

Brown W L, Jr. & Wilson E O. Character displacement. *Syst. Zool.* 5:49-64, 1956.  
[Museum of Comparative Zoology, Harvard University, Cambridge, MA]

*Character displacement* is the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone. The characters involved in this dual divergence-convergence pattern may be morphological, ecological, behavioral, or physiological. [The SCI® indicates that this paper has been cited in over 255 publications—the most-cited paper for this journal.]

William L. Brown, Jr.  
Department of Entomology  
Cornell University  
Ithaca, NY 14853-0999

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The success of a paper on geographical subspecies<sup>1</sup> by Edward Wilson and me was exhilarating enough to set off a train of what Wilson called *megathought* discussions over a wide range of evolutionary topics. At my urging, he had embarked upon a taxonomic revision of the widespread and common holarctic ant genus *Lasius* as the subject of his doctoral thesis.<sup>2</sup> We discussed the findings daily, and one of the most interesting of these was that certain pairs of species, distinct morphologically and ecologically where they occurred together over wide geographical areas, were in other regions replaced by populations that appeared to be intermediate to or a blend of the same two species. In other cases among plants and animals, such intermediate populations sometimes had been classed as hybrid swarms, and we considered this as a possibility for *Lasius*.

As one example, two common, small, yellow *Lasius*, *L. nearcticus* (shady forest) and *L. flavus* (open or dry woodland, forest borders), are distinct in a number of characters, including palpal segment proportions, antennal scape length, head shape, eye size, and queen size in the eastern US. Western populations, however, are often intermediate between *nearcticus* and *flavus* and show various combinations of these same characters.

A similar case was found in the *L. niger* group, taken on a holarctic basis, and Wilson mentioned two other, possibly parallel examples in the butterfly genus *Karanasa* and the composite plant genus *Ixeris*. About this time, I also came across Charles Vaurie's penetrating analysis of the rock nuthatch

species *Sitta neumayeri* and *S. tephronota*,<sup>3</sup> which differ greatly where their ranges overlap in Iran but are virtually identical outside Iran, where each species occurs alone over wide stretches of the Balkans and Central Asia, respectively.

In 1954 Wilson left for a long collecting tour in Melanesia and Australia, but I kept on looking for evidence of the phenomenon in question, which I now began to call *character displacement*. It didn't take long to discover that this evidence was everywhere in the zoological literature, and I compiled a set of summary case descriptions that were eventually put together in series to form the body of the manuscript for a paper. It turned out that several authors had interpreted particular situations in much the same ways that Wilson and I had, but what was new was the realization that the phenomenon of character displacement was well-nigh universal among animals and was of great theoretical interest in evolutionary and ecological studies.

On Wilson's return in 1955, we wrote a definition (see abstract), which is, of course, a descriptive one. Later redefinitions<sup>4</sup> confuse the phenomenon and its causes. Some commentators also tended to emphasize one or the other of the two likely selective causes we put forward to explain its dynamics: *reinforcement of reproductive isolating mechanisms* and *competitive divergence*. In practice, the two causes are often difficult or impossible to separate; for example, the larger bill of *S. tephronota* and the smaller one of *S. neumayeri* in the zone of sympatry in Iran may serve as a reproductive isolating mechanism as well as divergent specializations in the food-getting tool.

In 1972 P.R. Grant<sup>4</sup> published a paper criticizing (and redefining) the concept. He pointed out, quite rightly, that most of the cited cases were incompletely analyzed and that the proximate causal dynamics of particular situations had not been observed. (In this he overlooked our observations on the interaction of two fire ant species in the Florida panhandle.<sup>5</sup>) It is interesting to note that Grant, early skeptical about the existence of character displacement, is now deeply involved in producing the most detailed evidence for its causality, especially in Darwin's finches in the Galápagos.

One of the potentially most important points made in our paper concerned the so-called *species standard* as applied to allopatric populations. If populations of closely related species are different where they occur together, species occurring apart in isolation do not have to be different.

I was recently brought to realize what a long time has passed since Wilson and I had our excited discussions over noontime coffee when, during a seminar at Cornell, I mentioned a case of double invasion of an island off Australia by a genus of birds. An eager undergraduate sitting across the table patiently explained to me that what I was talking about had a name. "It's character displacement," he said.

1. Wilson E O & Brown W L, Jr. The subspecies concept and its taxonomic application. *Syst. Zool.* 2:97-111, 1953.
2. Wilson E O. A monographic revision of the ant genus *Lasius*. *Bull. Mus. Comp. Zool. Harv.* 113:1-205, 1955.
3. Vaurie C. Adaptive differences between two sympatric species of nuthatches (*Sitta*). (Hörstadius S. ed.) *Proceedings of the Xth International Ornithological Congress. Uppsala, Sweden. 1950.*  
Uppsala: Almqvist and Wiksell, 1951. p. 163-6.
4. Grant P R. Convergent and divergent character displacement. *Biol. J. Linn. Soc.* 4:39-68, 1972. (Cited 120 times.)
5. Wilson E O & Brown W L, Jr. Recent changes in the introduced population of the fire ant *Solenopsis saevissima* (Fr. Smith). *Evolution* 12:211-18, 1958.

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