

Concepts and Principles of Population Dynamics

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A *population* is a collection of individuals of a single species of organisms spatially or temporally isolated from other such groups. In some cases populations are geographically contiguous but exhibit gradual genetic variation across their range (clinal variation). In a qualitative sense, a population can be considered at various levels of spatial resolution and will exhibit different characteristics in terms of the means and variances of parameters descriptive of its morphology, behavior, biological attributes, and distribution. In comparing two or more populations within a species, such parameters can be used to quantify degrees of difference or similarity. For example, if the thermal optimum for development of *Meloidogyne incognita* (Kofoid and White) Chitwood, is calculated from the mean for samples of the population taken from each state in which it occurs, the mean of all the populations will have a large associated variance. If the mean is determined for the population in a single state, it will probably differ from the national average and have a much smaller variance. Similarly, if the mean is determined for the population in a single field, it will vary from both state and national averages and have a still smaller variance.

Similarly, the spatial characteristics and distributional measures of a population vary with the level of resolution at which they are measured. As the physical size of the sample unit decreases, the perception of aggregation in the population increases. *M. incognita* may appear relatively uniformly distributed across the southern United States. Within a single field, the nematode may appear to have an aggregated distribution with regions of high population density, regions of low population density, and regions of apparent absence of the population. At the level of resolu-

tion of a single plant root system, however, there are clearly islands of high aggregation (multiple females in single galls of the root producing egg masses) and large portions of the root and rhizosphere unoccupied by the nematode. As the physical resolution is defined at a still finer level, the measurement of aggregation may be reversed towards randomness or further to uniformity (for example, distribution of eggs within a single egg mass). This change in perception of aggregation with changing physical resolution is relevant in that it parallels the information on population dynamics of a species obtained by experimental techniques varying in their resolution. In other words, many of the quantitative measures of populations are a function of the magnitude of the system included in, or described by, these measures. For the purpose of this chapter, the boundary of the system under consideration is at the level of the population of a single species. Consequently, all factors within this boundary are considered intrinsic properties of the population. Factors outside the boundary, including food resources, environmental conditions, and other biotic agencies are considered extrinsic to the population and to the system.

The term *population dynamics* is used to convey changes in the numbers, age class distribution, sex ratio, and behavior of a population through time and space, determined by inherent characteristics of the individuals and mediated by environmental conditions, food resources, and interacting biotic agents. Populations have characteristics that are the basis of their dynamics and that are definable and measurable. They exhibit age-specific rates of development, mortality, and reproduction. They migrate into or out of an area at a definable rate. They have a measurable sex and age composition which may or may not be stable,

and which is also determinant of the dynamics of change in the population,

Intrinsic features of populations: Nematodes, like other organisms, have definable life history strategies. These strategies can be defined in terms of the number of life stages, the duration of the life stages, fecundity rates, life expectancy, sex ratios, and functionality of males. They can also be defined in terms of the feeding habits and mode of parasitism in the case of plant parasites. The strategies may be impacted by density-dependent and density-independent factors. Thus, resource limitation may impact the survival of organisms, their reproductive potential and their longevity. Temperature will affect the rates of metabolic processes and consequently duration of life stages and fecundity rates. We categorize organisms in terms of their life history strategy to aid in our understanding of the biology and in the development of concepts of the evolutionary and adaptive significance of these strategies.

Life history strategies may undergo tactical shifts in response to the impact of both density-dependent and density-independent conditions. Such alterations of the general strategies are examples of the plasticity and adaptability of the organism and are factors that promote its survival and success in its environment.

Life history strategies of plant-parasitic nematodes, in terms of their feeding habits and mode of parasitism, range from ectoparasitism through various intermediate categories to sedentary endoparasitism, involving varying levels of sophistication of the relationship between parasite and host. Life history attributes of plant-parasitic nematodes involve an egg stage, four juvenile stages, and male and female adults, although males are frequently rare or may be absent. In many cases, there is indication of a tendency to shortening or elimination of life stages. Thus, the first juvenile stage is frequently passed in the egg and some developmental stages may be relatively short. Tactical shift capabilities in life history strategies in response to resource limitation or adverse density independent conditions include: sex ratio alteration, which impacts the fecundity of the organism and which may promote ge-

netic recombination; parthenogenesis as an adaptation to the parasitic mode; diapause, aestivation, and cryptobiosis as mechanisms of survival of adverse conditions; and special mechanisms including host recognition and width of host range. At the population level, variability among individuals is important. The variability at the genetic level provides the basis for selection and adaptation to environmental change. It mediates and allows the evolution of the organism. Plasticity, in response to environmental shifts can be measured in terms of tactical variation in life history strategies and genetic breadth to provide germplasm adapted to changed conditions.

Interaction with extrinsic regulators: Resource availability is a primary density-dependent regulator of the population dynamics of nematodes and other organisms. The abundance and state of the food source (its physiological activity and health), its distribution in the soil matrix (horizontal and vertical), and its host status to the nematode all impact rates of population change. Resource availability affects and mediates intraspecific and interspecific competition among individuals. The status of the environment in terms of temperature, soil moisture, aeration, pH, salinity or osmotic potential, particle or pore size affect and constrain developmental rates, activity, mortality, and fecundity.

Unifying conceptual theories: Over the last century and a half, theories on the growth and dynamics of populations have been formalized into analytical models. Most such models are based on an adaptation of the logistic growth curve:

$$N_t = \frac{K}{1 + (1 - N_0/K)e^{-rt}}$$

However, most models of population process are more complex versions of these embodied concepts. The familiar derivative form of the logistic equation

$$dN/dt = rN [(K-N)/K]$$

indicates the expected rate of change in the population (dN/dt) at any point in time given the current size of the population (N), the carrying capacity of the environment (K), and the intrinsic rate of increase

of the population (r). The intrinsic rate of increase of the population is the change per individual under conditions of unlimited resources. As such, it is the integral result of births, deaths, immigration, and emigration for the extrinsic environment of the system at low population densities. The logistic equation as a descriptor of population growth was developed independently by Verhulst (11) and Pearl and Reed (9). A logistic model has been widely used for both animal and plant populations and has also been adapted to plant disease epidemiology (10), competition, and predator-prey interactions between two species (4,12).

Long-term discussions in ecology have explored the factors that govern the dynamics of populations. Nicholson and Bailey (8) stressed the importance of density-dependence in population regulation, that is, intraspecific competition for resources as a limitation in the size or growth of the population. In terms of an analytical model, their hypotheses centered around the carrying capacity (K) as a measure of environmental resources (food, space, pollution) and how close the current size of the population is to that carrying capacity. However, there are clearly instances at which the population of an organism is well below the apparent carrying capacity of the environment as determined by availability of resources. In these instances, competitive effects will have relatively small impact. In fact, in any other than microcosm situations, populations are frequently well below the carrying capacity of the environment due to biotic and abiotic factors (predation, parasitism, emigration, adverse conditions resulting in high mortality rates).

The effect of environmental conditions on the net rate of increase of the population (r in the logistic equation modified for current extrinsic conditions) was stressed by Anderwartha and Birch (1), recognizing r as a dynamic variable. Many extrinsic factors are considered density-independent since, at least superficially, they do not appear affected by availability of resources. However, the separation between density-dependence and density-independence is difficult to make since environmental conditions normally considered density-inde-

pendent may in fact be density-dependent if their affect is determined by nutritional status. As an example, if the population is at a high density there may be insufficient shelters or refuges for the organism to escape inclement conditions, or they may be more accessible to predation and parasitism.

The general consensus of current theory is evolving to a recognition of a midground in that density-dependent factors are obviously not always operating or may not be as important, especially at low densities, and density-independent factors are usually, but not exclusively, operating. MacArthur and Wilson (5) descriptively captured these notions by defining organisms as r or K strategists. The population dynamics and fitness of r strategists are largely mediated by the r value in the logistic. In other words, they have characteristics which maximize the net balance of births + immigration - deaths - emigration. On the other hand, K strategists are influenced by intraspecific competition and density-dependent feedback which may result in reductions in fecundity or shifts in sex ratios at high population densities. Those organisms or genotypes with high K values should be successful at high densities. MacArthur and Wilson's (5) characterization of r and K strategists was very useful in promoting understanding of the success of organisms of different life history strategy in various environments. Closer consideration, however, reveals that few organisms are exclusively r strategists or exclusively K strategists. Rather, there is a continuum between r and K strategies and many organisms exhibit features of both ends of the spectrum, probably reflective of their tactical adaptability and success in a wide range of environments. High r and K values are not mutually exclusive; a genotype with both high r and high K will have superior fitness at all densities (2).

The same r and K attributes that confer advantage to specific genotypes within a species also influence community dynamics and interspecific competition. Generalizing, those plant-parasitic nematodes that are successful in annual disturbed agricultural systems have many of the attributes of r strategists (opportunists with high reproductive rates). They

exhibit a wide host range, a potential for rapid population increase to high levels during the crop-growing season, may cause high levels of host damage and usually experience massive mortality during the overwinter period between crops. Plant-parasitic nematode species that are more successful in perennial crops, in comparison, frequently have **K** strategy attributes, including limited host damage at high population densities. Unless they are also *r* strategists, their success may be susceptible to environmental disturbances. These species may have a narrow host range, since opportunistic attributes receive lower selection pressure in the more stable perennial crop situations. However, the **K**-selected attributes for nematodes in perennial crops are less well-known than the *r*-related attributes providing fitness in annual crops, and further testing of hypotheses is necessary.

The complexity of biological systems in terms of heterogeneity in distribution, and variability in age and sex structure, is increasingly recognized. Similarly, the heterogeneity of the environment and its microclimate, as well as the distribution and activity of biological antagonists, is appropriately considered as population theory continues to develop. Den Boer (3) suggested that the heterogeneity present in populations and their habitats tends to stabilize numbers and to reduce chances of global extinction. In predator-prey systems, there is recognition that a local stability in predator-prey densities is unlikely and that heterogeneity in the systems will dictate and allow local extinction at the microcosm level, while maintaining relative stability at a more global level (7). Again, the level of resolution at which the system is examined is important. The effects of extreme conditions in one part of the habitat will be offset by the smaller effects of these conditions in other parts.

The variability in biological systems is expressed through differences in rates of development and rates of response to environmental conditions. Since these differences occur, the status of the environmental conditions (biotic and abiotic) at any point in time are selecting in favor of increased reproduction, survival, or fitness of an individual of particular genetic com-

plement at that point in time. Consequently, gradual or sudden shifts in the environment will select dramatically for some subset of the genotype favored by, or able to survive, these shifts. The study of variability in populations and the impact of selection pressures on various components of the population of given genotype forms the basis of *population genetics*. Here the attempt is made to predict or describe changes in populations through time and in response to varying conditions. This science is mainly concerned with the proportion of the different genes in the population and the attributes which these genes confer to the particular phenotype. Thus, if the rate of increase of the total population is described by: $dN/dt = rN(K-N)/K$. This increase is actually made up of differential increase of various subsets of the genotype:

$$\frac{dN}{dt} = (r_1n_1 + r_2n_2 \dots)(K-N)/K \\ = \bar{r}N(K-N)/K, \text{ where}$$

j is the number of genotype subsets and

$$N = \sum_{i=1}^j n_i, \bar{r} = \sum_{i=1}^j r_i n_i / N.$$

Furthermore, the response of each subset of the genotype to the resource limitation implied in the carrying capacity **K** may differ, so that the equation might be rewritten:

$$\frac{dN}{dt} = r_1n_1(k_1-N)/k_1 + r_2n_2(k_2-N)/k_2 \dots \\ = \bar{r}N(\bar{K}-N)\bar{K}, \text{ where}$$

$$\bar{K} = \sum_{i=1}^j k_i n_i / N.$$

Where the genotype subsets differ markedly, it may be necessary to convert the **N** value in the resource limitation term (i.e., $[k_i-N]/k_i$) into respective n_i equivalents. Consequently, the proportions of various genotypes in the population change as they are differentially selected for by current environmental conditions.

Population genotypic variability and distribution heterogeneity contribute to a complexity in biological systems that is difficult to capture in simple analytical models. Consequently, iterative, repeated calcula-

tion, approaches are used to solve the component equations of the increasingly complex models. The capabilities of high-speed computation have promoted the development of explanatory simulation models, which may employ a large number of equations to describe the various complexities and minutiae of the system. Algorithms have been developed and adopted from other disciplines to allow incorporation and consideration of the variance of population parameter values into "distributed-delay" models (6). Stochastic considerations in simulation models are addressed by incorporating probability functions for various processes and events in the model, and by varying the environmental data sets used to drive the models. Generally, such models are excellent tools for organizing and assessing the current state of knowledge of the biological system. They are a powerful resource for conducting research on the expected behavior of the system for given structures and combinations of state variables, and for given environmental conditions. However, the basic notions and underlying concepts embodied in these models are those expressed simply in the logistic equation. The following chapters will expand on the development and utility of models descriptive of nematode population dynamics and nematode population genetics. In reviewing these chapters,

the reader will benefit by attempting to categorize the information presented in terms of rates of population and genotype change, and affects of environment and resource limitation embodied in the components of the logistic model.

LITERATURE CITED

1. Anderwartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Chicago: University of Chicago Press.
2. Boyce, M. S. 1984. Restitution of r- and K-selection as a model of density-dependent natural selection. *Annual Review of Ecology and Systematics* 15:427-447.
3. Den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18:165-194.
4. Lotka, A. J. 1925. *Elements of physical biology*. Baltimore: Williams and Wilkins.
5. MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
6. Manetsch, T. J. 1976. Time-varying distributed delays and their use in aggregative models of large systems. *IEEE Trans. Systems, Man and Cybernetics* 6:547-553.
7. Murdoch, W. W., J. Chesson, and P. L. Chesson. 1985. Biological control in theory and practice. *American Naturalist* 125:344-366.
8. Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations, Part 1. *Proceedings of the Zoological Society of London* 3:551-598.
9. Pearl, R., and L. J. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proceedings of the National Academy of Science* 6:275-288.
10. Van der Plank, J. E. 1963. *Plant diseases: Epidemics and control*. New York: Academic Press.
11. Verhulst, P. F. 1838. Notice sur la loi que la population poursuit dans son accroissement. *Corresp. Math. Phys.* 10:113-121.
12. Volterra, V. 1931. Variations and fluctuations of the number of individuals in animal species living together. Pp. 409-448 in R. N. Chapman, ed. *Animal ecology*. New York: McGraw Hill.