EVOLUTION OF THE INSULAR HERPETOFAUNAS

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For the purposes of the present discussion the islands off southern California and the Pacific coast of northern Baja California, Mexico, may be grouped into three geographic units, (1) the Northern Channel Islands: San Miguel, Santa Rosa, Santa Cruz, and the Anacapas; (2) the Southern Channel Islands: Santa Barbara, San Nicolas, Santa Catalina, and San Clemente; and (3) the islands off Baja California: Los Coronados, Todos Santos, San Martin, San Geronimo, Cedros, the San Benitos, Natividad, and Guadalupe. The herpetofauna of the northern group consists of two salamanders, one frog, three lizards, and three snakes, for a total of nine species. The Southern Channel Islands support a fauna of 12 species: two salamanders, one frog, four lizards, and five snakes. The Baja California series includes two salamanders, one frog, 11 lizards, and eight snakes, for a total herpetofauna of 22 species. In total, 28 species of amphibians and reptiles are known from these islands (table 1). Twenty-four of the insular forms are also found on the nearby mainland. Three species endemic to Isla de Cedros (*Gerrhonotus cedroensis*, *Phrynosoma cerroense*, and *Crotalus exsul*) are allopatric insular derivatives of widespread mainland forms. One genus and species of lizards is endemic to certain of the Southern Channel Islands, and one salamander from the northern group is known elsewhere from scattered localities in California and Baja California far removed from its insular habitat.

The Northern and Southern Channel Islands are covered predominantly by coastal sage scrub vegetation. Chaparral and oak woodland occur on the largest islands. The small islands off northern Baja California also support coastal sage scrub communities. Natividad, the San Benitos, and most of Cedros are covered by a desert scrub vegetation. A closed-cone pine association mixed with chaparral occurs at high elevations on the latter island. The flora of Guadalupe has been discussed in detail in the present symposium by Dr. Reid Moran, and the major aspects of its vegetation correspond to those of Cedros. Because of the moderating effects of the sea and the greater rainfall, the islands have a milder and more moist climate than the immediately adja-

	San Miguel	Santa Rosa	Santa Cruz	Anacapas	Santa Barbara	San Nicolas	Santa Catalina	San Clemente	Los Coronados	Todos Santos	San Martin	San Geronimo	Cedros	San Benitos	Natividad	Guadalupe
SALAMANDERS																
Aneides lugubris							x		x							
Batrachoseps pacificus	x	x	x	x			x		x	x						
Batrachoseps sp.			x													
FROGS																
Hyla regilla		x	x				x						x			
LIZARDS																
Coleonyx variegatus													x			
Crotaphytus wislizenii													x			
Uta stansburiana			x	x		x	x	x	x	x	x	x	x	x	x	
Sceloporus magister													x			
Sceloporus occidentalis	x	x	x													
Phrynosoma cerroense													x			
Klauberina riversiana					x	x		x								
Cnemidophorus tigris									x				x		x	
Eumeces skiltonianus							x		x	x						
Gerrhonotus cedroensis													x			
Gerrhonotus multicarinatus	x	x	x	x			x		x		x					
Anniella geronimensis												x				
Anniella pulchra									x	x						
SNAKES																
Leptotyphlops humilis													x			
Lichanura trivirgata															x	
Thamnophis couchii							x									
Diadophis punctatus							x			x	x					
Coluber constrictor			x													
Lampropeltis getulus							x									
Lampropeltis zonata										x						
Pituophis melanoleucus			x				x		x		x		x			
Hypsiglena ochrorhyncha			x						x		x		x			
Crotalus exsul													x			
Crotalus viridis							x		x							
TOTALS	3	4	9	3	1	2	11	2	10	6	5	2	12	1	3	0
Km from mainland	42	44	30	20	61	98	32	79	13	6	5	9	23	66	7	252
Area Km^2	37	217	249	2.9	2.6	58	194	145	2.5	1.2	2.3	0.4	348	6.4	7.2	255
Km^2/species	12	54	28	1.0	2.6	29	18	73	0.3	0.2	0.5	0.2	29	6.4	2.4	–

cent mainland areas; and the more humid and uniform climate is reflected in vegetation and fauna.

By comparison with the species of amphibians and reptiles found in similar plant communities in Ventura, Los Angeles, and San Diego counties, the island herpetofaunas appear to be depauperate mainland derivatives. In Ventura County, opposite the Northern Channel Islands, comparable habitats support three salamanders, two frogs, seven lizards, and eight snakes, for a total of 20 species. Santa Cruz, the largest island in this group, has a fauna of only nine forms. Santa Catalina in the southern group has a herpetofauna of 11 species as compared to five salamanders, four frogs, nine lizards, and 16 snakes (a total of 34 forms) from similar habitats in Los Angeles County. Because of maritime conditions, the islands off Baja California resemble San Diego County more closely in vegetation and fauna than they do the immediately adjacent areas of the xeric Baja coast. A total of 36 amphibians and reptiles (comprised of four salamanders, four frogs, 11 lizards, and 17 snakes) are found in appropriate habitats in San Diego County, as compared to 12 species on Isla de Cedros.

The relationship of insular surface area to the number of species found on a particular island has been discussed by MacArthur and Wilson (1963) and by Raven (in this symposium). In an attempt to determine the relative role of distance from the mainland and the area of each island as factors in limiting species diversity, a log-log graph (fig. 1) of species number versus area has been prepared from the presented data (table 1). The Santa Monica Mountains of Los Angeles County, with an area of about 829 square kilometers and a herpetofauna of 34 species, have been used as a mainland point of reference. On the basis of these data and the graph, it is obvious that the herpetofaunal composition of the various islands is not strictly correlated with area. Nevertheless, one series of islands (the San Benitos, San Miguel, Santa Catalina, Santa Cruz, and Cedros) supports herpetofaunas directly proportional to area. A second group (Santa Barbara, San Geronimo, Natividad, the Anacapas, San Martin, Todos Santos, and Los Coronados) has significantly larger herpetofaunas than would be expected if area alone were responsible. A third group (Guadalupe, San Clemente, San Nicolas, and Santa Rosa) has significantly fewer species in the herpetofaunas than would be anticipated on the basis of island size.

The islands fall into three geographic categories on the basis of size and distance from the adjacent mainland:

I. Inshore Islands, less than 75 kilometers from mainland

A. Small Islands, less than 10 square kilometers:

the San Benitos, Santa Barbara, San Geronimo, Nativi-

dad, the Anacapas, San Martin, Todos Santos, and Los Coronados

B. Large Islands, more than 10 square kilometers:

San Miguel, Santa Rosa, Santa Cruz, Santa Catalina, and Cedros

II. Large Offshore Islands, more than 10 square kilometers and more than 75 kilometers from mainland:

Guadalupe, San Clemente, and San Nicolas

Among inshore islands the large islands, exclusive of Santa Rosa, support a herpetofauna proportional to area as compared to the mainland (values of 12-29 km^2/species on the islands, 25 km^2/species for the Santa Monica Mountains). The small inshore islands, exclusive of the San Benitos, have herpetofaunas proportionally larger per unit area as compared to the mainland or large inshore islands (values to 2.6 km^2/species). Two of the offshore islands, Guadalupe and San Clemente, have extremely depauperate faunas (values of greater than 70 km^2/species). On the other hand, San Nicolas, a large offshore island, is comparable to Cedros Island (29 km^2/species); and Santa Rosa, a large inshore island, (with 54 km^2/species) is somewhat intermediate between the large offshore and the other large inshore islands. The value for the San Benitos, a small inshore island group, is close to those for other small islands but approaches the value for large inshore islands, perhaps a reflection of its considerable distance from the mainland (66 km).

These data indicate that the compositions of insular biotas are most strongly influenced by the area of the islands, particularly in inshore areas, and by the distance from shore. As seen in the table (table 1) and reflected in the graph (fig. 1), the number of species on the large islands decreases generally proportionally to distance from the mainland. If San Geronimo and Natividad are ignored, a similar trend is seen for the small inshore islands. The data further suggest that any recent land connection of the offshore to the mainland is unlikely; otherwise species/area relationships for the offshore islands would deviate less significantly from the line for inshore large islands. The high number of species per unit area for small inshore islands might, at first sight, suggest previous land connections; but the depauperate composition and distinctive non-recurrent species assemblages tend to refute such a view. In addition, if a connection existed, the values for species/area for the small islands should be proportional to mainland areas, which they are not except in the case of the San Benitos. Inshore large islands, although comparable in species/area relations to the mainland, also tend to have distinctive non-recurrent herpetofaunas, strong evidence that no

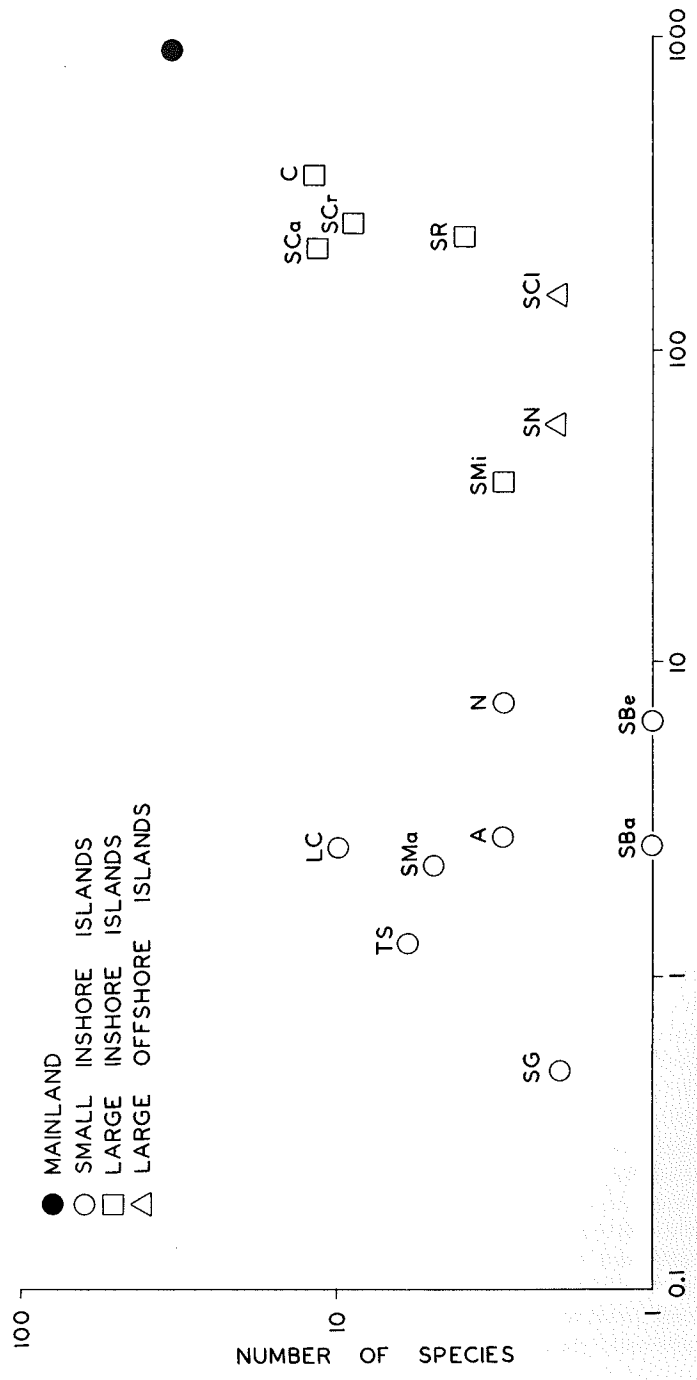

Fig. 1. Graph of relation between size of herpetofauna and insular area for the Southern California Islands and the islands off Baja California. Abbreviations for islands as follows: A = the Anacapas, C = Cedros, LC = Los Coronados, N = Natividad, SBa = Santa Barbara, SBe = the San Benitos, SCa = Santa Catalina, SCl = San Clemente, SCr = Santa Cruz, SG = San Geronimo, SMa = San Martin, SMi = San Miguel, SN = San Nicolas, SR = Santa Rosa, TS = Todos Santos. The mainland is represented by the Santa Monica Mountains.

connections to the mainland existed in the recent past. The composition of the present day herpetofauna of all the islands, characterized by a depauperate and in most cases unique assemblage of wide-ranging forms from the adjacent mainland, favors the concept that the islands were all populated by overwater, chance distribution.

On the basis of the geologic, geofloral, and herpetofaunal history of southern California outlined by Peabody and Savage (1958) and Savage (1960), it appears likely that the ingredients of the present insular herpetofaunas invaded the islands during late Pleistocene times. Almost all of the species currently represented on the islands are representatives of wide-ranging successful forms usually associated with semi-arid environments peripheral to desert areas in western North America. Most of these groups did not occur in southern California and Baja California before Pliocene times and probably did not invade what is now the coastal region until it was uplifted in Pleistocene (Corey, 1954). Climatic fluctuations during the latter period also tended to eliminate many species from the islands and adjacent mainland. The differences among the island herpetofaunas today derive mainly from the vagarities of fortuitous distribution, area, distance from shore, and Pleistocene climatic fluctuations. Since no convincing evidence of any Pleistocene land connection between any of the islands and the mainland is available, as shown by Dr. D. W. Weaver in this symposium, and since the herpetofaunas now found on the islands are depauperate and composed of vagile forms, it seems probable that all of the islands were invaded by late Pleistocene over-water immigrants. Nothing in the biological evidence speaks strongly for land connections as an explanation of modern distribution patterns, and it seems futile to build imaginary bridges where none are known to have existed and when the facts of the situation do not require it.

Two exceptions to these statements must be noted. The salamanders of the genus *Batrachoseps* are represented on all of the northern series and Santa Catalina by a mainland form (*B. pacificus*), probably a recent arrival, and by a recently discovered species known from Santa Cruz Island. The latter form appears to be a relict of a once wider-ranging species that is found in isolated mainland populations on the Monterey Peninsula, in the southern Sierra Nevada, and at high elevations in the Sierra San Pedro Martir of Baja California. Since parts of the Northern Channel Islands area have been land positive since Miocene, it seems likely that this primitive *Batrachoseps* has persisted as isolated colonies there and on the mainland while being replaced elsewhere by more successful derivative species.

The second case involves the primitive monotypic night lizard genus, *Klauberina*, endemic to San Nicolas, Santa Barbara and

San Clemente islands. The closest allies and only other members of the family Xantusiidae include *Xantusia* of arid and semi-arid regions of the southwestern United States and northern Mexico, *Lepidophyma* of tropical Middle America, the monotypic *Cricosaura* of Cuba, and *Paleoxantusia* of the Oligocene of Wyoming. All of these genera appear to have been derived from an ancestor similar to *Klauberina*. It seems probable that this lizard became associated with coastal California by late Miocene. Since that time it has disappeared from the mainland and occurs only where there is an absence of snake predators and severe competition with other lizards.

Muller and Axelrod (in this symposium) have commented at some length on the role of these islands as conservatories of relicts, rather than as centers for the evolution of new forms. The herpetological evidence confirms their view, since the only peculiar endemics in the island groups, *Batrachoseps* sp. and *Klauberina*, are obviously forms in the process of being eliminated from the mainland or already eliminated, respectively. The several insular endemics on Isla de Cedros do not detract from this concept in any way since they actually form allopatric insular populations of wide-ranging mainland species (*Phrynosoma coronatum - P. cerroense, Gerrhonotus multicarinatus - G. cedroensis* and *Crotalus ruber - C. exsul*).

Another possible example of a potential insular relict is provided in the lizard genus *Anniella* of the monotypic family Anniellidae. Only two species of this limbless burrowing lizard are known. One form, *A. pulchra*, has a wide range from northern Baja California to the San Francisco Bay area and is known from coastal, inland, and desert slope areas. *A. geronimensis* is found on Isla San Geronimo and adjacent coastal Baja California north almost to Colonia Guerrero. The two species are virtually sympatric over a 40 kilometer stretch of coastal dunes near Bahia San Quintin. Apparently *A. geronimensis*, which appears to be the more primitive of the two, is being replaced on the mainland by *A. pulchra*. Eventually, if this trend continues, *A. geronimensis* may become an insular relict.

The herpetofaunas of the islands under discussion are typical of continental islands that have not been connected recently by land to the mainland. Two major lines of evidence demonstrate that the present faunas of all the islands are rather recent overwater immigrants. First are the differences among the islands in their herpetofaunal composition and the absence of many common successful species known from similar habitats on the adjacent mainland. No two islands with more than two species have the same faunal composition, and no island supports more than 35 per cent of the species from comparable mainland areas. These facts strongly suggest random immigration. Second, the relationship

between species/area, as previously outlined (fig. 1), emphasizes the insularity of the herpetofaunas. On the basis of the assumptions involved in this relationship (MacArthur and Wilson, 1963), values for adjacent areas that were colonized by means of a land connection will lie on the same curve. If the values lie on the same curve for both mainland and insular localities, land connection is a possibility; but a similar result could be produced by over-water dispersal. If the values deviate markedly from the curve, they provide evidence that no land connection existed at the time of immigration. The data for the large inshore islands agree with mainland data and lie on the same species/area curve for the Santa Monica Mountains, a condition that neither confirms nor refutes either the hypothesis of over-water dispersal or the hypothesis of a land connection. The values for the other types of islands clarify the situation. The number of species on the large offshore islands are so low that it seems obvious that they have not recently been connected to the faunal source area. On the other hand, most of the small inshore islands have more species than would have been predicted because of area. Presumably if they had been invaded over a land connection, the values would lie on the same species/area curve as for the mainland. Whatever the reasons for this difference, it is probably a function of the amount of time during which immigration took place, and it indicates that the small inshore islands must have been colonized by over-water transport. Since most of the small inshore islands lie closer to shore than any of the large islands, it seems reasonable to conclude that none of the islands discussed in this paper have been connected to the adjacent mainland during the period of herpetofaunal immigration. Pleistocene connections between the islands and the mainland or with distant islands, as proposed by Clements (1955), are definitely contrary to the herpetofaunal evidence.

In summary: The modern herpetofaunas of the Southern California and Baja California islands are depauperate chance samples of the faunas of the adjacent mainland. The most distinctive elements in the insular herpetofauna appear to be relict forms formerly ranging widely on the continent. On the basis of the species composition and species/area relations of the insular faunas, it seems logical to conclude that the islands have been colonized during Pleistocene by fortuitous over-water waif distribution.

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LITERATURE CITED

Clements, T. 1955. The Pleistocene history of the Channel Island Region, southern California. *In* Essays in the natural sciences in honor of Captain Allan Hancock, pp. 311-323. Los Angeles.

Corey, W. H. 1954. Tertiary basins of southern California. Calif. Dept. Nat. Resources, Div. Mines Bull., 170, chap. 3:73-83.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution, 17(4):373-387.

Peabody, F. E., and J. M. Savage. 1958. Evolution of a Coast Range corridor in California and its effects on the origin and dispersion of living amphibians and reptiles. Amer. Ass. Advance. Sci., 51:159-186.

Savage, J. M. 1960. Evolution of a peninsular herpetofauna. Syst. Zool., 9(3):184-212.