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Schoener T W. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704-26, 1968.
[Biological Laboratories, Harvard University, Cambridge, MA]

The tiny island of South Bimini contains four species of the largely arboreal lizard genus *Anolis*, a number exceeded only on a handful of much larger islands. The species differ remarkably in where they occur in vegetation; in interspecific comparisons, sex-age classes most similar in vegetational habitat are especially dissimilar in sizes of prey consumed. These lizards provide a particularly striking example of niche overdispersion. [The *SCI*® indicates that this paper has been cited in more than 340 publications.]

Overdispersed Niches on a Crowded Island

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In 1966, as a second-year graduate student, I had just completed a project on the lizard *Anolis conspersus*,[1] the sole anoline species of an island in the central Caribbean. These lizards were very abundant and tractable, and I was curious to see how this single-species fauna would compare with what I called the "complex" fauna of four anoline species found in the northern Caribbean. An ideal location for study seemed to be Bimini, as it had a scientific research station, the Lerner Marine Laboratories. J.A. Oliver[2] had written the only paper devoted to Bimini's *Anolis*; it described classical niche differences among the species, with the exception of *angusticeps* which seemingly overlapped a great deal in vegetational microhabitat with two of the others. As the species are fairly similar in size, and Bimini is rather uniform in climatic habitat, this fauna seemed a possible exception to the then-prevailing expectation that no two species would use resources in a very similar way.

Provided with an informal taxonomic key by Ernest Williams, I traveled in late November to Bimini. I quickly discovered that the "island" was in fact an archipelago, that the laboratories were located on the urbanized North Bimini, and that I needed to work on South Bimini where much pristine habitat remained. Fortunately, small boats are readily available at marine laboratories; unfortunately, these could only be used during "working" hours; but fortunately again, lizard schedules during this chilly time of year closely matched those of the laboratory staff.

Several weeks later, I had the resolution of the apparent paradox of too much niche overlap: the four species separated nicely in their primary vegetational microhabitat, being almost Copernican: *carolinensis* was on the outermost leaves and twigs, *angusticeps* was on bare twigs and small branches (contra Oliver[2]), *distichus* was on large branches and upper trunks, and *sagrei* was on lower trunks, the understory, and the ground. Moreover, in interspecific comparisons, sex-age classes similar in vegetational microhabitat were especially dissimilar in prey size, and vice versa. Rather than exceptional, the niches of these top carnivores were highly overdispersed, apparently showing the evolutionary imprint of competition.

Why has the paper been frequently cited? Most ecological *Citation Classics* seem to be theoretical, broadly synthetic, or both; my three previous classics all conform here, whereas the present one does not—it is a highly specific field study. I would like to think its results were irresistibly fascinating to biologists, generating attention and comment from the intriguing new phenomenology. Probably this is in part correct, but I suspect at least three other reasons. First, the paper apparently contained the first usage of the widely adopted term "resource partitioning," connoting how species in a community differ in their resource utilization. Second, the relation between overlap in vegetational microhabitat and nonoverlap in prey size was one of the first (see also M.L. Cody[3]) examples of complementarity of separation along several niche dimensions, later generalized as a kind of principle when interspecific competition is influential.[4] Third, the paper contained the first statement of a particular formula for ecological overlap; this was a simple "percent" measure, and possibly because of its relatively straightforward nature has been in constant use ever since.

In part because of multiple explanations for niche overdispersion phenomena, purely observational studies of resource partitioning have not fared so well recently; we now hasten to perform field experiments to demonstrate underlying processes.[5,6]

1. **Schoener T W.** The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155:474-7, 1967. (Cited 150 times.)
2. **Oliver J A.** The anoline lizards of Bimini, Bahamas. *Amer. Mus. Novitates* 1383:1-36, 1948.
3. **Cody M L.** On the methods of resource division in grassland bird communities. *Amer. Naturalist* 102:107-47, 1968. (Cited 195 times.)
4. **Schoener T W.** Resource partitioning in ecological communities. *Science* 185:27-39, 1974. (Cited 785 times.) [See also: **Schoener T W.** Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 18(44):18, 14 September 1987.]
5. ————. (Kikkawa J & Anderson D J, eds.) *Resource partitioning*. Melbourne, Australia: Blackwell, 1986. p. 91-126.
6. ————. (Cherrett J M, ed.) *The ecological niche*. London: Blackwell, 1989. p. 79-113.

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