

**Jolly G M.** Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225-47, 1965. [Agr. Res. Council Unit of Stat., Aberdeen, Scotland, UK]

**An efficient mark-recapture method is given for estimating population size, survival rate, and number of recruits in a natural population subject to both death and recruitment. The estimates are found to be very simple functions of numbers of captures and recaptures. [The SCI<sup>®</sup> indicates that this paper has been cited over 170 times since 1965.]**

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"In 1963, when the ARC unit of statistics was in Aberdeen, I had published<sup>1</sup> a mark-recapture method for estimating the size of a population subject to both death (or permanent emigration) and recruitment. This was a generalization of methods developed by others, but, like theirs, it used certain supposedly simplifying but unrealistic assumptions. I then set out to explore a similar model based on more realistic, fully probabilistic assumptions. Happily, after many pages of algebra, I arrived at a solution to the maximum likelihood equations. As in the earlier model, the key to the solution lay in estimating the number of *marked* animals in the population, but not caught, at a given sampling time, and, not surprisingly, some involved calculation was necessary.

"Next I tried out my solution on the same insect data used to illustrate the 1963 method in which the number of marked was estimated as a weighted mean of recaptures with rather complicated weights. By a stroke of luck, I

noticed that by setting all the weights to unity, the old and new estimates were arithmetically equivalent. This strongly suggested that the new estimate was, after all, a very simple function of numbers recaptured, and, after a few more pages of algebra, this indeed turned out to be true. In effect, all that was necessary to estimate the number of marked in the population not caught at that time was to divide the number of those caught in later samples by the proportion of the number released at that time that were subsequently caught. Estimates of total population, survival rate, and number of recruits for intervals between sampling followed immediately.

"On submitting the 1965 paper for publication I learned from the editor of *Biometrika* that George Seber (a name then unknown to me) had simultaneously submitted a paper<sup>2</sup> containing the same result in a slightly less general form. Also, at the same time as I had been ploughing through my algebra, a lecturer colleague, Richard Cormack, in the Aberdeen University statistics department, had been encountering similar problems in the course of obtaining an efficient estimate of survival for a colony of fulmar petrels.<sup>3</sup> Although we met daily over coffee and occasionally played squash together, neither had thought of discussing current research problems with the other, and we were doubly surprised to find that, with George Seber, all three of us had independently arrived at the same estimate of survival rate!

"The method has come to be known as the Jolly-Seber method and is cited as a standard procedure by biologists using mark-recapture techniques. Its simplicity and intuitive interpretation clearly have an appeal. Theoretically, it has also proved to be a central pivot in the development of biologically more sophisticated models."

1. **Jolly G M.** Estimates of population parameters from multiple recapture data with both death and dilution—deterministic model. *Biometrika* 50:113-28, 1963.
2. **Seber G A F.** A note on the multiple-recapture census. *Biometrika* 52:249-59, 1965.
3. **Cormack R M.** Estimates of survival from the sighting of marked animals. *Biometrika* 51:429-38, 1964.