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IS THE PENINSULAR EFFECT A RED HERRING?

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Since Simpson (1964) recognized that mammalian species density decreased from base to tip on North American peninsulas, many authors have debated the presence or absence of such a trend in other animal groups and other peninsulas (MacArthur and Wilson 1967; Cook 1969; Kiester 1971; Taylor and Regal 1978; Wamer 1978; Lee 1980; Seib 1980, 1981; Gilpin 1981). Simpson explained this "peninsular effect" as a result of the higher rate of extinction and lower rate of immigration on peninsulas when compared to the adjacent mainland. Taylor and Regal (1978) prepared a model of Simpson's hypothesis and used this model to explain the diversity gradient in heteromyid rodents inhabiting the Baja California peninsula. Gilpin (1981) objected to the assumptions of Taylor and Regal's model and demonstrated how the molecular theory of island biogeography could be applied to peninsular diversity patterns. Seib (1980) could not find a peninsular effect in lizard and snake species density on the Baja California peninsula and preferred to explain the distributions of these groups in terms of historical events which produced a gradual interdigitation of northern and southern faunas. Recently, however, Seib (1981) has acknowledged that a peninsular effect may be present.

Because of the scarcity of data for most major peninsulas of the world, the general applicability of the peninsular effect as a biogeographic phenomenon is uncertain. The lizard and snake faunas of Baja California, Florida, Yucatán, and Iberia are well known; we have critically examined the species density patterns of these vertebrates on these four peninsulas and demonstrate (1) that the peninsular effect (*sensu* Simpson 1964) is not a concomitant feature of peninsulas and may not be a general biogeographic pattern and (2) that historical events probably exert a greater influence on peninsular diversity than the shape of the landmass.

MATERIAL AND METHODS

To construct species density diagrams for Iberia and Florida (fig. 1), we laid a grid of squares representing 100 km^2 over species distribution maps (Salvador [1974] for Iberia and Conant [1975] for Florida) and tabulated the number of

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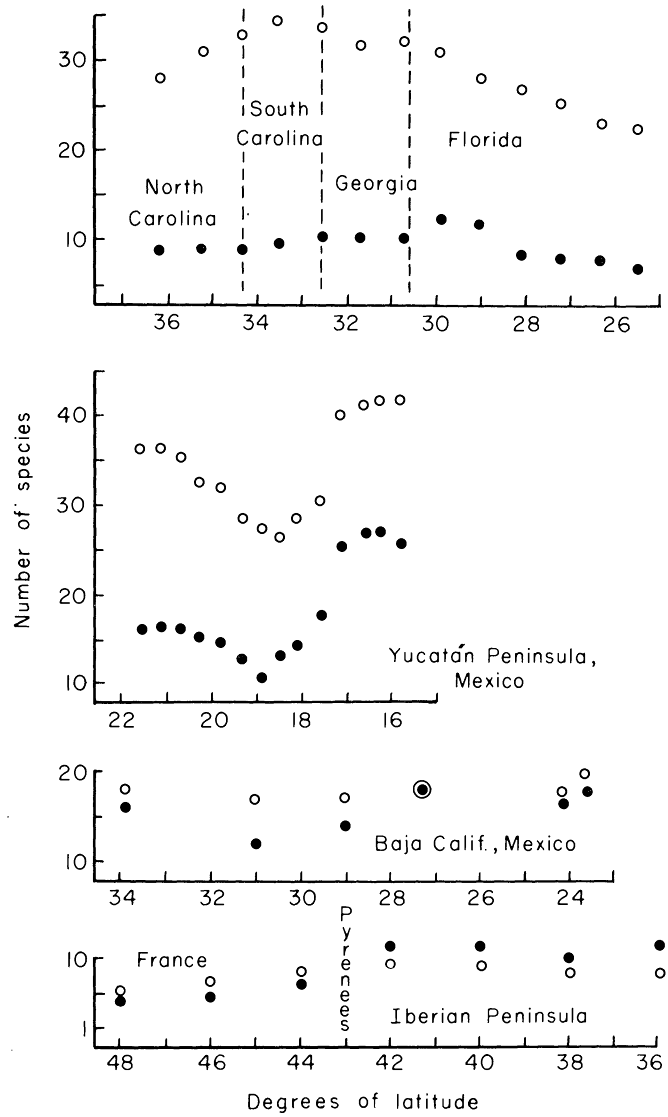

FIG. 1.—Average number of species of lizards (closed circles) and snakes (open circles) at various latitudes on four peninsulas.

sympatric species of lizards and snakes present at the center of each square. We then summed and averaged the species densities of cells in each row. This average provided a single estimate of the number of species present at representative degrees of latitude. To further enhance our analysis, we used distributional data available for France (Parent 1981) and the eastern United States (Conant 1975). Our figures for species numbers along 48°, 46°, and 44° of latitude in Europe were obtained by averaging the number of species found in each of 15 (at 48°), 9 (at 46°), and 9 (at 44°) Departments of France which range in area from 610 to 9,237 km^2

(Paxton 1976). The species density diagram for Yucatán (fig. 1) was constructed by averaging rows of 50-km^2 species-density cells found in Lee (1980, fig. 7); data for Baja California (fig. 1) are from Seib (1980, table 2, personal communication).

Preston (1962) presented empirical evidence demonstrating that the number of species (S) inhabiting an area of size A could be described by the power function $S = cA^z$. In this relationship, the value of the coefficient (c) is determined by taxonomic group and biogeographic region and the exponent (z) is related to the degree of isolation the region has undergone. MacArthur and Wilson (1967) reviewed available literature and reported that observed exponents (z) generally fell between 0.17 and 0.35 with many islands at one end of the scale and most mainland observations at the other; old peninsulas are expected to fall in the middle. Recent attention has focused on the proper use and interpretation of the species area curve (Haas 1975; Gould 1979; Sugihara 1980). Connor and McCoy (1979) assert that species-area curves are useful in comparing diversities between geographical regions.

Because degree of historical isolation of an area may be reflected in the value of z in the species-area relationship (i.e., as z approaches unity, a greater degree of isolation is indicated), we undertook an examination of this parameter in a comparison of the four herpetofaunas. If a peninsula effects islandlike isolation, the degree of this isolation should be indicated by its z value. A peninsular effect should produce an exponent intermediate between the values described for continental areas and those so frequently seen for islands; peninsulas with strong effects might be expected to show exponents which approximate those of island areas.

Species-area data and sources for each of the four peninsulas and adjacent areas are listed in table 1; each area is independent and exclusive of every other area studied. The area of the Baja California peninsula was determined (Bonine et al. 1970) and, by weighing each of four biogeographic regions cut from a map of Baja California (Savage 1960, fig. 2), we were able to approximate the area of each region. Areas of Mexican states, when not provided by sources referenced in table 1, are from Paxton (1976). Species-area data for native Florida lizards and snakes, primarily from Ashton (1976) and Ashton and Ashton (1981), were updated by records from the geographic distribution section of SSAR *Herpetological Review*. South Florida includes all of Broward, Collier, Dade, Hendry, Lee, Monroe, and Palm Beach counties and the Florida Panhandle includes all Florida counties west of the Appalachicola River. Mainland United States areas are all within the coastal plain. Solved directly as power functions, these data describe equations for which values of c, z, and r^2 are presented in table 2 (in using lizard species data for Iberia, the digit 1 was added to each datum to eliminate zeros).

RESULTS

Species Density Patterns

Of the four peninsulas, only Florida shows a decreasing gradient in lizard and snake species density, the classic peninsular effect (fig. 1). Baja California (Seib

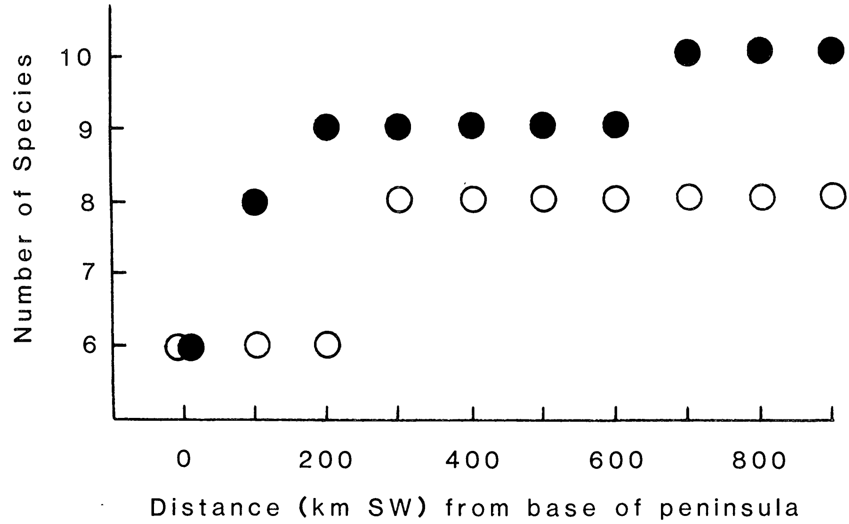

FIG. 2.—Average number of species of lizards (closed circles) and snakes (open circles) at varying distances from the base of the Iberian peninsula.

1980) and Iberia both exhibit relatively uniform densities of lizard and snake species. Since Iberia has a southwestern orientation in relation to Europe, instead of the north-south orientation seen in American peninsulas, we also considered distance from the base of the peninsula in one transect. A line connecting San Sebastian and Tarragona approximates the orientation of Iberia's base; by drawing a line perpendicular to this base, we created a transect oriented from peninsular base to tip. Sampling at 100-km intervals along this transect provided the data for figure 2. As distance from the base of the peninsula increases, the numbers of species of lizards and snakes either increases or remains the same.

Species densities generally decrease with increasing latitude north of Florida and Iberia while on Yucatán species densities of lizards and snakes are lowest at midpeninsula relative to the base and tip (fig. 1). Although species density patterns are instructive, they may also be misleading if considered in conjunction with latitudinal gradients. If Florida were not a peninsula, one would expect an increase in species density to accompany a decrease in latitude. That the inverse is true indicates that factors other than latitude are influencing species density. In Iberia, by the same reasoning, species density should increase with decreasing latitude. That it remains relatively uniform may be a peninsular effect in itself. Seib (1981) has recently come to a similar conclusion with Baja California lizards and snakes. Although species densities are relatively uniform down the peninsula, he believes that the Cape Region province may be undersaturated for reptile species because of its complex flora and higher rainfall relative to midpeninsula. Of the four peninsulas, Yucatán is unusual in that it is oriented in a south to north direction (base to tip) instead of north to south. Because of this orientation, any latitudinal gradient in species density would amplify, rather than conceal a peninsular effect. The observed patterns (fig. 1) of low species density at midpeninsula,

TABLE 1

LOCALITIES, AREAS, NUMBERS OF SNAKE AND LIZARD SPECIES, AND SOURCES FOR NUMBERS OF SPECIES

Locality	Area (km²)	Snakes	Lizards	Source (see also text)
IBERIA				
Sites within Provinces of Iberia				
Cádiz				
Algeciras	203	1	2	Busack & Jaksić 1982:3B
Campano	214	2	0	Busack & Jaksić 1982:1D
Jerez de la Frontera	311	4	2	Busack & Jaksić 1982:2A
Las Lomas	312	5	3	Busack & Jaksić 1982:2D
Medina Sidonia	314	2	1	Busack & Jaksić 1982:2C
San Fernando	201	3	3	Busack & Jaksić 1982:1C
San José del Valle	304	2	3	Busack & Jaksić 1982:2B
Sanlúcar de Barrameda	214	2	2	Busack & Jaksić 1982:1B
Sotogrande	135	1	1	Busack & Jaksić 1982:2E
Tarifa	112	2	2	Busack & Jaksić 1982:1E
Trebujena	183	2	0	Busack & Jaksić 1982:1A
Ubrique	278	1	4	Busack & Jaksić 1982:3A
Lugo				
Caurel	19.3	7	7	Bas López 1982
Provinces				
Cádiz (minus above sites)	4,604	8	10	Busack 1977, personal observation
Guipúzcoa	1,997	5	6	Bea 1981
Navarra	10,421	9	6	Escala & Perez Mendia 1979
Salamanca	12,336	6	10	Martínez-Rica 1979
Countries				
Portugal	91,970	9	13	Salvador 1974
Spain (minus above localities)	565,009.7	13	18	Salvador 1974
BAJA CALIFORNIA, MEXICO				
Sites on Peninsula				
San Felipe	814	12	17	Seib 1980
Bahía de Los Angeles	814	14	17	Seib 1980
San Ignacio	814	18	18	Seib 1980
La Paz	814	18	17	Seib 1980
Buena Vista	814	20	18	Seib 1980
Biogeographic Regions				
Californian	28,269	22	16	Savage 1960; Seib 1980, pers. commun.
Colorado (minus sites included above)	19,577	19	20	Savage 1960; Seib 1980, pers. commun.
Peninsular (minus sites included above)	69,046	20	23	Savage 1960; Seib 1980, pers. commun.
San Lucan	22,818	21	23	Savage 1960; Seib 1980, pers. commun.

YUCATÁN PENINSULA, MEXICO				
Sites on Peninsula				
Santa Rosa	0.01	32	13	Lee 1980
Tunkas	0.01	36	13	Lee 1980
Row 2, cell no. 5	2,500	38	15	Lee 1980
Row 2, cell no. 6	2,500	39	17	Lee 1980
States on Peninsula				
Campeche	56,114	42	26	Lee 1980
Quintana Roo	42,030	45	25	Lee 1980
Yucatán (W. of 89° long.)	19,343	39	20	Lee 1980
MAINLAND MEXICO AND GUATEMALA				
Mexico				
Chiapas	73,887	115	102	Smith & Smith 1976
Distrito Federal	1,499	43	19	Smith & Smith 1976
Guerrero	63,794	100	81	Smith & Smith 1976
Puebla	33,919	77	46	Smith & Smith 1976
Tabasco	24,661	55	30	Smith & Smith 1976
Morelos	4,941	55	37	Smith & Smith 1976
Guatemala				
El Ceibal	0.01	35	23	Lee 1980
La Libertad	0.01	26	9	Lee 1980
Poptun	0.01	24	8	Lee 1980
Tikal	0.01	39	26	Lee 1980
Row 14, cell no. 1	2,500	42	26	Lee 1980
Row 14, cell no. 2	2,500	42	25	Lee 1980
Row 14, cell no. 3	2,500	42	27	Lee 1980
ALABAMA, GEORGIA, AND FLORIDA				
Mainland				
Lower coastal plain, Ala.	20,515	40	11	Mount 1975
Red Hills, Ala.	20,510	35	11	Mount 1975
Fort Stewart, Ga.	1,131	33	10	Williamson & Moulis 1979
Hunter Army Airfield, Ga.	21.9	23	8	Williamson & Moulis 1979
Panhandle of Florida	19,502	35	10	Ashton 1976; Ashton & Ashton 1981
Osceola National Forest, Fla.	622	28	9	USFWS 1978
Liberty Co., Fla.	2,173	28	9	USFWS 1979; P. Moler, pers. commun.
Wakulla Co., Fla.	1,557	31	10	USFWS 1979; P. Moler, pers. commun.
Peninsular Florida				
South Florida	27,827	27	13	Ashton 1976; Ashton & Ashton 1981
Marion Co.	4,141	32	13	P. Moler, pers. commun.; Fla. Game & Freshwater Fish Comm. 1976
Alachua Co.	2,372	36	11	P. Moler, pers. commun.; Fla. Game & Freshwater Fish Comm. 1976
Archbold Biol. Stn.	15.4	22	9	J. N. Layne, pers. commun.

relative to the base and tip, clearly cannot be ascribed to either a latitudinal gradient or peninsular geometry (Lee 1980).

Equilibrium Theory Analysis

When untransformed data representing the number of lizard and snake species known to occur in defined areas of the four peninsulas (table 1) are entered directly into the $S = cA^z$ relationship the slopes (z) of the resultant curves should be higher than those for nearby mainland areas if peninsulas are more isolated. Most z values for the four peninsulas were lower than expected, and none was significantly different from adjacent mainland values (table 2); no statistically defensible peninsular effect can be demonstrated when equilibrium theory is applied to these data.

Descriptive Biogeographical Analysis

Iberian vertebrates currently face two barriers to dispersal: the Pyrenees Mountains to the north, and the Strait of Gibraltar to the south. In terms of faunal exchange, these barriers make today's Iberia an island rather than a peninsula; but this was not always the case. Northern Iberia was alternately isolated from and open to faunal exchange with northern Europe during the Miocene. North-central Iberia was separated from southeastern Iberia and Morocco by an Atlantic connection with the western Tethys during mid-Miocene. During the late Miocene this connection was severed (Tjalsma 1971) and the two land areas became connected (Ruggieri 1967; Le Pichon 1968). Later, the eroded Pyrenees were uplifted, forests receded, central Iberia became more open (Crusafont Pairó 1958), and the formation of the Strait of Gibraltar ($\approx$ 6 M.Y.B.P.) completed the isolation from Europe and Africa (Berggren and Van Couvering 1974; Hsü et al. 1977; Mantura 1977; Ager 1980; Loutit and Keigwin 1982).

The mammalian fossil record adds support to this scenario in that no African mammals are found in the European fauna before the Burdigalian stage (Miocene, 19–14 M.Y.B.P.); mammal faunas of the Turolian (the final Miocene stage) contained many species which had arrived in Iberia through passage across northern Africa (Crusafont Pairó 1958; Coryndon and Savage 1973). The fossil record is insufficiently known for reptiles, but the present distributions of snake and lizard species on the Iberian peninsula do not contradict the pattern shown by mammals. Busack (1977) examined lizard and snake species in Spain's southernmost province (Cádiz) and determined that five lizard species were of European origin, three were African, one was endemic, and two were of uncertain origin. Of seven snake species, four were European, two were African, and one was of uncertain origin. An examination of the distributions of the entire Iberian lizard fauna (based on maps in Salvador [1974]) shows that, of the 19 species, six species occur only to the north, two occur only to the south, and 11 occupy areas both to the north and to the south of midpeninsula. The 13 snake species show a similar distribution. Six species are found both above and below, five are only found above, and two are

TABLE 2

SNAKE AND LIZARD SPECIES-AREA CURVE DATA (Coefficients of determination [r^2], probabilities [P] associated with r^2, c, and z values, and associated 95% confidence levels [in parentheses] are presented.)

Snakes	r^2	P	c	z
Iberia	.472	.001	.8 (0.3–1.5)	.22 (.106–.326)
Florida				
Peninsular	.412	.179	21.3 (11.4–34.4)	.04 (−.025–.101)
Mainland	.834	.001	18.6 (15.2–22.4)	.07 (.044–.090)
Mexico				
Peninsular				
Baja California	.388	.037	10.5 (5.8–16.6)	.06 (.005–.123)
Yucatán	.729	.007	35.8 (33.7–38.0)	.01 (.006–.021)
Mainland	.625	.007	36.7 (29.6–44.6)	.06 (.030–.080)
Lizards				
Iberia	.511	.0003	.9 (0.3–1.8)	.23 (.123–.335)
Florida				
Peninsular	.984	.004	7.8 (7.3–8.4)	.05 (.040–.056)
Mainland	.792	.002	7.1 (6.1–8.0)	.04 (.024–.060)
Mexico				
Peninsular				
Baja California	.405	.033	12.9 (8.9–17.6)	.04 (.005–.083)
Yucatán	.710	.009	14.7 (12.4–17.2)	.04 (.015–.055)
Mainland	.538	.002	19.0 (12.9–26.2)	.08 (.035–.121)

only found below, midpeninsula. Busack and Jaksić (1982) discussed retarded species-saturation on Iberia in terms of historical factors and concluded that those species surviving climatic, faunistic, floristic, and physiographic changes had been those more ecologically generalized.

Seib (1980), who found similar distributional patterns on Baja California, inferred that ecological constraints and competitive exclusion effected a gradation between northern and southern faunas.

Pleistocene climatic changes are thought to be responsible for the isolation and subsequent evolution of herpetofaunal endemics on the Yucatán peninsula; evidence for a peninsular effect in species density was not found by Lee (1980). Species patterns for Yucatán lizards and snakes are correlated with structural habitat characteristics (plant height, cover, and volume diversity).

A species density gradient in Florida is found not only in lizards and snakes (Kiester 1971; this paper) but also in mammals (Simpson 1964) and birds (Cook 1969). Although paleoclimatic hypotheses have been suggested as influencing bird species densities in Florida, Wamer (1978) considered current vegetation patterns to be more important. The decrease in bird species density from north to south on the peninsula results from steady reduction in habitat quality (low within-habitat diversity) to the south. Although habitat quality may not explain diversity gradients in other Florida vertebrates, the classic "peninsular effect" must be qualified and may not apply generally to vertebrates.

CONCLUSIONS

We must agree with Gilpin (1981) and conclude that many biogeographic parameters are responsible for the departures from theory demonstrated by the lizard and snake assemblages of these four peninsulas. Since all are peninsulas, and only one (Florida) exhibits a decreasing gradient in species density with respect to snake and lizard faunas, we also question the idea of peninsular effect as a general phenomenon. The absence of this effect in faunas on some peninsulas indicates that historical factors and their effects are more deterministic of animal distributions than the geometric nature of the landfall on which they reside.

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