Supersaturated Island Faunas: A Species-Age Relationship for Lizards on Post-Pleistocene Land-Bridge Islands

Bruce A. Wilcox

Science, New Series, Vol. 199, No. 4332. (Mar. 3, 1978), pp. 996-998.

References and Notes

1. D. J. Cram and J. M. Cram, *Science* **183**, 803 (1974); J. M. Girodeau, J. M. Lehn, J. P. Sauvage, *Angew. Chem.* **14**, 764 (1975).
2. D. J. Cram, in *Applications of Biochemical Systems in Organic Chemistry*, J. B. Jones, Ed. (Wiley, New York, 1976), part 2; ——, R. C. Helgeson, L. R. Sousa, J. M. Timko, M. Newcomb, P. Moreau, F. de Jong, G. W. Gokel, D. H. Hoffman, L. A. Domier, S. C. Peacock, K. Madan, L. Kaplan, *Pure Appl. Chem.* **43**, 327 (1975); E. P. Kyba, R. C. Helgeson, K. Madan, G. W. Gokel, T. L. Tarnowski, S. S. Moore, D. J. Cram, *J. Am. Chem. Soc.* **99**, 2564 (1977); W. D. Curtis, D. A. Laidler, J. F. Stoddart, G. H. Jones, *J. Chem. Soc. Chem. Commun.*, 835 (1975); J. Behr, J. Lehn, P. Vierling, *ibid.*, 621 (1976).
3. J. H. Moreno and J. M. Diamond, in *Membranes*, G. Eisenman, Ed. (Dekker, New York, 1975), vol. 3, pp. 383–497; K. A. Rubinson, *J. Chem. Ed.*, **54**, 345 (1977).
4. E. Grell, T. Funck, F. Eggers, in *ibid.*, pp. 1–126; Yu. A. Ovchinnikov, V. T. Ivanov, A. M. Shkrob, *Membrane-Active Complexones* (Elsevier, New York, 1974); B. C. Pressman, *Annu. Rev. Biochem.* **45**, 925 (1976).
5. G. Szabo, G. Eisenman, R. LaPrade, S. M. Ciani, S. Krasne, in *Membranes*, G. Eisenman, Ed. (Dekker, New York, 1973), vol. 2, pp. 179–328.
6. D. F. Martin and B. B. Martin, *J. Chem. Ed.* **53**, 614 (1976).
7. R. M. Izatt, J. H. Rytting, D. P. Nelson, B. L. Haymore, J. J. Christensen, *Science* **164**, 443 (1969); *J. Am. Chem. Soc.* **93**, 1619 (1971).
8. J. J. Christensen, D. J. Eatough, R. M. Izatt, *Chem. Rev.* **74**, 351 (1974); R. M. Izatt, D. J. Eatough, J. J. Christensen, *Struct. Bond.* **16**, 161 (1973); R. M. Izatt, R. E. Terry, D. P. Nelson, Y. Chan, D. J. Eatough, J. S. Bradshaw, L. D. Hansen, J. J. Christensen, *J. Am. Chem. Soc.* **98**, 7626 (1976); R. M. Izatt, J. D. Lamb, G. E. Maas, R. E. Asay, J. S. Bradshaw, J. J. Christensen, *ibid.* **99**, 2365 (1977).
9. R. M. Izatt, R. E. Terry, B. L. Haymore, L. D. Hansen, N. K. Dalley, A. G. Avondet, J. J. Christensen, *J. Am. Chem. Soc.* **98**, 7620 (1976).
10. We thank the National Science Foundation for financial support through grant CHE 76-10991. This is contribution No. 104 from the Thermochemical Institute.

28 March 1977; revised 13 June 1977

Supersaturated Island Faunas: A Species-Age Relationship for Lizards on Post-Pleistocene Land-Bridge Islands

Abstract. *Lizard faunas on post-Pleistocene land-bridge islands in the region of Baja California were examined for the effect of island age on species diversity. Species diversity and age are significantly correlated; and when the variation in species diversity attributable to area and latitude are removed, the corrected species diversity plotted against island age produces a relaxation or extinction curve. These results provide evidence for supersaturated faunas which are relaxing to lower levels of species diversity consistent with the equilibrium theory of island biogeography.*

The equilibrium theory of island biogeography (*1*) proposes that the number of species in some biotas may be explained by an equilibrium resulting from a balance of immigration by extinction. Although the theory has been broadly applied (*2*) and widely accepted, it has recently been impugned for a lack of conclusive evidence for the existence of an immigration-extinction equilibrium in nature (*3*).

Paradoxically, some of the most convincing evidence for the theory to date comes from apparent nonequilibrium faunas. These are post-Pleistocene isolate faunas, such as on islands that are presumed to represent the dwindling portions of once larger faunas. These isolates were either part of a continental fauna from which they have become separated or were part of an already existing isolate that has been shrinking in size because of the rise of the sea level. The greater-than-expected numbers of species found in some of these faunas, relative to what is predicted for similar faunas in regions of comparable size but with a stable geological past, can be explained by the equilibrium theory. The theory would predict that they are supersaturated and in the process of shrinking or relaxing to equilibrium states with fewer species.

Diamond (*4*) and Terborgh (*5*), working independently in the southwest Pacific and Neotropics, respectively, have reported the existence of supersaturated bird faunas. Further, they have obtained remarkably similar results for relaxation rates dependent on island size, and for equilibrium species numbers. Soulé and Sloan (*6*) earlier provided evidence for supersaturated lizard faunas on islands in the Gulf of California. Subsequently, Case (*7*) produced more evidence for the supersaturated status of some of the same faunas, and also made estimates of the dependence of relaxation rates on island size which corroborate the above results for bird faunas. Some workers nevertheless question whether positive results from such studies are evidence for the equilibrium theory, and have either disregarded them (*3*), or questioned their validity (*8, 9*). For example, Abbott and Grant (*9*) state that there are no undisputed cases of nonequilibrium faunas due to a lack of sufficient time to attain their equilibria.

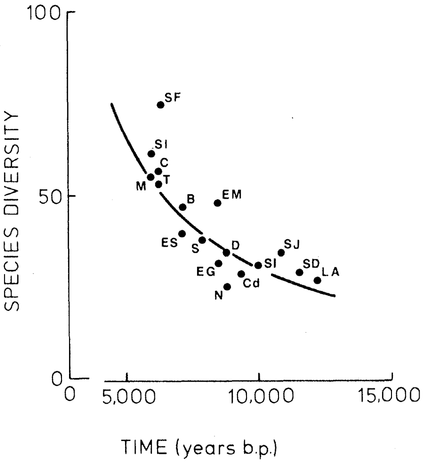

Fig. 1. Species diversity, corrected by partialing out variation due to area and latitude, plotted as a function of isolation time. *SF*, San Francisco; *SI*, San Ildefonso; *SM*, San Marcos; *M*, Mejia; *T*, Tiburon; *B*, Ballena; *EM*, El Muerto; *ES*, Espíritu Santo; *S*, Smith; *D*, Danzante; *EG*, Encantado Grande; *N*, Natividad; *Cd*, Cedros; *C*, Coronado; *SJ*, San Jose; *SD*, San Diego, *LA*, Las Animas.

Such caution is reasonable in that the identification of supersaturated faunas is based on estimates of initial and final (equilibrium) numbers of species as predicted from other faunas of the same taxa and region that are assumed to represent both of the above extremes. Thus evidence for the equilibrium theory from such studies is necessarily indirect. Here I ask whether it is possible to obtain evidence for supersaturated nonequilibrium faunas without making these assumptions.

In previous studies, it was assumed that upper- or post-Pleistocene land-bridge islands became isolated 10,000 years ago (*4, 5*). Actually, isolation times have been variable, occurring between approximately 6,000 and 14,000 years ago as the eustatic sea level rose gradually. Therefore, land-bridge islands became isolated from the mainland at different times and should demonstrate a correlation between time since isolation and the degrees of supersaturation of faunas, given that a sufficient number of the island faunas remain supersaturated. Obtaining a quantitative relationship between island age and species number would provide direct evidence for nonequilibrium supersaturated faunas.

I have tested for such a relationship by considering 17 land-bridge islands in the region of Baja California. These islands were chosen because they are upper- or post-Pleistocene land-bridge islands, their lizard faunas are derived from virtually the same mainland pool (*10*), and the lizard species composition of each is known (*6, 11*). Stepwise multiple regression and correlation were used to determine which of several variables, including time since isolation (age), explain a significant amount of variation in lizard species diversity between islands. Lizard species diversity is here defined as $S = (N/P)100$, where N is the number of species on an island and P is the number

Table 1. List of islands and variables. Abbreviations: N, number of species; S, species diversity; A, area; D, distance; E, elevation; L, latitude; T, time of isolation; I_1 and I_2, isolation indices.

Island	N	S	A (km^2)	D (km)	E (m)	L	T (years ago)	I_1	I_2
El Muerto	2	13.3	<1	6	191	30.16	8,300	3,751	938
Encantado Grande	2	13.3	7	6	222	29.91	8,300	3,750	938
Smith	3	20.0	4.5	5	474	29.00	7,700	5,500	1698
Tiburon	12	92.0	1196	2	1218	29.00	6,100	5,046	1670
San Marcos	10	66.0	31.5	4	271	27.25	6,100	3,000	600
Danzante	5	33.0	4.9	1	106	25.75	8,600	5,511	1835
Coronado	9	60.0	8.5	2	283	26.83	5,800	3,888	950
San Ildefonso	3	20.0	2.6	10	118	26.60	9,800	937	59
San Diego	3	20.0	1.3	17	220	25.25	11,400	1,032	69
Las Animas	2	13.0	<1	14	27	25.16	12,000	632	33
San José	11	73.0	194	5	633	25.00	10,600	3,010	602
Espíritu Santo	11	73.0	99	6	595	24.60	6,900	2,500	417
Ballena	4	36.0	<1	6	228	24.60	6,900	1,971	1141
Natividad	2	16.7	7.2	7	150	27.90	8,600	1,841	198
Cedros	7	58.7	348	23	1204	28.16	9,100	639	27
Mejia*	3	37.5	3.5	1	693	28.66	5,800	8,585	8030
San Francisco*	8	72.0	2.6	8	210	24.92	6,100	2,586	471

*Land-bridge islands isolated from larger islands, not the mainland.

Table 2. Correlation matrices. The matrix above the diagonal consists of r values from untransformed variables. The matrix below the diagonal is for r values from log-linear correlations, where the values of the variables on the left have been transformed.

Variable	S	A	D	E	L	T	I_1	I_2
S		.60	−.20	.63	−.24	−.50	.11	.00
A	.77		−.05	.77	.25	−.19	.12	.00
D	−.25	−.15		.12	−.16	.62	−.74	−.48
E	.64	.56	−.08		.28	−.26	.21	.24
L	−.24	.25	−.16	.28		−.25	.44	.30
T	−.52	−.20	.61	−.26	−.21		−.60	−.44
I_1	.21	.11	−.87	.11	.39	−.69		.85
I_2	.20	.08	−.88	.09	.30	−.70	.90	

composing the nearest mainland pool. Thus with S for each island as the dependent variable, the following independent variables were considered, both as linear and log transformed functions: area of the island, A; topographic relief expressed as elevation, E; shortest distance to the mainland, D; latitude at the approximate center of the island, L; and the estimated time since the island became isolated from the mainland, T (*12*). In addition, two isolation indices were considered. For isolation index 1, I_1 was defined as

$$I_1 = \sum_{i=1}^{n} \frac{N_i A_i}{D_i}$$

For isolation index 2, I_2 was defined as

$$I_2 = \sum_{i=1}^{n} \frac{N_i A_i}{D^2_i}$$

where D is the distance to the ith source of potential immigrants (which includes the nearest mainland region and each island within a radius of approximately 50 km), N is the number of species on the ith source and A is the area of the ith source (1000 was used as the value of A for the mainland) (*13*). The data are summarized in Table 1 and the correlation matrices are given in Table 2.

The bivariate correlation between S and each of the independent variables reveals significant correlations ($P < .05$) between S and both simple and log transformed values of A, E, and T. The best regression model resulting from the stepwise analysis is

$$S = 1026 + 20(\log A) - 121(\log T) - 372(\log L)$$

and $r^2 = .91$, $P < .01$. The bivariate correlations for S with area and elevation are similar to those found by Case (*8*) for eight of these same islands.

In general, biogeographic studies have shown species diversity to be correlated with distance. This distance effect is attributable to the lower rate of immigration with increasing distance from the mainland. In my study there is no significant correlation between S and distance (Table 2); this lack of correlation was also observed by Case (*7*). In fact, none of the three isolation or distance variables was significantly correlated with S in either the bivariate correlation or in the stepwise regression analysis. Yet distance is correlated with lizard species diversity for the oceanic islands of the Gulf of California (*6, 7*) and for the California Islands (*14*). Two categories of hypotheses may explain the absence of a distance effect for the islands in my study. First, the rate at which potential immigrants arrive on these islands is too low to affect species diversity in the short time since they have been isolated from the mainland. Second, the rate of arrival of potential immigrants on these islands may be high enough to affect species diversity, but the distance effect is not yet detectable for the following reasons. Almost half of these islands still retain a majority of the mainland species. Hence, the probability is low that a species will arrive that is not already represented. Also, there is a correlation between distance and age, so that the closest islands are also the most recently isolated from the mainland. In turn, these islands tend to have a larger proportion of the mainland species. Immigration is, a priori, not as important as extinction in supersaturated faunas.

The existence of supersaturated land-bridge islands can be demonstrated graphically. The calculation of the residual variation in S for each island, from the regession on area and latitude alone, has the effect of holding these two variables constant. This residual variation in S calculated for each island should be attributable to island age and random error (*15*). Adding the mean value of S over all the islands to each residual value of S (*16*), and plotting these as a function of island age, gives a plot of the corrected species diversity, S^*, as a function of the time since isolation. This plot is given in Fig. 1.

This result is equivalent to a plot of species diversity as a function of time (or, a relaxation curve) for a hypothetical island with mean area and latitude. A linear regression of log transformed values of both variables produces a fitted curve described by the exponential function

$$S^* = 10^6 T^{-1.13}$$

with a correlation coefficient of $-.82$ ($P < .01$). Thus S^* represents a standardized level of species diversity to which each fauna has relaxed up to the present time. The relaxation process has both an immigration and extinction component. Since immigration is not detectable, however, the relaxation curve here is approximately equivalent to an extinction curve. These results are consistent with the hypothesis that these are nonequilibrium supersaturated faunas which are relaxing to states with fewer species.

Recently, Simberloff (*3*) questioned the validity of the equilibrium theory of island biogeography, citing a lack of rigorous proof of species turnover, or evidence that a fauna is approximately balanced, within an ecological time scale (*17*). The demonstration that nonequilibrium biotas behave dynamically in predicted ways is perhaps better evidence for the equilibrium theory than is the existence of biotas in apparent equilibrium. Thus, the equilibrium condition could be considered just one possible state predicted by the theory.

BRUCE A. WILCOX
Department of Biology, University of California, San Diego, La Jolla 92093

References and Notes

1. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, N.J., 1967).
2. For example, applications of the theory have been attempted for diatom communities [R. Patrick, *Proc. Natl. Acad. Sci. U.S.A.* **58**, 1335 (1967)], plant communities [M. P. Johnson and P. R. Raven, *Science* **179**, 893 (1973)], bird communities (*4, 5, 9*), lizard communities (*6, 7*), and conservation [(*8*); J. M. Diamond, *Biol. Conserv.* **7**, 129 (1975)].
3. D. Simberloff, *Science* **194**, 572 (1976).
4. J. M. Diamond, *Proc. Natl. Acad. Sci. U.S.A.* **67**, 1715 (1972).
5. J. Terborgh, *BioScience* **24**, 715 (1974).
6. M. Soulé and A. J. Sloan, *Trans. San Diego Soc. Nat. Hist.* **14**, 137 (1966).
7. T. J. Case, *Ecology* **56**, 3 (1975).
8. D. S. Simberloff and L. G. Abele, *Science* **191**, 285 (1976).
9. I. Abbott and P. R. Grant, *Am. Nat.* **110**, 507 (1976).
10. Constituents of the species pool for the region adjacent to each island were determined with range maps from R. C. Stebbins [*A Field Guide to the Western Reptiles and Amphibians* (Houghton Mifflin, Boston, 1966)]. The pool size was taken as 15 for all but five islands. The exceptions were Tiburon, 13; Cedros and Natividad, 12; San Francisco, 11; and Mejia, 8.
11. J. M. Savage, in *Proceedings of the Symposium on the Biology of the California Islands*, R. N. Philbrick, Ed. (Santa Barbara Botanic Garden, Santa Barbara, 1967), p. 219.
12. The general importance of A, D, and E as biogeographic variables has been established; see (*1*) and T. H. Hamilton, I. Rubinoff, R. H. Barth, Jr., G. L. Bush, *Science* **142**, 1575 (1963). However, L and T are explained as follows. *Latitude*: the islands in this study occur over a latitudinal gradient of more than 5 degrees, with the northernmost extending into a Mediterranean climatic zone and the southernmost into an arid-subtropical zone [J. R. Hastings and R. M. Turner, "Meteorology and climatology of arid regions," *Univ. Ariz. Inst. Atmos. Phys. Tech. Rep. No. 18* (1969)]. Associated with this climatic difference is an increasing structural and taxonomic diversity of the vegetation southward [F. Schreve and I. L. Wiggins, *Vegetation and Flora of the Sonoran Desert* (Stanford Univ. Press, Stanford, Calif., 1964), vols. 1 and 2; J. R. Hastings and R. M. Turner, "Meteorology and climatology of arid regions," *Univ. Ariz. Inst. Atmos. Phys. Tech. Rep. No. 21* (1972)]. The moderating effect of the subtropical climate and the increased structural diversity of the habitats should improve the chances of species coexistence [E. R. Pianka, *Ecology* **48**, 333 (1967)] and thus increase successful colonizations and reduce extinctions. *Age*: an examination of the submarine topography surrounding these islands (Defense Mapping Agency Hydrographic Charts, Nos. 21005, 21008, 21011, and 21014) reveals that each island is now separated from the mainland by a minimum ocean depth that may range from 11 to 93 meters. Since this region has been relatively tectonically stable during postglacial times (G. Gastil, personal communication) it should be possible to estimate the dates of isolation of each island from the mainland on the basis of the rate of post-Wisconsin eustatic sea level rise with time. The general features of the eustatic sea level rise with time have been established by an accumulation of corroborative evidence [F. P. Shepard and J. R. Curray, *Prog. Oceanogr.* **4**, 283 (1967); J. D. Milliman and K. O. Emery, *Science* **162**, 1121 (1968); A. L. Bloom, "Glacial isostatic and eustatic controls of sea level change since the last glaciation," in *The Late Cenozoic Glacial Ages*, K. Turekian, Ed. (Yale Univ. Press, New Haven, Conn., 1971)], p. 355. This evidence suggests an approximate scheme of sea level rise with time as summarized in a plot by Milliman and Emery (cited above). From their curve, I have estimated the dates of isolation for each island by extrapolation from the ocean depth between each island and the mainland.
13. The values 100 and 10,000 were also used for the mainland area. However, similar results were obtained in the correlation analysis regardless of the value used.
14. B. A. Wilcox, in preparation.
15. The residuals were calculated from the regression equation
$$S = 440 + 23(\log A) - 294(\log L)$$
16. This step results in the elimination of negative residuals and allows for log transformation of S^* values.
17. Subsequently, J. M. Diamond and R. M. May [*Science* **197**, 266 (1977)] have shown that existing evidence may be stronger than was previously apparent.
18. I thank M. Soulé for continued help throughout this study and M. Rosenzweig and J. Senner for helpful suggestions. This work was supported by NIH grant 6M 07242, NSF grant DEB 76-18604, and the Theodore Roosevelt Memorial Fund.

22 August 1977; revised 31 October 1977

Directional Selectivity in Hamster Superior Colliculus Is Modified by Strobe-Rearing But Not by Dark-Rearing

Abstract. *Visual response properties of superior collicular neurons of normal hamsters were compared with those of animals reared from birth to adulthood in either total darkness or with stroboscopic illumination. Directional selectivity was markedly reduced only in the strobe-reared animals, thus demonstrating visual plasticity in a system that develops apparently normally without visual experience.*

Since the early 1960's many studies have been concerned with the role of early experience in the functional organization of the brain's visual centers (*1, 2*). Two types of manipulations have been commonly employed: (i) visual deprivation, attained by dark-rearing or eyelid suturing; and (ii) visual restriction, in which the animal's early experience is limited along one or more stimulus dimensions. Most of these studies have dealt with the visual system of the cat, and in this species dramatic effects of visual deprivation, as well as restriction, have been demonstrated in the cortex and, more recently, in the superior colliculus (*3–5*). However, there appear to be important species differences with regard to the degree of plasticity exhibited by the mammalian visual system. Thus, in rabbit, visual restriction during development failed to modify the functional organization of single neurons in visual cortex (*6*). Furthermore, in comparison to the cat, visual deprivation in rabbit results in relatively subtle effects upon the response characteristics of either cortical or superior collicular neurons (*2, 7*).

We now report a demonstration of plasticity in response to environmental restriction in a visual system that develops relatively normally without visual experience. These results were obtained in the golden hamster (*Mesocricetus auratus*), where we have found that dark-rearing produces only subtle changes in the receptive-field properties of superior collicular neurons, whereas rearing in a stroboscopic environment results in dramatic modifications in the functional organization of this midbrain structure. The most clear-cut effect of stroboscopic rearing was on directional selectivity, and this finding is the main focus of this report (*8*).

We used three groups of animals: group 1 included normal hamsters, reared on a 12-hour light/dark cycle ($N = 33$); group 2 included visually deprived animals, raised from birth to adulthood in total darkness ($N = 13$); and group 3 included visually restricted hamsters that were raised from birth to adulthood in an environment illuminated

0036-8075/78/0303-0998$00.50/0 Copyright © 1978 AAAS