

Pianka E R. The structure of lizard communities.

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Lizards partition environmental resources in three major ways: by being active at different times, by spending time in different places, and by eating different foods. These three niche dimensions are not independent, but together they serve to separate most pairs of sympatric species. Intercontinental comparisons of desert-lizard assemblages from three independently evolved systems with differing diversities demonstrate no differences in niche breadth, which is often bimodally distributed among species suggesting a natural dichotomy of generalists and specialists. [The *SC1*\* indicates that this paper has been cited in over 270 publications.]

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This review paper was solicited in 1972 by an editorial committee (I suspect that Gordon Orians was pivotal in offering me this opportunity). I was pleased to receive the invitation since I was nearing completion of a decade of intense fieldwork and data collection that had taken me to three independently evolved desert-lizard systems scattered around the world. The opportunity to write this review spurred me to analyze major patterns in my data quickly, and I was able for the first time to put together a preliminary synthesis.

Earth's most diverse lizard faunas occur in the Great Victoria Desert of Western Australia. As many as 42 different species occur in sympatry there. In contrast, only 6-18 lizard species occur together on comparable sites in the flatland deserts of western North America and in the Kalahari semidesert of southern Africa.<sup>1</sup> Explaining the awesome diversity of Australian desert lizards has consumed me ever since I first discovered these rich saurofaunas in 1966-1968.<sup>2,5</sup> Understanding diversity and community organization is of fundamental interest in community ecology as well as being of substantial practical importance for wise exploitation of both natural and artificial ecosystems. Unfortunately, research at the community level lags far behind that at other levels of biological organization (molecular, cellular, organismal, and population biology). We simply cannot afford to remain so ignorant about the design and operation of ecological systems.

In recent reviews of various factors that promote lizard diversity in Australia,<sup>1,4,6</sup> six major factors have been postulated: 1) usurpation of the ecological roles occupied by other taxa elsewhere, 2) the unique tussock grass life-form of spinnifex (*Triodia*), 3) nocturnality, 4) arboreality, 5) habitat specificity, and

6) soil nutrient limitation. A more elaborate and comprehensive synthetic theory involving infertile soils, unpredictable precipitation and primary productivity, *Triodia*, and termites was recently proposed by S.R. Morton and C.D. James.<sup>6</sup>

Another extremely important and interesting mechanism for the maintenance of habitat heterogeneity and lizard diversity involves disturbance and a complex fire succession cycle.<sup>1</sup> Fires are a predictable event in arid Australia and generate a spatial mosaic of patches of habitat at various stages of post-fire succession. A more or less regular agent of disturbance, bushfires are usually started by lightning and rage completely out of control for weeks on end across many square kilometers of desert.

Fires vary considerably in intensity and extensiveness. *Eucalyptus* trees are fire-resistant and usually survive a hot but brief ground fire carried by the exceedingly flammable *Triodia* grass tussocks. Certain lizard species are arboreal and/or associated with trees. Moreover, fires frequently reticulate, missing an occasional isolated grass tussock or even large tracts embedded in or immediately adjacent to burns. Effects on lizards and lizard microhabitats are drastic, yet exceedingly heterogeneous in space. Many or even most individual lizards may survive such burns, although survivorship is probably drastically reduced for some time afterwards.

Some lizard species with open-habitat requirements repopulate burned areas rapidly, quickly reaching high densities in their "preferred" open habitat. Other lizard species require large spinnifex tussocks for microhabitats, nearly vanishing over extensive open areas following a burn. However, these "climax" species continue to exist in the isolated pockets and patches of unburned habitat. Spinnifex rejuvenates rapidly, probably from live roots as well as by seedling establishment. Newly burned areas are very open with lots of bare ground and tiny, well-spaced clumps of *Triodia*. Unburned patches, in contrast, are composed of large, ancient tussocks, frequently close together with little open space between them. As time progresses, *Triodia* clumps grow and "close in," gradually becoming more and more vulnerable to carrying another fire. Throughout this process, lizard microhabitats (and associated food resources) change. These elements can be exploited to develop a dynamic model of fire succession, incorporating disturbance probabilities, flammabilities, the resulting spatial heterogeneity of microhabitats, as well as species-specific habitat requirements and colonization abilities.

Panglobal comparative ecological studies are badly needed for other taxa, but few researchers are prepared to dedicate the time and effort needed, and funding opportunities are essentially nonexistent. Nevertheless, interest in such work is keen, as reflected by frequent citations.

1. Pianka E R. *Ecology and natural history of desert lizards. Analyses of the ecological niche and community structure.* Princeton, NJ: Princeton University Press, 1986. 208 p.
2. ———. Niche overlap and diffuse competition. *Proc. Nat. Acad. Sci. USA* 71:2141-5, 1974. (Cited 135 times.)
3. ———. Niche relations of desert lizards. (Cody M & Diamond J, eds.) *Ecology and evolution of communities.* Cambridge, MA: Harvard University Press, 1975. p. 292-314.
4. ———. Diversity and adaptive radiations of Australian desert lizards. (Keast A, ed.) *Ecological biogeography in Australia.* The Hague, The Netherlands: Junk, 1981. p. 1375-92.
5. ———. Some intercontinental comparisons of desert lizards. *Nat. Geogr. Res.* 1:490-504, 1985.
6. Morton S R & James C D. The diversity and abundance of lizards in arid Australia: a new hypothesis. *Amer. Naturalist* (In press.)

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