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100 YEARS AGO IN THE AOU

## 100 Years Ago in the American Ornithologists' Union

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One of the most important papers ever published in *The Auk* appeared in 1917. Joseph Grinnell (Figure 1) presented his extensive observations of the California Thrasher (*Toxostoma redivivum*) and introduced the concept of the niche (Grinnell 1917). How many journal articles are still being cited over 75 times a year 100 years after publication?

Grinnell was not the first person to coin the term *niche*, but he is generally credited with publishing the first paper that codified the concept on the basis of habitat. It and two other works—Sir Charles Elton's (1927) definition of the niche based on food relations and G. Evelyn Hutchinson's (1957) characterization of the niche as a hypervolume—were the basis for niche theory in the last century.

Grinnell was a keen observer of nature and took copious notes on animal behavior and ecology (e.g., Grinnell 1912). He was interested in what restricted birds' ranges and suggested that it would be best to examine the habitat in which a particular bird occurred. He further suggested that as many points as possible within a species' range should be sampled and analyzed to reveal “the elements common to all these points, and of these the ones not in evidence beyond the limits of the bird's range.” Grinnell was way ahead of his time with this kind of thinking, foreshadowing the use of multivariate statistics. For example, if one were to look at habitat variables between species, it would be appropriate to look at the first several components of a principal component analysis because they would represent the maximum sources of variance. However, within a species, one might examine habitat variables associated with the last principal component, those that account for the least amount of variance, or Grinnell's common elements.

To illustrate his point, Grinnell chose to study the California Thrasher (Figure 2), a species that he thought had one of the most restricted ranges in California: the Upper Sonoran division of the Austral zone, better known as chaparral. These divisions and zones had been proposed by C. Hart Merriam (1894), based primarily on temperature. The map of California that accompanied Grinnell's article showed how closely the distribution of the thrasher

matched that of the Upper Sonoran division, but he acknowledged that there may be some circular reasoning, in that Merriam used the thrasher as one of the animals to define the Upper Sonoran division.

To account for the coloration of the three races of California Thrasher, Grinnell chose to emphasize the role of relative humidity: birds were gray in areas with low humidity, slate in areas with moderate humidity, and brown in areas with the highest humidity (often referred to as “Gloger's rule”). There may be some truth to this, based on feather-degrading bacteria being more common in high humidity, necessitating stronger, more heavily pigmented feathers (Burt and Ichida 2004). Nonetheless, coloration is one of the adaptations to living in the chaparral: the color of the birds matched the color of vegetation, allowing them at times to “escape detection altogether.”

Next Grinnell turned to the morphology of the thrasher. The long, curved bill was certainly an issue, but studies had shown the diet of thrashers to be quite varied. Grinnell's observations were that thrashers rarely forage out in the open or above the ground. When they do forage in shrubs, they still remain quite inconspicuous, rarely showing themselves. More commonly they forage on the ground in the open spaces underneath the thick evergreen shrub layer of chaparral vegetation. Under these shrubs, thrashers (as the name implies) use their bill to forage in leaf litter, “whisking” it away from side to side. Thrashers also forage by probing in the ground, such that the areas in which they feed show numerous little pits in the soil. Grinnell concluded that there was nothing in the chaparral habitat per se that would account for the bill morphology. Such a bill might be just as good in a variety of other habitats.

Noting again that California Thrashers spend most of their time under shrubs, Grinnell concluded that locomotion in chaparral was the most important feature of the bird's morphology. Long, strong legs and feet, muscular thighs, a “conspicuously” long tail, and comparatively short wings were all adaptations to living in the chaparral habitat, typically running rather than flying.

In the penultimate paragraph, Grinnell concluded: “These various circumstances, which emphasize depen-



**FIGURE 1.** Joseph Grinnell, in his private office in the original M.V.Z. building, shortly before moving into the Life Sciences Building, March 4, 1930. Photographer: Berkeley Commercial Photo Company. With the permission of The Museum of Vertebrate Zoology, University of California, Berkeley.

dence upon cover, and adaptation in physical structure and temperament thereto, go to demonstrate the nature of the ultimate associational niche occupied by the California Thrasher.” He stated that it is the collection of niches of plants and animals that defines the chaparral, but he referred to the thrasher’s as a “minor niche”—so some niches must be more important than others? Also, he observed that two species cannot have the same niche. He later expanded these ideas, emphasizing the environment’s role in natural selection and the importance of biological interactions (Grinnell 1924, another paper that still gets cited regularly) and reiterating his belief (Grinnell 1927) in the importance of climate and the ecological niche for determining species distributions.

Grinnell also established a system for organizing field notes and survey data (Herman 1986), which almost all researchers at the Museum of Vertebrate Zoology have used over the last century. In another amazing revelation, Grinnell (1910) suggested that his data might be useful maybe a century later. In fact, his field notes were so detailed that researchers were able to reconstruct his surveys 100 years later and document faunal changes. For example, Morgan Tingley and his colleagues (2009) were able to document changes in bird distributions, which they attributed to climate changes, concluding that birds had moved their Grinnellian niche over the course of the century.

Like Grinnell, Hutchinson (1957) emphasized the role of biological interactions, particularly in reducing the fundamental niche of an organism to its realized niche. Hutchinson’s characterization of the niche as an  $n$ -dimensional hypervolume led the way to the use of multivariate statistics, which Frances James, the first



**FIGURE 2.** California Thrasher (*Toxostoma redivivum*). Photo credit: Kevin Cole

woman president of the AOU, introduced to the ornithological world in her analysis of habitat relationships of birds in northwestern Arkansas (James 1971). Considered a “Citation Classic,” in which she coined the term *niche-gestalt*, it has been cited well over 500 times.

Although the Hutchinsonian niche concept has endured (e.g., Holt 2009), there was some criticism of his approach during the 1960s and ’70s, prompting Fran James to reexamine the usefulness of the Grinnellian niche using modern statistical techniques. She and colleagues (James et al. 1984) chose the habitat relationships of the Wood Thrush (*Hylocichla mustelina*) throughout its range in eastern North America, concluding that there were some advantages to the Grinnellian approach over the Hutchinsonian duality of fundamental and realized niches.

Joseph Grinnell (1877–1939) was, of course, one of the leading ornithologists of the first half of the last century. He was instrumental in establishing the Museum of Vertebrate Zoology at the University of California, Berkeley, where he spent most of his career. He was an authority on the birds and mammals of California, and it was said that no one had traveled as extensively within the state as he. Very active in the Cooper Ornithological Society, he joined the AOU in 1894 and was elected a Fellow in 1901 at the age of 24. At the time, he was the youngest Fellow ever elected, a distinction that may still hold true today.

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