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Species Number, Stability, and Equilibrium Status of Reptile Faunas on the California Islands

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INTRODUCTION

Island biogeography is the study of species distribution among islands. Its purpose is to develop principles that explain patterns of species distribution and species composition of island biotas through ecological, evolutionary, and historical mechanisms.

The most notable feature of the biogeography of the islands off the coast of southern California and Baja California, Mexico is the paucity of land vertebrate species, especially on the northernmost islands. This pattern was especially noted for reptiles and amphibians in an earlier analysis of the herpetofaunas of these islands by Savage (1967). No causal explanation was offered, save the suggestion that previous land bridge connections to the mainland were nonexistent. At the time of Savage's analysis, our understanding of island biogeography was, in general, poorly developed. The primary purpose of this paper is to re-evaluate the depauperate status of the reptile faunas of the California Islands in light of what is now known of the mechanisms controlling species diversity on islands, and to discuss the significance of the findings in terms of current island biogeographic theory.

THE THEORY OF ISLAND BIOGEOGRAPHY

In the interval between Savage's analysis and the present study, major advances have been made in our understanding of island biotas. Whereas in the past most of the emphasis was on dispersal, many recent studies emphasize the importance of extinction in determining the composition of island faunas. Extinction is apparently not an uncommon event, at least among island vertebrate populations (see Diamond and Jones 1980, Wilcox 1978). Thus, present species distribution on islands may only partially reflect the previous status of land bridge connections or successful over-water colonization events. From a consideration of the processes of extinction and immigration of species on islands, and the characteristics of insular biotas influencing their rates, a general theory of island biogeography has emerged.

The theory of island biogeography centers on the concept of an equilibrium between the rate of addition of new species to an island biota, immigration, and the rate of species loss through extinction (Preston 1962, MacArthur and Wilson 1963, 1967). These authors further proposed that the immigration rate should be dependent on the degree of isolation of an island, which is usually quantified as the shortest distance from an island to the mainland. They proposed that the other important variable, extinction, should be dependent on the size of an island. This is because, on smaller islands with limited habitats, population sizes may be so small that typical population fluctuations imposed by environmental vagaries are more likely to result in extinction. Thus, an island's area and its degree of isolation from other landmasses may largely define the equilibrium number of species. A relationship between species number and area and mainland distance has been established for numerous biotas (see Diamond and May 1976 for the

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most recent review). Such relationships have also been established for the reptile faunas of the California Islands (Savage 1967) and islands in the Gulf of California (Soulé and Sloan 1966, Case 1975, and Wilcox 1978).

SPECIES NUMBER AND THE CALIFORNIA ISLAND REPTILE FAUNAS

Defining the Problem

Armed with the equilibrium theory of island biogeography, we return to the problem of depauperate reptile faunas on the California Islands. We may now say, *a priori*, that any island biota should be depauperate relative to the adjacent mainland. This is because of the effect of reduced area and isolation from other terrestrial regions. It should hold true regardless of previous land bridge connections since extinction will eliminate at least some land bridge migrants.

The problem of the depauperate reptile faunas can now be more rigorously examined. Our first question is whether the reptile faunas are more depauperate than expected. To help answer this, it should be useful to compare the number of reptile species in these faunas with the number of species in reptile faunas elsewhere.

A Comparison with Islands in the Gulf of California

On the basis of the equilibrium theory, islands with similar areas and mainland distances (given that they are faunistically, ecologically, and historically comparable) should have similar numbers of species. It should be reasonable, therefore, to compare the California Island reptile faunas with similar faunas on islands in the Gulf of California. The two island groups are not strictly ecologically comparable. The regions, however, are zoogeographically similar and share many species.

The comparison will be confined to the eight Channel Islands since they are the most apparently depauperate and form a single biogeographic unit, which will be described later. These will be compared with islands in the Gulf of California which are also beyond the 130-meter depth contour. Thus, these Gulf islands and the Channel Islands are *deep-water* islands. It is assumed that they have had no land bridge connections to the mainland in geologically recent time (*i.e.*, since at least prior to the last glacial stage, the Wisconsin, when eustatic sea-level lowering did not exceed approximately 130 meters [Milliman and Emery 1968]).

The biogeographic data are given in Table 1 and island locations in Figure 1. The Channel Islands would be expected to have more species if the Pleistocene land bridge connection from the mainland to the Northern Channel Islands were verified. Nevertheless, the comparison reveals the following. Anacapa of the Channel Islands, for example, with an area of 2.9 km^2 and a distance to the mainland of 20 km, has only two recorded reptile species. The Gulf islands of Partida Norte, Raza, Salsipuedes, and San Pedro Mártir are all smaller and, on the average, farther from the mainland, yet have four, two, four, and three reptile species, respectively. Comparisons among the larger islands are more striking. Matching Santa Cruz and Santa Catalina of the Channel Islands to the Gulf islands of San Esteban, San Lorenzo, and Santa Catalina, which are roughly equivalent in distance from the mainland but are almost an order of magnitude smaller, shows that all have remarkably similar numbers of reptile species. Darlington (1957) had suggested a rule of thumb now well known to zoogeographers that states a tenfold increase in island size corresponds to a doubling in the number of species. The rule is clearly not upheld in this instance; Santa Cruz and Santa Catalina of the Channel Islands should have twice as many species as the Gulf Islands.

A more systematic comparison is made by plotting the log of the number of species against the log of area for both groups of islands (Fig. 2). The San Benito Islands are included with the Gulf islands since they are geographically closer and historically more similar, as discussed in detail later. From the regression lines in Figure 2 it can be seen that, for any given size, islands in the Gulf sample have, on the average, two to three times more reptile species than the Channel Islands. In other words, this twofold to threefold difference in the number of reptile species must be explained on the basis of something other than area.

The mean distance to the mainland is twice as great for the Channel Islands (50 km) as for the Gulf island sample (25 km). This undoubtedly accounts for some of the overall deficiency in the Channel Island faunas. As the island-by-island comparison showed, however, the Channel Islands consistently have fewer species than expected for islands of comparable area and distance from the mainland.

The expectation that islands of similar size and isolation should have similar numbers of species assumes that everything else is equal, *i.e.*, evolutionary, ecological, and historical mechanisms have been operating to an equivalent degree on both groups of islands. Each class of mechanisms will be examined to determine whether or not this is the case.

Evolutionary Mechanisms

The equilibrium theory of island biogeography is explicitly an ecological theory and does not account for evolutionary change. Evolutionary mechanisms may affect species diversity on islands in two ways. Species multiplication within a single island or an archipelago can enhance species diversity. Conversely, ecological release in early colonizing species can prevent invasion of new species (MacArthur 1972, Lack 1976), thus limiting species diversity.

Unequal faunal enrichment between the two groups of islands through speciation can be eliminated as a possibility. There is no evidence for speciation events other than those due to the divergence of a single population for any of the islands under consideration here. Further, as an indication of lack of multiple invasions, there are no cases of sympatry between island endemics and the ancestral species from which they were derived. Unequal evolutionary depression of species diversity through ecological release can probably also be eliminated. Ecological release is apparent for some of the island lizard species; however, evidence for such cases exists only for some of the Gulf island populations (Soulé 1966).

Ecological Mechanisms

In the context of equilibrium theory, ecological differences of importance are those which may affect immigration and/or extinction rates characterizing the two groups of islands. The supposition here that islands with similar areas and mainland distances should have similar extinction and immigration rates assumes that numerous ecological variables, including the quality and types of available habitats, are held constant. In general, the Channel Islands and the Gulf islands are ecologically dissimilar. The Gulf islands are arid and characterized by thorn scrub vegetation, while the Channel Islands are characterized by sage scrub and chaparral, including oak woodland on the larger islands. Unfortunately, the ways in which these differences might affect immigration and extinction rates in their respective faunas are unclear, and detailed analyses of the ecological requirements of the species composing these faunas are beyond the scope of this study.

There are, however, at least two identifiable factors that could lead to higher immigration rates for the reptile faunas of the Gulf islands. First, islands in the Gulf can potentially receive immigrants from two mainland regions—the Baja peninsula and Sonora. Second, the number of reptile species available as potential colonists is greater for the Gulf region. According to Stebbins (1966), there are 22 species of lizards and snakes on the mainland adjacent to the northernmost Channel Islands. This number increases to 26 adjacent to the southernmost Channel Islands. Species ranges are not as well established for the Baja peninsula and Sonora;

TABLE 1. Numbers of reptile species and island characteristics.

	Number of reptile species	Area (km²)	Distance from mainland (km)
	California Islands		
1 San Miguel	2	37	42
2 Santa Rosa	3	217	44
3 Santa Cruz (Norte)	6	249	30
4 Anacapa	2	2.9	20
5 San Nicolas	2	58	98
6 Santa Barbara	1	2.6	61
7 Santa Catalina (Norte)	8	194	32
8 San Clemente	2	145	79
9 Los Coronados	8	2.5	13
10 Todos Santos	7	1.2	6
11 San Martín	5	2.3	5
12 San Geronimo	3	0.4	9
13 San Benito	2	6.3	66
14 Cedros	12	348	23
15 Natividad	3	7.2	7
	Gulf of California Deep-water Islands		
16 Ángel de la Guarda	12	1,001	13
17 Partida Norte	4	2.1	12
18 Raza	2	1.1	18
19 Salsipuedes	4	1.8	19
20 San Esteban	8	43	37
21 Las Ánimas (Norte)	5	7.5	18
22 San Lorenzo	5	44.5	18
23 San Pedro Mártir	3	1.5	48
24 San Pedro Nolasco	5	3.5	10
25 Tortuga	4	6.3	37
26 Santa Catalina (Sur)	9	43	24
27 Santa Cruz (Sur)	4	11.6	17
28 Cerralbo	18	163	9

Note: Guadalupe is omitted since it is not known to have reptiles.

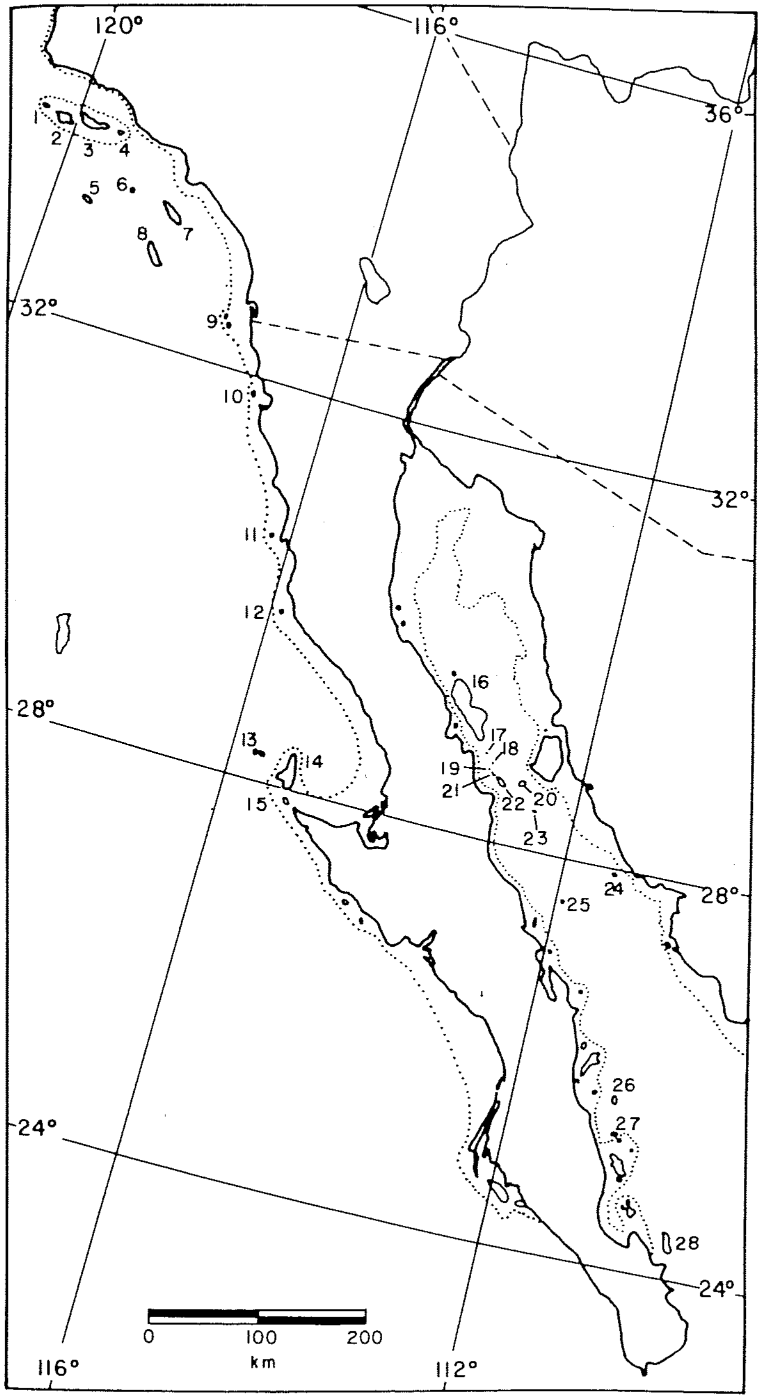

FIGURE 1. *Map of the California and Gulf of California Islands. Numbers refer to island names in Table 1.*

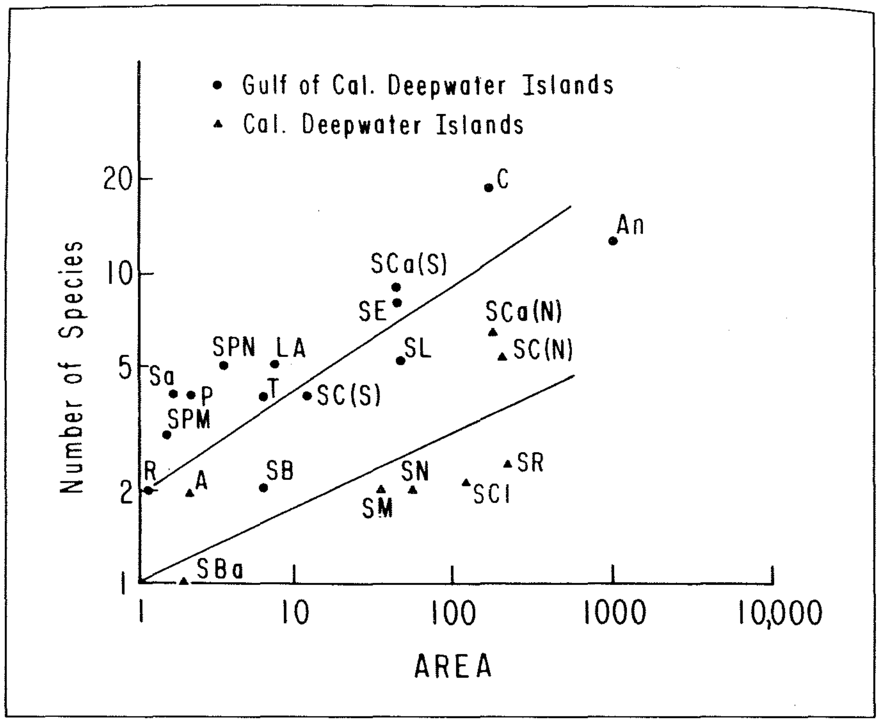

FIGURE 2. *Log of the number of reptile species plotted against the log of island area. SB = San Benitos, An = Ángel de la Guarda, P = Partida Norte, R = Raza, Sa = Salsipuedes, SE = San Esteban, LA = Las Ánimas (Norte), SL = San Lorenzo, SPM = San Pedro Mártir, SPN = San Pedro Nolasco, T = Tortuga, SCa(S) = Santa Catalina (Sur), SC(S) = Santa Cruz (Sur), C = Cerralbo, SM = San Miguel, SR = Santa Rosa, SC(N) = Santa Cruz (Norte), A = Anacapa, SN = San Nicolas, SBa = Santa Barbara, SCa(N) = Santa Catalina (Norte), SCI = San Clemente. The regression equations are as follows. For the Channel Islands, log species number = 0.21 (log area) + 0.02, r = 0.68. For the Gulf of California* deep-water *islands, log species number = 0.26 (log area) + 0.43, r = 0.80.*

nevertheless, coastal regions in the Gulf of California extending over a distance approximating the length of the southern California coastline may have from 30 to 40 species (Murphy unpubl. data).

It is difficult to estimate the effect these differences should have on immigration rates; it is questionable, however, that they can account for a doubling or tripling in species number. This leads to the third and, in this case, possibly the most important class of mechanisms explaining biogeographic patterns.

Historical Mechanisms: A Climatic Instability Hypothesis

Several reptile species occurring throughout much of mainland coastal southern California and Baja California are relatively uncommon or absent on the Channel Islands. Strikingly, these species—the side-blotched lizard (*Uta stansburiana*), the western whiptail lizard (*Cnemidophorus tigris*), the night snake (*Hypsiglena torquata*), and the coachwhip (*Masticophis flagellum*)—are among the most common species found on lower-latitude islands, including the islands of the Gulf and the other California Islands. As such, they are demonstrably good colonizers and capable of persisting on islands. The failure of these four species to occur on the Channel Islands with a frequency similar to that on the Mexican islands is virtually sufficient by itself to account for the low levels of reptile species diversity on the Channel Islands. Why are these species less common on these islands?

The present mainland ranges of these species all coincide (Stebbins 1966). While some differences occur east of the coast mountain ranges, along coastal California their distributions are indistinguishable. Their joint range is shown in Figure 3. All are apparently incapable of expanding their ranges into the cool and humid coastal region north of Point Conception.

A cool and humid climate prevailed throughout most of California, including the islands, during periods of Pleistocene glacial maxima (Axelrod 1967). The recurrent climatic and vegetation shifts concomitant with the glacial advances and retreats are estimated to have extended over about 500 miles of latitude (Durham 1950, Chaney and Mason 1930). Thus, a southward retreat of xerophilic reptile forms to desert refugia would have accompanied each glacial advance (Savage 1960). Figure 4 is a reconstruction of the probable mainland distribution of these xerophilic forms at the time of the glacial maxima. There are at least eleven other reptile species presently occurring in coastal southern California which may have been similarly affected, but most do not have ranges extending the length of the Baja peninsula.

The climatic instability during the Pleistocene could have resulted in the reduction of species diversity on the Channel Islands by the exclusion of xerophilic reptile forms in three ways. First, their intermittent displacement from the mainland region adjacent to the Channel Islands would have reduced the rate of immigration to the islands. Second, had any xerophilic species successfully colonized during an interglacial period, as *Uta* and *Hypsiglena* may have done during the present interglacial period, they would have been extirpated with the southward advance of the subsequent glacial environment. Third, the existence of inter-island or island-mainland land bridge connections during periods of glacial maxima when the sea level was at its minimum would have been of little consequence to these species since they would have been absent from the region.

Species distribution on the Channel Islands further supports the hypothesis that climatic instability is responsible for the islands' depauperate nature. Of the 27 occurrences of reptiles (Table 2), only five are of xerophilic forms. The mainland distributions of the remainder (except for the endemic lizard *Klauberina riversiana*, whose ancestral form is not known with certainty) clearly demonstrate their capability of persisting in a cool, humid, glacial environment.

However, if the climatic instability hypothesis is correct in its entirety, then the colonization of five xerophilic forms on the Channel Islands since the present climatic regime stabilized 6,000 to 7,000 years ago must be explained. Considering that four of the five occurrences are of *Uta stansburiana*, the climatic instability hypothesis seems reasonable. Among the local reptiles, *Uta* is unsurpassed in colonizing ability (Case 1975). There are other lines of evidence that specifically suggest that the *Uta* populations on these islands are the result of post-Pleistocene colonization. First, if the Santa Cruz and Anacapa *Uta* pre-date the present interglacial period, the absence of *Uta* on Santa Rosa and San Miguel is surprising since all four islands were presumably connected during the late Pleistocene. Second, according to Ballinger and Tinkle (1972), none of the Channel Island *Uta* are taxonomically distinct, but several subspecies and species are recognized on Mexican islands.

In summary, the Channel Islands appear to have an incomplete assemblage of xerophilic reptile forms. The xerophilic forms that do occur on the islands appear to be the result of

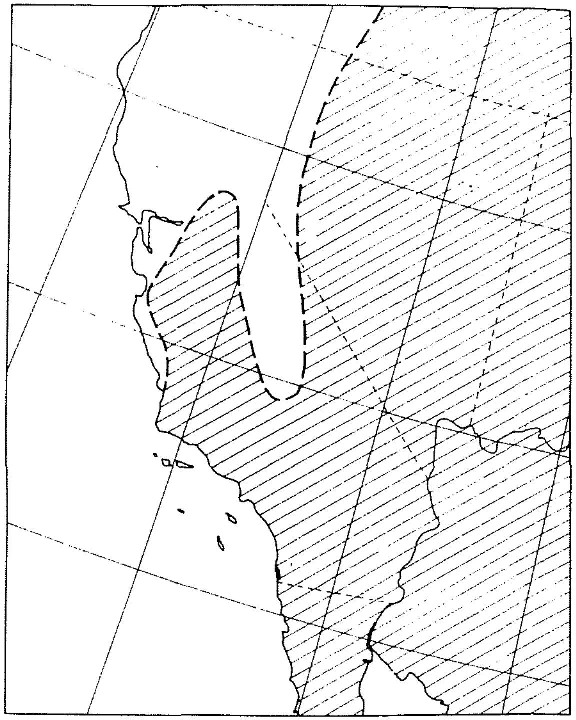

FIGURE 3. *Present joint distribution of several xerophilic reptile forms (see text).*

colonization events since the beginning of the present interglacial period. This implies that the islands will continue to acquire xerophilic forms until they become saturated and the loss of species through extinction balances immigration. Thus, it can be said that the reptile faunas in the Channel Islands are presently below equilibria.

DISCUSSION

Since the equilibrium theory was introduced, biogeographers have not been wholly successful in identifying faunas where species number is the result of a balanced equilibrium between immigration and extinction (Simberloff 1976). There are conditions, however, under which nonequilibrium faunas may actually be anticipated. The conditions depend both upon factors intrinsically characteristic of a taxon (*e.g.*, the specific immigration and extinction rates), and on variables characteristic of a given island (*e.g.*, size, environmental stability, and geologic history). The following considerations of these factors and how they might interact to result in faunas of differing equilibrium status provide the basis for an understanding of biogeographic patterns among the California Islands.

The probability of extinction for an island reptile is presumed to be less than that for an endothermic vertebrate. This was first pointed out specifically for lizards by Williams (1969), and seems reasonable since, because of their lower metabolic demands, reptiles should maintain higher population densities and withstand longer periods of deprivation than birds or mammals. In addition to their ability to persist on islands, reptiles also differ substantially from birds, yet are similar to or slightly superior to land mammals, in their capability for over-water dispersal.

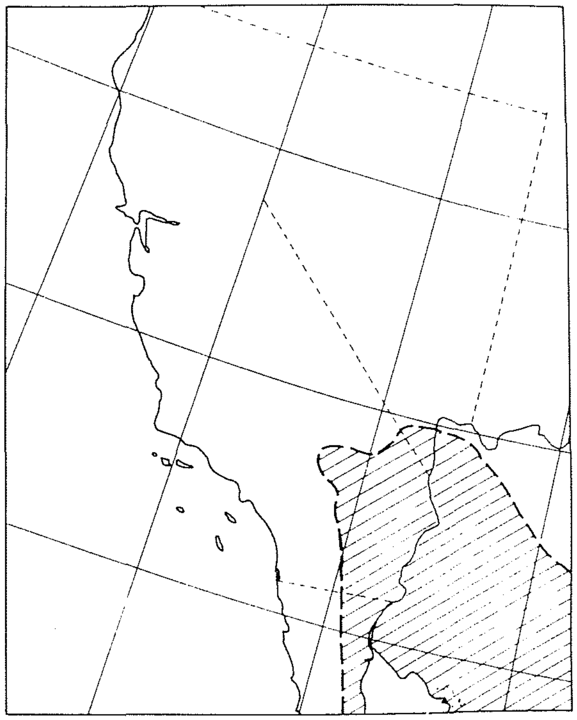

FIGURE 4. *Probable joint distribution of the same xerophilic reptile forms in Figure 3 at glacial maxima.*

The consequences of these probable differences in immigration and extinction rates between the vertebrate taxa are twofold. First, in the case of equilibrium faunas, taxon-specific differences determine relative species numbers on an island. For example, although reptiles and mammals probably have similar dispersal abilities, reptiles, because of lower extinction rates, are expected to produce island faunas which achieve equilibrium at a greater number of species. Second, and of primary interest in this study, nonequilibrium faunas may behave in dynamically predictable ways, differing in the rate of approach to equilibrium, depending on the taxon.

On islands where historical events such as past volcanic activity or changes in climate have reduced biotic diversity, those taxa with poor dispersal ability should take longer to reach equilibrium. Thus, reptile and mammal faunas will be more commonly found below equilibrium, or *subsaturated*, than will avifaunas. Pleistocene climatic fluctuations undoubtedly affected the Channel Island avifaunas and mammal faunas in addition to the reptile faunas. Nevertheless, the avifaunas should have adjusted rapidly to the changing conditions. Studies by Diamond (1969), Diamond and Jones (1980), and Jones and Diamond (1976) suggest these faunas are at their equilibria. Like the reptiles, mammals are also notably depauperate on the Channel Islands; perhaps, having even more limited over-water dispersal capabilities than reptiles, they may be similarly subsaturated. Alternatively, they simply may have attained equilibrium at fewer species because of higher extinction rates and lower immigration rates.

Nonequilibrium faunas have been suggested more frequently to be above equilibrium, or *supersaturated*. These faunas are found primarily on late or post-Pleistocene land bridge islands isolated with the rising sea level. The area is reduced in size and no longer receives the

TABLE 2. Reptile faunas of the California Islands.*

	San Miguel	Santa Rosa	Santa Cruz	Anacapa	Santa Barbara	San Nicolas	Santa Catalina	San Clemente	Los Coronados	Todos Santos	San Martín	San Geronimo	Cedros	San Benito	Natividad
Lizards															
Coleonyx variegatus													X		
Crotaphytus wislizenii													X		
Uta stansburiana			X	X			X	X	X	X	X	X	X		X
Uta stellata														X	
Sceloporus magister													X		
Sceloporus occidentalis	X	X	X												
Phrynosoma cerroense													X		
Klauberina riversiana					X	X		X							
Cnemidophorus tigris									X				X	X	X
Eumeces skiltonianus							X		X	X					
Gerrhonotus cedroensis													X		
Gerrhonotus multicarinatus	X	X	X	X		X	X		X		X				
Anniella geronimensis												X			
Anniella pulchra									X	X					
Snakes															
Salvadora hexalepis										X		X			
Chilomeniscus cinctus													X		
Leptotyphlops humilis													X		
Lichanura trivirgata															X
Thamnophis couchii							X								
Diadophis punctatus ringneck							X			X	X				
Coluber constrictor racer			X												
Lampropeltis getulus							X								
Lampropeltis zonata										X					
Pituophis melanoleucus		X	X				X		X		X		X		
Hypsiglena torquata night snake			X						X		X		X		
Crotalus exsul													X		
Crotalus viridis							X		X						

*The distributional data are derived largely from Savage (1967); however, there have been the following additions and a deletion. Bostic (1975) records *Salvadora hexalepis* from Todos Santos and San Geronimo, as well as *Chilomeniscus cinctus* from Cedros; a specimen of *Pituophis melanoleucus* was recently collected on Santa Rosa by Paul Collins; the occurrence of *Uta stansburiana* on San Nicolas as reported by Savage (1967) is unsubstantiated (R. Bezy, pers. comm.) and is deleted from this table.

constant influx or recruitment of individuals from adjacent regions. A new, lower equilibrium species number is defined by the reduced immigration and increased extinction rates. The rate of approach to this new equilibrium is inversely proportional to island size (Diamond 1972, Terborgh 1974, Case 1975, Soulé *et al.* 1978) and the taxon-specific extinction rate (Wilcox in prep.). Thus, on similar-sized islands, reptiles are expected to approach equilibrium more slowly than do birds or mammals. The existence of supersaturated faunas is well documented. Studies of land bridge island faunas, including avifaunas of the southwest Pacific (Diamond 1972) and neotropics (Terborgh 1974), lizard faunas (Case 1975, Wilcox in prep.), reptile faunas (Soulé and Sloan 1976, Wilcox in prep.), and mammal faunas (Wilcox in prep.) of the Gulf of California, suggest the importance of geologically recent land bridge connections. These connections clearly can account for the greater number of species on such islands where *relaxation* to equilibrium has not yet been completed. Six of the California Islands (Los Coronados, Todos Santos, San Martín, San Geronimo, Cedros, and Natividad) are potential candidates for supersaturated status since they all occur well within the contour of late Pleistocene minimum sea level. On the basis of Milliman and Emery's (1968) estimates of eustatic sea-level rise, most of these islands were isolated less than 10,000 years ago.

As seen in Table 1, each of these islands has much larger faunas than either the Channel Islands or Gulf islands, considering their sizes. Most are closer to the mainland, so it would seem likely that they should have more species by virtue of higher immigration rates. This, in fact, may not be the case. Studies of lizard faunas (Case 1976, Wilcox 1978) and reptile faunas (Wilcox in prep.) on land bridge islands in the Gulf indicate that immigration influences species numbers only very weakly, if at all, on supersaturated islands.

On islands that have sufficient geological and climatic stability, faunas are expected to have had time to reach equilibrium. Low-latitude, *deep-water* islands, including the Gulf deep-water islands and the San Benitos of the California Islands, may thus have faunas in equilibrium. Historically, then, the San Benitos are more similar to the Gulf islands since they are also of relatively low latitude and probably did not experience severe climatic shifts. That the San Benitos have one of the most divergent populations of island *Uta* (Ballinger and Tinkle 1972) further attests to the relative antiquity of their reptile fauna.

CONCLUSION AND SUMMARY

According to current island biogeographic theory, three types of faunas are possible with regard to equilibrium status: subsaturated, supersaturated, and in equilibrium. The variation in reptile species diversity and the climatic and geological history of the California Islands suggest that each of the types is represented. Climatic instability associated with Pleistocene glacial advances and retreats may be largely responsible for the low diversity of reptile species on the high-latitude California Islands, the Channel Islands. Thus, they are regarded as relatively subsaturated. Geologically recent land bridge connections to the mainland for six of the remaining California Islands inhabited by reptiles may be largely responsible for high reptile species diversity. Thus, they are regarded as relatively supersaturated. The remaining California Island, San Benito, because of its latitude and the depth of the surrounding ocean, should be immune to recent climatic and geological instability. Thus, a balanced equilibrium fauna is more likely.

Most island biogeographic studies stress the role of island size and isolation as factors controlling species diversity at dynamic equilibrium. In this study on numbers of reptile species, historical factors are emphasized and faunas that are apparently not at equilibrium are suggested.

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Divergence in the Island Night Lizard *Xantusia riversiana* (Sauria: Xantusiidae)

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INTRODUCTION

The island night lizard, *Xantusia riversiana* Cope (Fig. 1), is found only on Santa Barbara, San Clemente, and San Nicolas Islands off southern California (Fig. 2). The species is sufficiently divergent in morphology from its mainland relatives, *X. vigilis* Baird and *X. henshawi* Stejneger (Fig. 1), that it has been placed in the monotypic genus *Klauberina* by Savage (1957, 1963). Regardless of whether it is accorded generic (Savage 1957) or subgeneric (Bezy 1972) rank, *X. riversiana* is clearly more divergent than the other living vertebrates of the California Channel Islands, suggesting that it may have been present longer than other species on one or more of the islands. Moreover, casual observations indicate that there may be greater morphological differences between the island populations of *X. riversiana* than were documented by earlier work (Savage 1951, Smith 1946). In an effort to further clarify the evolutionary history of the species, we have compared electrophoretically determined genetic distances and divergence time estimates between the island populations with those between the species of *Xantusia*, and have reappraised inter-island differences in karyotypes, scalation, coloration, body size, clutch size, and variability.

MATERIALS AND METHODS

Two separate electrophoretic analyses were performed. In the first, 22 presumptive loci were scored for 15 *X. riversiana* from San Clemente Island, 15 from San Nicolas Island, and five from Santa Barbara Island. In the second study, 30 presumptive loci were analyzed for six *X. riversiana* from San Nicolas Island, six *X. riversiana* from San Clemente Island, six *X. henshawi* from the San Jacinto Mountains, and 20 *X. vigilis* from Antelope Valley, California (see Specimens Examined for exact localities). The procedures for preparing the gels, stains, and interpreting alleles follow Selander *et al.* (1971), with minor modifications (Yang *et al.* 1974, Kim *et al.* 1976).

The chromosomal methods utilized were described by Bezy (1972). Scalation was analyzed univariately with the BMDP3D program and multivariately by stepwise discriminant analysis (SDA) utilizing BMDP7M (Dixon 1975).

RESULTS

Electrophoresis

The 22-locus study indicated that 18 presumptive loci are fixed for identical electromorphs (alleles) in all three island samples. Polymorphisms were observed for MDH (San Nicolas Island), PGM-2 (San Clemente and Santa Barbara Islands), and GOT-2 and PGI (San Clemente and San Nicolas Islands) (Table 1). In the 30-locus study, identical alleles were fixed at 27 loci for San Clemente and San Nicolas; polymorphisms occurred for MDH-2 on San Nicolas and for ADH and PGM-2 on San Clemente (Table 2). Allele frequencies were used to compute genetic similarity and distance (Nei 1972). Inter-island genetic distances (Table 3) are, of course,