

Wilson D S. The adequacy of body size as a niche difference.

Amer. Naturalist 109:769-84, 1975.

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Ecologists frequently invoke differences in body size to explain the coexistence of species. Often, however, large species are competitively superior to small species, and differences in body size do not allow coexistence. This paper incorporates an interesting asymmetry in the resource utilization curves of predators into a theoretical model that reconciles these seemingly discrepant observations. [The *SCI*® indicates that this paper has been cited in over 170 publications.]

Body Size and Species Coexistence

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During the early 1970s, two seemingly contradictory ecological ideas were in vogue. The first was G.E. Hutchinson's idea¹ that species must be different from each other to coexist. Body size was the most common difference that was invoked, and there was even talk of a critical ratio of linear dimensions (1:1.2) required for the coexistence of closely related species. Theoretically, limiting similarity was modeled by assuming a resource that varied along a single axis (such as particle size) and consumer species whose utilization of the resource resembled overlapping bell-shaped curves. Different sizes of animals eat different sizes of food or otherwise utilize different resources, until at some point there is enough nonoverlap to allow coexistence.

The second idea was J.L. Brooks and S.I. Dodson's² "size-efficiency hypothesis," which was advanced to explain the structure of zooplankton communities. They supposed that bigger is better as far as competition for resources is concerned and that small zoo-

plankton are maintained in lakes only by fish predators that remove the large zooplankton.

As an undergraduate student, I was interested in zooplankton and conducted an experiment at Woods Hole that involved feeding algae-sized plastic beads to a marine copepod.³ The ingested beads could be clearly seen through the body wall, which allowed me to measure food size as a function of zooplankton body size. Two years later, as a student in an Organization for Tropical Studies course, I did a little project on ant lions, bizarre and wonderful insects that dig conical pits in the sand to entrap their prey.⁴ The sucked-out carcasses are thrown out of the pit and accumulate along the rim, which once again made it easy to relate the size of the predator to the size of its prey.

Although ant lions and copepods are utterly different creatures, their utilization curves were remarkably similar and revealed an interesting asymmetry. Big consumers could eat bigger food items but the reverse wasn't as true; smaller items were accepted by big and small consumers alike. I didn't have to be a great naturalist to realize that this pattern could be generalized. Furthermore, when symmetrical bell-shaped utilization curves were replaced by asymmetrical curves, a single theoretical model could explain both the limiting similarity idea of Hutchinson and the bigger-is-better idea of Brooks and Dodson, depending on where the consumer utilization curves sat in relation to a prey size-frequency distribution.

I am delighted that this paper became influential, especially because I was so young and naive when I wrote it. Compared to great theorists like MacArthur and great field biologists like Janzen, I felt like a baby trying to stack blocks. But the idea was elementary—therefore fundamental—and that is what counts.

I have not followed the fate of this paper in detail because shortly after writing it, I discovered a seemingly general model of group selection⁵ that has occupied me ever since.⁶ Dare I hope that I might someday write a *Citation Classic* essay on that subject?

1. Hutchinson G E. Homage to Santa Rosalia, or why are there so many kinds of animals? *Amer. Naturalist* 93:145-59, 1959. (Cited 560 times.)
2. Brooks J L & Dodson S I. Predation, body size and the composition of plankton. *Science* 150:28-35, 1965. (Cited 655 times.)
3. Wilson D S. Food size selection among copepods. *Ecology* 54:909-14, 1973. (Cited 85 times.)
4. ———. Prey capture and competition among ant lions. *Biotropica* 6:187-93, 1974. (Cited 20 times.)
5. ———. A theory of group selection. *Proc. Nat. Acad. Sci. USA* 72:143-6, 1975. (Cited 115 times.)
6. Wilson D S & Sober E. Reviving the superorganism. *J. Theor. Biol.* 136:337-56, 1989.