

**Cody M L.** On the methods of resource division in grassland bird communities.  
*Amer. Naturalist* 102:107-47, 1968.  
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In grassland bird communities, ecological segregation occurs by dint of species using different habitats, feeding at different heights, or foraging in different ways with  $\pm$  dissimilar morphologies. Although the relative importance of one or another means of segregation differs with vegetation structure, the species at different sites show comparable limiting similarity in resource use. Since these patterns apply to bird communities over a variety of habitats both within and between continents, they provide evidence for convergent evolution and parallel selection, via resource competition, for similar levels of ecological divergence within communities. [The *SC*<sup>®</sup> indicates that this paper has been cited in over 190 publications.]

**Niche Segregation from  
Eijafjordur to Tierra del Fuego**

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I spent my last summer as an undergraduate, 1963, with an Edinburgh University expedition surveying the geology and biota of a bleak peninsula on the north coast of Iceland. There I spent most of my time looking at the habitat preferences and associated differences in foraging behavior of the three passerine birds breeding on the fells above Eijafjordur: snow-bunting, wheatear, and meadow pipit. I still remember how enthusiastically my account of this rather naive study was received that following fall by my new graduate advisor at Penn, Robert MacArthur; thus was my work for the next three years, on resource partitioning in grassland birds, launched.

The *Citation Classic* that describes the dissertation research seems to have several facets that contrib-

ute to its frequent citation: (a) it described three aspects of niche segregation—by habitat, foraging behavior/morphology, and foraging site/height—in purely quantitative terms, and assembled them into a single value of ecological “distance”; (b) it supported the idea that, in grassland bird communities of different species numbers in various habitats, species are similarly limited ecologically by natural selection via competition for limited resources; and (c) that this pattern holds in grasslands occupied by unrelated birds (but comprising morphological, behavioral, and ecological counterparts) on two continents, from Canada to Tierra del Fuego. Further (d) it employed, I believe for the first time, the statistical techniques of discriminant functions to define the birds’ habitat preferences (laboriously worked out by “hand” on an old rotary calculator)!

Many references to the article must stem from the subsequent development of niche theory, its quantification and testing in birds and other taxa; my 1974 book<sup>1</sup> summarizes an extended view of the some years later. There is another reason it is cited, however, and that is as a prime example of a competition-mediated, equilibrium, point of view, to which authors then proceed to offer alternative views or cite contrary data. In fact, ecologists presently are by no means united in their opinions on the extent, consistency, or meaning of ecological segregation in bird (or any other sort of) communities. Current journal editors would insist nowadays that the self-confident assurance of my 1968 paper be tempered considerably, and a wide range of dissenting views would have to be quoted and parried, if not accommodated! Some of this lack of accord is undoubtedly taxon-based, or else results from studies in which community equilibria or resource limitation are precluded by the vagaries of resource supply or by other influences on consumer populations (see, for example, reference 2). Yet even within bird communities there are data suggesting that in certain habitats, at least in certain years, bird consumers are mismatched to their food resources (see, for example, reference 3). I have tried,<sup>4</sup> I hope with some success, to reconcile some of the divergent opinions and conflicting data by reference to year-to-year variations in resource productivity in both breeding and overwintering habitats, but present-day perspectives are still hazy on whether (and which) generalizations are possible and/or useful.

1. Cody M L. *Competition and the structure of bird communities*. Princeton, NJ: Princeton University Press. 1974. 318 p. (Cited 435 times.)
2. Diamond J M & Case T J, eds. *Community ecology*. San Francisco, CA: Harper & Row. 1986. 665 p.
3. Wiens J A & Rotenberry J T. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. *Ecol. Monogr.* 50:287-308, 1980. (Cited 65 times.)
4. Cody M L. Habitat selection in grassland and open-country birds. (Cody M L, ed.) *Habitat selection in birds*. Orlando, FL: Academic Press, 1985. p. 191-226. (Cited 25 times.)