

Lloyd M. 'Mean crowding.' *J. Anim. Ecol.* 36:1-30, 1967.

[Bureau of Animal Population, Department of Zoological Field Studies, Oxford University, England]

This paper proposed \bar{m} , the mean number per individual of other individuals in the same quadrat, as a useful ecological measure of crowding and its ratio to mean density (\bar{m}/m) as a measure of patchiness. It provided large-sample standard errors for both measures. [The *SCI*® indicates that this paper has been cited in over 250 publications since 1967.]

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In 1957 I went to Oxford for a postdoc with Charles Elton, who suggested studying patchy distributions of arthropods in forest litter. One afternoon over tea I remarked that I had found a species of centipede, *Lithobius muticus*, randomly distributed. Elton said, "Do you mean it has no habits at all?"

Teatime conversations were intense. Density dependence—was that really what limited numbers in natural populations? Or was it predation? Or perhaps competition? Having studied cannibalism in *Tribolium* at the University of Chicago with Thomas Park, I was prepared to believe in the importance of crowding. But if animals are really all that crowded in nature, then why are most of them so patchily distributed? Why don't they spread out, get away from each other, and use the habitat more uniformly? Is habitat favorability really so variable from spot to spot on the forest floor as the patchy dis-

tributions of animals would imply, or is there some other explanation?

"Ecologists don't know how to measure habitats," Elton would say. Look closely enough, and every square foot of the forest floor is unique. Most of these differences probably don't matter to the centipedes, but then, what *does* matter to them, and how can one possibly measure whatever this is?

Wandering around Wytham Woods one wet afternoon, I finally had to admit to myself that I would never be able to answer this question. Even so, there is one thing about the habitat that can be measured and is undoubtedly important to the centipedes, namely, the number of other centipedes in their immediate vicinity. If the overall distribution is highly patchy—for whatever reason—then the average individual will encounter others of its own kind more frequently than it would if the distribution were less patchy but had the same mean density. Since variance-to-mean ratio is related to patchiness, perhaps there is some function of mean and variance that measures this thing, viz., the average number of other individuals per quadrat, per individual. That evening I sat down and soon saw that it is simply

$$\bar{m} = m + (\sigma^2/m) - 1.$$

I had no idea how to come up with a standard error for \bar{m} , since it is quadrats, not individuals, that are independent observations. P.H. Leslie came to my rescue. Without his help, I would have had much less to write about.

I suppose this paper has often been cited because it was an early attempt to deal with the fact that natural populations are spatially structured—something that engages the attention of more ecologists now than it did then. The \bar{m} - m plot of Iwao¹ is still, I think, a most elegant means of extracting ecologically meaningful conclusions from quadrat data, especially where other species are not likely to be important.²

1. Iwao S. A new regression method for analyzing the aggregation pattern of animal populations. *Res. Pop. Ecol.* 10:1-20, 1968. (Cited 125 times.)

2. Simon C, Karban R & Lloyd M. Patchiness, density, and aggregative behavior in sympatric allochronic populations of 17-year cicadas. *Ecology* 62:1525-35, 1981.