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This Week's Citation Classic®

Schoener T W. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 19:189-213, 1965. [Biological Laboratories, Harvard University, Cambridge, MA]

Differences in bill size among species frequently reflect differences in their food resources and are thought to facilitate coexistence. Large bill-size ratios are usually found (1) among specialists on scarce food, (2) on islands, and (3) among large kinds of birds. Faunal buildup is likely to proceed first via food-size and related differences and subsequently via differences in habitat. [The *SCI*® indicates that this paper has been cited in more than 205 publications.]

Why Do Large Size Differences Sometimes Evolve and Sometimes Not?

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This paper, my first publication, originated in a graduate course in biogeography that I took in 1963 while a sophomore at Harvard. The faculty roster was historic: P.J. Darlington, E. Mayr, B. Patterson, G.G. Simpson, E.E. Williams, and E.O. Wilson, among others. Perhaps in compensation for my near speechlessness in these eminent presences, my term paper was very long: The portion resulting in this *Citation Classic?* began as an examination of P.H. Klopfer and R.H. MacArthur's[1] proposal that closely related bird species had greater niche overlap in the tropics than in temperate latitudes, this being reflected in smaller bill-size differences. My own data and arguments suggested that they were wrong about both the claimed manifestation and its theoretical justification. I sent a draft of an intended publication to MacArthur himself, at the time a rather recent PhD of G.E. Hutchinson and the crown prince (or better) of the niche approach to ecology. MacArthur's neatly handwritten replies were always prompt and brief: This one began with the intimidating: "I will give quite blunt criticism in the hope that it will help you...." It continued: "Your criticism of the...paper is surely justified. However, I feel your demonstration leaves even more to be desired than ours." And later: "There is something nobler about a constructive paper than a destructive one.... Why not collect some more critical data...[before publication]." Such comments from arguably the most original thinker in ecology couldn't help but stall my sophomoric rush to publication; the version finally reaching print (during my senior year) had substantially more data as well as more carefully (albeit complexly) presented arguments.

The major empirical findings were that bill-size differences are relatively large among (1) species specializing on relatively scarce food, (2) island species, and (3) species having large individuals. Its crude models related minimal population size to food abundance: The more abundant the food, the smaller the food-size range each species could have, and the less likely that food-size partitioning per se would allow coexistence. Morphological constraints were viewed as restricting generalization with respectto food more than habitat; this would cause faunal buildup to proceed first by partitioning the size and physical properties of food and its immediate environment rather than by partitioning habitat.

Early on, the paper was often cited for its conceptual content. Later, however, with the advent of more sophisticated theory that included actual mechanisms of evolution,[2-3] its theoretical contributions became less emphasized. Its empirical content, and even the raw data (presented in a seven-page double-columned table), were used rather continually, especially once "null model" approaches took hold.[4-5] In the latter, rather than comparing kinds of species or localities with respect to size differences, differences among actually co-occurring species are compared to differences among "randomly" co-occurring species, the latter sometimes calculated from scrambled versions of the former[6] (this procedure has both advantages and disadvantages, as might be imagined). In short, the paper survives today because of the detailed data it contains rather than either the theory or the methodology—take heart empiricists!

1. Klopfer P H & MacArthur R H. On the causes of tropical species diversity: niche overlap. *Amer. Naturalist* 95:223-6, 1961.
2. **Roughgarden J.** Resource partitioning among competing species—a coevolutionary approach. *Theor. Pop. Biol.* 9:388-424. 1976. (Cited 135 times.)
3. **Slatkin M W.** Ecological character displacement. *Ecology* 61:163-77. 1980.
4. Simberloff D & Boecklen W. Santa Rosalia reconsidered. *Evolution* 35:1206-28, 1981. (Cited 125 times.)
5. **Strong D R, Jr., Szyska L A & Simberloff D S**. Tests of community-wide character displacement against null hypotheses. *Evolution* 33:897-913. 1979. (Cited 150 times.)
6. **Schoener T W.** Size differences among sympatric, bird-eating hawks: a worldwide survey. (Strong D R, Simberloff D. Abele L G & Thistle A B, eds.) *Ecological communities: conceptual issues and the evidence.* Princeton. NJ: Princeton University Press, 1984. p. 254-81.
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