

Birch L. C. The intrinsic rate of natural increase of an insect population.
J. Anim. Ecol. 17:15-26, 1948.
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This was the first application of the statistic known as the intrinsic rate of natural increase to an insect population, namely, the weevil *Calandra oryzae*. It was calculated from experimental data on the age schedule of births and deaths in controlled environments. [The SCI® indicates that this paper has been cited over 235 times since 1961.]

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January 25, 1982

"During World War II, I had made laboratory measurements on the influence of temperature and moisture on the chance of grain weevils to survive and reproduce. The objective was a practical one of determining the most favourable environments for the storage of huge quantities of grain stockpiled in Australia during the war years. This meant finding the environments least favourable for the multiplication of the insect pests of stored grain. I had tried to put the chance to survive and reproduce into a single index which I called the 'biotic potential.' But I was unaware at the time of a much better measure of the chance to survive and reproduce introduced into human demography by A.J. Lotka in 1924.¹ This was called the intrinsic rate of natural increase. Lotka was employed by a US insurance company in New York and developed this statistic in connection with his actuarial work. But it was quickly taken up by demographers interested in human population growth. Lotka showed how it could be calculated from age schedules of births and deaths obtained from registers of births and deaths. It gives the exponential rate of growth of a population whose death rates

and birth rates are known. Lotka's work was brought to my attention by P.H. Leslie of the Bureau of Animal Population in Oxford. He had recognized the relevance of this statistic for estimating rates of growth of populations of voles which at that time was occupying the attention of ecologists in Oxford. Indeed, Leslie and R.M. Ranson in 1940 estimated the intrinsic rate of increase of the vole, the first estimate for a nonhuman animal.² This was obviously the statistic I needed for my grain weevils, so with Leslie's help I calculated the statistic from data I had on birth rates and death rates of *Calandra oryzae*, the grain weevil. The method used in the calculations provided a means of determining the extent to which the various components, the life table, the fecundity table, and the length of the pre-reproductive states, enter into the value of the intrinsic rate of natural increase. For example, with *C. oryzae* the intrinsic rate of natural increase is determined to a much greater extent by the rate of egg-laying in the first two weeks of life than by the total number of eggs laid in the entire life of 30 weeks. The paper suggested that analyses of this sort may provide a clue to the life patterns characteristic of different species. This latter aspect was reviewed by S.C. Stearns in 1976.³ In the meantime, H.G. Andrewartha and I had incorporated a chapter on the statistic in our book in 1954.⁴ Many ecologists made estimates of the statistic for many different species, first of animals and more recently of plants. With some difficulty I persuaded population geneticists to consider it as one measure of Darwinian fitness, as indeed R.A. Fisher⁵ had done much earlier in a theoretical context. So there is now a wealth of studies on the intrinsic rate of natural increase of animals and plants and microorganisms and on the way in which life-history patterns contribute to the chance to survive and reproduce. I think it can now be regarded as a basic statistic in population ecology and population genetics.

"This paper is highly cited because it is the first application of the statistic 'intrinsic rate of natural increase' to a nonmammal population and it has apparently served as an introduction to the concept for many ecologists and geneticists."

1. Lotka A J. *Elements of physical biology*. Baltimore, MD: Williams & Wilkins, 1924. 460 p.
2. Leslie P H & Ranson R M. The mortality, fertility and rate of natural increase of the vole (*Microtus agrestis*) as observed in the laboratory. *J. Anim. Ecol.* 9:27-52, 1940.
3. Stearns S C. Life-history tactics: a review of the ideas. *Quart. Rev. Biol.* 51:3-47, 1976.
4. Andrewartha H G & Birch L C. *The distribution and abundance of animals*. Chicago: University of Chicago Press, 1954. 782 p.
5. Fisher R A. *The genetical theory of natural selection*. Oxford: Clarendon Press, 1930. 272 p.