversity of mammals on the montane islands, it is necessary to exclude three alternative explanations: (1) Differences in habitat between islands may be sufficiently great to obscure the distance effect (see Diamond 1969). The montane islands of the Great Basin have similar vegetation, climate, and geomorphology; but they differ somewhat in elevation, which may affect the amount and diversity of boreal habitats

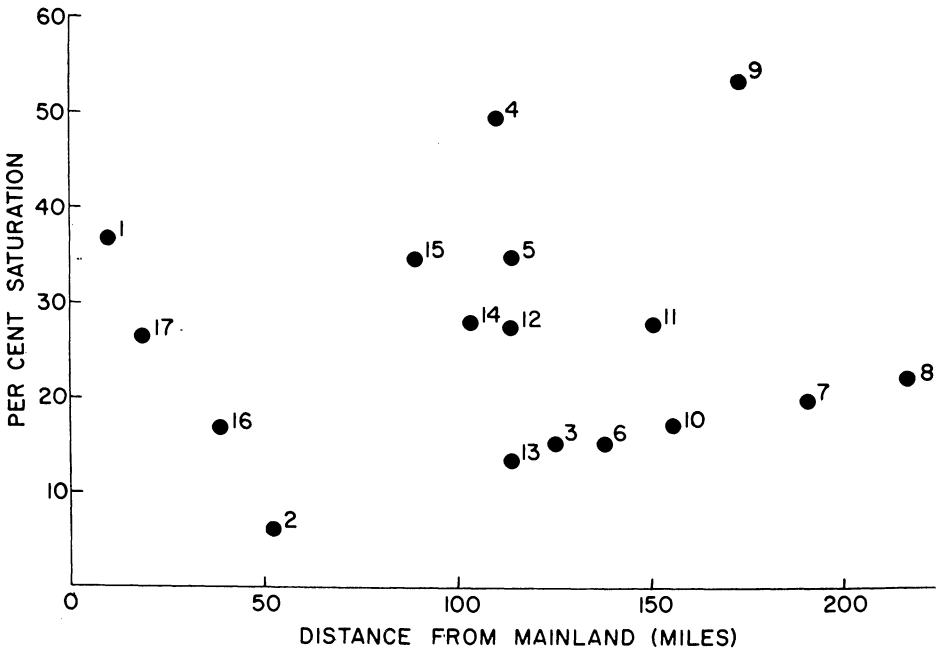


FIG. 4.—Percentage of faunal saturation plotted against distance from the Sierra Nevada or Rocky Mountains, whichever is nearer, for the 17 montane islands listed in table 1. Percentage of saturation is defined in the text.

in a manner different from insular area. (2) The islands may acquire most of their mammalian colonists from other islands (by a stepping-stone process) rather than directly from the nearest mainland, so that distance between islands might be an important variable affecting immigration. If this is so, the nearest island with more species is the most likely source of colonists if it is nearer than the closest mainland. (3) The effectiveness of the desert barriers surrounding the islands rather than the distance between mountains may be the most important variable influencing the rate of colonization. If this is true, the altitude of the highest pass should be the best measure available of the severity of the climatic and habitat barriers which separate the mountain ranges.

The possibility that any of these three explanations may account for some of the variability in insular-species diversity and provide evidence of the effects of immigration can be evaluated by subjecting the data in table 1 to stepwise multiple regression analysis. The results of such analysis using a linear model are shown in table 3. Again it is apparent that the number of mammalian species inhabiting an island is closely related to insular area, although the correlation is not as good as when a logarithmic model is used. Neither elevation of the highest peak nor any of the three variables (distance from nearest mainland, distance from nearest mountain with more species, elevation of highest intervening pass) which might be expected to

TABLE 3
 INFLUENCE OF SEVERAL VARIABLES ON THE NUMBER OF SPECIES OF SMALL MAMMALS
 INHABITING MONTANE ISLANDS IN THE GREAT BASIN ANALYZED BY
 STEPWISE MULTIPLE REGRESSION USING LINEAR MODEL^a

Variable	Contribution to R^2	F Value	Order Entered in Equation
Area49421	14.65*	1
Highest peak00006	0.32	2
Nearest mainland00042	0.83	3
Nearest island00002	0.16	4
Highest pass00000	0.04	5
Total R^249471

^a Data are from table 1.

* Significant at 1% level; the other F values are not significant.

influence immigration rate contributes significantly to the reduction of the remaining variability in the number of insular species. Apparently, at the present time the rate of colonization of the islands is effectively zero. The desert valleys of the Great Basin are virtually absolute barriers to dispersal by small boreal mammals.

I conclude that the boreal mammalian faunas of the montane islands of the Great Basin do not represent equilibria between recurrent rates of colonization and extinction. This is somewhat surprising, because conditions of dynamic equilibria with surprisingly high and measurable steady state turnover rates have been documented for some oceanic islands (see MacArthur and Wilson 1967, on Krakatau; Simberloff and Wilson 1969, Diamond 1969). However, my explanation for the distribution of boreal mammals on the montane islands of the Great Basin—that all the islands were inhabited by a common pool of species at some time in the past and subsequent extinctions have reduced the number of species on individual islands to their present levels—is consistent with what we know of the paleoclimatic history of the Southwest and the way small mammals disperse over land.

At intervals during the Pleistocene, colder climates in the Southwest forced piñon-juniper woodland down to elevations approximately 2,000 feet below their present distribution (Wells and Berger 1967). This was sufficient to make piñon-juniper and associated streamside and meadow habitats contiguous across most of the Great Basin perhaps as recently as 8,000 years ago. The climatic and habitat barriers between the isolated peaks and the mainlands were removed for an entire set of species; these paleoclimatic and habitat shifts are sufficient to account for all 15 species of boreal mammals now found on the montane islands. Two lines of evidence indicate that the islands were colonized in this manner. First, the limited fossil evidence indicates that some of the boreal mammals that are now confined to only a few of the islands were more widely distributed in the late Pleistocene; for example, Wells and Jorgensen (1964) found fossils of *Marmota flaviventer* in the Spring Range in southern Nevada. Second, paleobotanical evidence indicates that the climate changes during the Pleistocene were not sufficient

to connect the dense coniferous forests of yellow pine, spruce, and fir between the islands and the mainlands. Those mammalian species which are restricted to such forests in the Sierra Nevada and Rocky Mountains are absent from all of the isolated peaks in the Great Basin, even though there are large areas of suitable habitat on several of the larger islands. It is apparent that the islands have been colonized only during those periods in the past when the climatic and habitat barriers which now isolate them were temporarily abolished.

A few thousand feet of elevation, with the associated differences in climate and habitat, constitute a nearly absolute barrier to dispersal by small mammals (with the exception of bats). This is not surprising in view of the fact that small mammals must disperse over land on foot. It may take several days for an individual to travel only a few miles, and during this period it must obtain food and avoid predation in an unfamiliar habitat and survive the stresses imposed by a different climate.

GENERAL DISCUSSION

The mammalian faunas of the isolated mountains in the Great Basin do not represent equilibria between rates of extinction and colonization. This is shown by the unusually steep slope of the species-area curve and by the lack of correlation between the percentage saturation of the insular faunas and any of the variables (distance to mainland, distance between islands, and elevation of surrounding valleys) likely to influence the probability of immigration to an island. The diversity of mammalian species on the mountaintops must be explained by historical events (climatic changes during the Pleistocene) which temporarily abolished the isolation of the mountains and permitted their colonization by a group of mammalian species. Subsequent extinctions, related to island size, have reduced the faunas of each island but not sufficiently to restore equilibrium with the vanishingly small rates of colonization. Approximately 8,000 years after their isolation, the largest islands still have almost all of their original species of boreal mammals, and even on the smallest islands one or more species remain. This suggests that the rate of extinction is very low once the biota of the island has initially adjusted to its isolation; when colonization rates approach zero, extinction of all species is reached only in geological time spans.

Island biotas which do not represent equilibria between rates of extinction and colonization should be fairly common, particularly in the temperate zones where the climatic fluctuations of the Pleistocene have drastically altered the distribution of terrestrial and freshwater habitats. Some organisms are capable of crossing the barriers between isolated habitats, and these may be expected to have distributions predicted by the equilibrium model. Examples are the birds, bats, flying insects, and most kinds of plants on montane islands. However, other groups of organisms

are unable to cross the barriers between insular habitats, and these should be distributed as relicts in a nonequilibrium pattern similar to the montane mammals described here. Likely examples are amphibians, reptiles, and large, nonflying arthropods on mountaintops and fish in isolated bodies of fresh water. The fish fauna of the isolated springs and streams of the Great Basin clearly does not represent an equilibrium situation; these habitats were colonized in the Pleistocene when there were aquatic connections between them, and extinctions have subsequently reduced the fauna of each isolate to its present composition (Hubbs and Miller 1948). Certainly, other nonequilibrium patterns of island distributions will be described. In those cases where environmental changes (often the result of human activity) have caused massive extinctions, the number of species on an island will be less than the equilibrium number.

SUMMARY

An analysis of the distribution of the small boreal mammals (excluding bats) on isolated mountaintops in the Great Basin led to the following conclusions:

1. The species-area curve is considerably steeper ($z = .43$) than the curves usually obtained for insular biotas.
2. There is no correlation between number of species of boreal mammals and variables which are likely to affect the probability of colonization, such as distance between island and mainland, distance between islands, and elevation of intervening passes. Apparently the present rate of immigration of boreal mammals to isolated mountains is effectively zero.
3. Paleontological evidence suggests that the mountains were colonized by a group of species during the Pleistocene when the climatic barriers that currently isolate them were abolished.
4. Subsequent to isolation of the mountains, extinctions have reduced the faunal diversity to present levels. Probability of extinction is inversely related to population size and, therefore, is influenced by body size, diet, and habitat. The rate of extinction has been low, and all of the islands still have one or more species of boreal mammals.
5. The mammalian faunas of the mountaintops are true relicts and do not represent equilibria between rates of colonization and extinction.

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