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Brown J H. Mammals on mountaintops: nonequilibrium insular biogeography. *Amer. Naturalist* 105:467-78, 1971.
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The small mammals inhabiting forested mountaintops in the Great Basin Desert do not represent an equilibrium between opposing rates of colonization and extinction. The insular faunas have been derived by extinction from more diverse, widespread Pleistocene faunas that colonized when woodlands occurred at low elevations. [The *SCI*® and *SSCI*® indicate that this paper has been cited in over 185 publications.]

Combining Historical and Ecological Biogeography

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Biogeography was always more a scientific hobby than a main theme of my research. In the late 1960s, I taught at the University of California, Los Angeles, and spent the summers studying competition in chipmunks in the mountains of Nevada (in what is now Great Basin National Park). When I read R.H. MacArthur and E.O. Wilson's *The Theory of Island Biogeography*,[1] I realized that I could test the predictions of their model using the distributions of small mammals that inhabit the islands of boreal forests that rise from the sagebrush desert. I found the predicted relationship of number of mammal species with island area but not with any reasonable measure of insular isolation.

I was so convinced by MacArthur and Wilson's logic that I thought that either the data contained errors or I had made a mistake in my analysis. I stopped work on the project and only began again at the urging of my wife. Then I read that P.V. Wells and R. Berger[2] had found late Pleistocene fossils of coniferous trees in the desert hundreds of meters below their current elevational limits. This suggested that mammals might have been isolated on the mountains since the Pleistocene when they had ready access along corridors of suitable habitat. The lack of any detectable effect of current desert barriers and many other aspects of the distributions were consistent with the hypothesis that the boreal mammal faunas have experienced extinctions but virtually no colonizations since their isolation.

Although subsequent work on fossil plants[3] and mammals[4] has corrected some of the details, my general hypothesis has been supported. Discovery of mammal fossils on mountain ranges where those species no longer occur confirms the occurrence of widespread past distributions and subsequent extinctions.[4] Reanalysis of the contemporary distributions supports the important effects of area and extinction and the insignificant role of contemporary isolation and colonization in determining the composition of the mountaintop faunas.[5] This body of work illustrates how historical and ecological perspectives can be integrated to understand the geographic distributions of organisms.

1. **MacArthur R H & Wilson E O.** *The theory of island biogeography*. Princeton, NJ: Princeton University Press, 1967. 203 p. (Cited 1,895 times.) [See also: **Wilson E O.** Citation Classic. Commentary on *The theory of island biogeography*. Princeton, NJ: Princeton University Press, 1967. 203 p. *Current Contents/Agriculture, Biology & Environmental Sciences* 19(36):14, 5 September 1988.]
2. **Wells P V & Berger R.** Late Pleistocene history of coniferous woodland in the Mojave Desert. *Science* 155:1640-7, 1967. (Cited 65 times.)
3. **Wells P V.** Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecol. Monogr.* 53:341-82, 1983. (Cited 25 times.)
4. **Grayson D K.** The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. *J. Mammalogy* 68:359-75, 1987.
5. **Lomolino M V.** Mammalian community structure on islands: the importance of immigration, extinction, and interactive effects. *Biol. J. Linn. Soc.* 28:1-21, 1986. (Cited 5 times.)