
REVIEW

Ecological Strategy of Bacteria: Specific Nature of the Problem

E. L. Golovlev

*Skryabin Institute of Biochemistry and Physiology of Microorganisms,
Russian Academy of Sciences, pr. Nauki 5, Pushchino, Moscow oblast, 142290 Russia*

Received April 5, 1999; in final form, February 6, 2001

Abstract—An attempt is made to sum up the results of the many years of using the conception of ecological strategy in bacterial ecology. Taking into account the specificities of microorganisms and their natural selection and the coevolution of microorganisms within evolving microbial communities, an inference is derived that the ecological strategy of most bacteria is the sum of a number of particular canonical strategies, some of which are common to higher organisms. It is proposed to call these particular strategies *ecological tactics*. The author considers this review to be a basis for a discussion.

Key words: ecological strategy, ecological tactic, bacteria, microbial ecology, coevolution, the forms of selection.

THE CONCEPTION OF THE ECOLOGICAL STRATEGY OF LIVING ORGANISMS

It is known that bacteria may respond differently to identical changes in environmental conditions. They can grow rapidly or slowly, produce refractory or lysing cell forms, synthesize storage substances in fresh media or in the late exponential growth phase, utilize growth substrates efficiently or inefficiently, maintain an equilibrium population or give peaks in the population density within certain periods of time, form competitive or uncompetitive cell forms, and so on. The explanation of these different responses by the taxonomic or phylogenetic differences of bacteria makes little biological sense.

In attempts to solve this problem, researchers suggested the conception of ecological or life strategies. The theory of different types of natural selection and their associated ecological strategies has been formulated by phytocenologists and zoologists. The present paper is not intended to review a great body of literature on this topic, as the reader can find relevant information in available reviews and monographs [1–9]; it rather aims at analyzing the application of the conception of ecological strategies to microbiology and at evaluating the degree of its success (or failure), whereas the basic ideas of this conception will be stated only in short.

One of the basic ideas of this theory relies on the Dobzhansky' observation [8] that in diverse biocenoses, such as tropical forest and tundra, natural selection acts in different ways. The effect of a tropical forest on a population depends on the population density. The latter limits the growth of the population because of limited resources. An intense species formation in the forest results from severe competition for the

resources; in this case, selection is aimed at the survival of the species that utilize the resources most efficiently. Steady environmental conditions, which are typical of this habitat, cause a steady population density. Conversely, in the moderate climatic zone, the population dynamics depends on environmental conditions rather than on the population density. High death rates caused by unfavorable conditions, for example, in spring in the middle and subpolar latitudes or in the rainfall period in arid areas, lead to a population that develops under conditions of an excess of resources and a low population density. In such a case, natural selection is aimed at the survival of the fastest-growing species.

These observations have formed the basis for the notions of the so-called *K*-type and *r*-type ecological (or life) strategies. Here, *K* and *r* are the parameters of the logistic population equation, which express the holding capacity of the medium and the reproduction rate, respectively [3, 4, 6].

The conception of the ecological strategy has been invoked, with more or less success, by researchers working in different fields of microbiology since 1971 [10–20]. However, it has found particular application in phytopathology for predicting the propagation of phytopathogenic bacteria, in microbiotechnology for interpreting the transition growth periods of microbial cultures, and in soil microbiology for analyzing the dynamics of soil microbial populations. It should be noted that researchers primarily identify two types of life strategies, *r*-strategy and *K*-strategy, in the microbial world, although as early as in 1975, Whittaker [5] proposed a third type of ecological strategy, the *L*-strategy, which is implemented by the microorganisms (such as spore-forming bacteria) that are well adapted to the adverse environment. To understand the underly-

ing reason, we now turn to the methodology used in the relevant studies.

IDENTIFICATION OF DIFFERENT ECOLOGICAL STRATEGIES

Whittaker proposed a simple method [5] (suffering, however, from serious shortcomings) for the differentiation of *r*-, *K*-, and *L*-strategies, which lies in the evaluation of the size and dynamics of microbial populations. *K*-strategists are characterized by a stable population density close to the holding capacity of the medium. The population density of *L*-strategists is also stable, but it is close to a minimum level below which the population disappears. The population density of *r*-strategists fluctuates between the values typical of the *K*- and *L*-strategists.

Some authors determine the type of ecological strategy based on the characteristics of substrate succession. For instance, the high abundance of a microbial species at the late successional stages is considered to be a sufficient condition for its identification as a *K*-strategist [21, 22]. This approach also evokes objections (see below).

K- and *r*-strategists can also be identified based on their growth rates and the efficiency of resource utilization. In the absence of competitors, *r*-strategists must reproduce more rapidly and utilize resources less efficiently. These characteristics can be easily obtained in terms of the growth kinetics of microorganisms cultivated in a batch or continuous mode. *r*-Strategists are considered to possess the maximum rates of growth and substrate consumption, a high growth rate in response to the appearance of a substrate in the cultivation medium, high maintenance expenses, a low yield of the biomass with respect to the substrate consumed, and a high minimal concentration of the substrate still capable of maintaining the growth of the microorganism. Conversely, *K*-strategists are believed to possess low growth rates and maintenance expenses, a low value of the minimal concentration of the substrate capable of maintaining the growth of the microorganism, a high yield of the biomass, etc. [19, 23–25].

INCONSISTENCIES AND CONTRADICTIONS

From the small amount of research along this line, it became clear that an organism may implement more than one life strategy. For instance, the dandelion accomplishes all three canonical life strategies: *r*-, *K*-, and *L*-. Among microorganisms, the ability to implement several canonical life strategies is even more frequent than among plants. To illustrate this, let us consider the results obtained by Panchishkin *et al.* [21], who attempted to identify *K*-strategists in the temperate climatic zone soils based on the evidence for their dense and equilibrium populations. Environmental conditions in such soils, even in summer, are far from those satisfying the requirements of *K*-strategists. Actu-

ally, the arthrobaeters identified by Panchishkin *et al.* as the *K*-strategists presumably accomplish *L*-strategy, which allows them to maintain a steady level of the population when unfavorable environmental conditions set in. On the other hand, these arthrobaeters cannot be called *L*-strategists, since, according to the definition of Whittaker [5], the *L*-strategy implies a very low population density.

It should be noted that the population density of bacilli in natural environments can be relatively high. For instance, the number of the bacilli in the Kyzylkum sand at a depth of 5 cm is as high as 10^7 cells/g [26], which is uncommon to *K*-strategists. Furthermore, under optimum growth conditions, bacilli may exhibit the values of the growth parameter typical of *r*-strategists. Therefore, it is reasonable to suggest that the bacilli accomplish a mixed type of life strategy with elements of several canonical strategies. Formally, the results of the investigation of the mixed-type life strategy can be presented as datum points in a multidimensional space, which is an intricate task.

In recent years, there has been decreasing interest in studying the life strategies of microorganisms. This can in part be explained by the researchers' endeavor to reveal a pure type of the life strategy, which was not always possible. On the other hand, the discovery that many non-spore-forming bacteria may occur in the so-called viable but nonculturable state (VNS) (for review, see [27]) considerably enlarged the range of the bacteria that, like bacilli, possess a perfect mechanism for maintaining their high population densities under unfavorable conditions and, therefore, are *L*-strategists.

With the discovery of VNS, it became clear that the dynamics of the microbial populations in natural habitats is primarily determined by their ability to survive in unfavorable conditions and not by the proportion between the reproduction and death rates. The time within which bacteria remain viable (i.e., their life span) may be very long (this explains high population densities of bacilli in arid environments [26]). Actually, as compared with the life spans of animals and even plants, bacteria are immortal.

Taking into account the existence of the VNS, the interpretation of seasonal variations in the population density of some bacteria as a manifestation of the *r*-strategy is no longer satisfactory [26]. For instance, the drastic increase in the population of fluorescent pseudomonads in the temperate-zone soils and bodies of waters observed at the beginning of summer is obviously due to the resuscitation of dormant pseudomonads from the VNS and not to their rapid reproduction. It should be noted that routine culture methods allow the actual population (i.e., the number of vegetative, metabolically active cells) and the potential population (the number of spores) of bacilli to be determined, since bacillar spores easily germinate in nutritionally rich media, whereas the resuscitation of dormant bacterial forms from the VNS needs a special resuscitating procedure.

A second reason why the conception of an ecological strategy in microbial ecology is subject to criticism lies in the specific properties of facultative oligotrophs, dissimilators, extremophiles, and extremotolerant bacteria. Analysis showed that the bacteria were identified as *K*-strategists from the fact of their detection in the late stages of substrate succession [20, 22, 23] may actually belong to one of the aforementioned bacterial groups. Generally, the bacterial phenotype of the late succession stage is determined by different factors, such as the adaptation of bacteria to specific substrates that are accumulated in the medium by the end of succession. In particular, arthrobacters and rhodococci that occur at the late stages of succession begin to utilize organic acids and various aromatic compounds produced from the original substrates (plant polymers and easily metabolizable sugars and amino acids). Such adaptation can hardly be called *K*-strategy, since it is independent of the population density. Furthermore, experiments on the long-term starvation of arthrobacters and rhodococci in tap water showed that these microorganisms maintain their populations due to the high viability of vegetative cells under unfavorable conditions. This follows from their tolerance to broad ranges of pH, temperature, oxygen concentration, etc. [26]. General consideration shows that the arthrobacters and rhodococci cannot originate from a relatively stable community due to the action of the *K*-type selection.

Dissimilators, which are adapted to consume dissipated nutrients, can utilize a wide range of specific substrates. Therefore, their phenotypes correspond to ecotypical and phenocenotic patients and not to violators (*K*-strategists), according to the terminology of phytocenologists.

With the accumulation of data on the kinetic parameters of the growth of bacterial populations, it became clear that *r*- and *K*-strategists cannot be differentiated on the basis of their growth parameters. Indeed, the characteristics that had been considered to be typical of *K*-strategists (the high biomass yield, low maintenance expenses, etc.) turned out to be also common to oligotrophs, i.e., patients [26].

Analysis of the data available in the literature shows that the assignment of bacteria to *K*-strategists is not always substantiated to a sufficient degree. I do not mean such stable habitats as humid tropical forests or equatorial bodies of water, whose conditions are evidently propitious to *K*-strategists. I mean certain niches in the temperate climatic zone, where bacterial populations may depend on their density and the time of existence of these niches, allow for *K*-selection. These are primarily the plant phylloplane [28], rhizoplane, and rhizosphere [29]. Of interest is the fact that the rhizosphere fluorescent pseudomonads have the characteristics of *K*-strategists [29].

In the temperate climatic zone, the conditions that favor *K*-selection exist only during warm seasons. Therefore, like *L*-strategists, *K*-strategists must survive

unfavorable conditions during cold seasons and then, like *r*-strategists, must rapidly reproduce and colonize the leaf surface. Pseudomonads, which implement *r*-strategy when grown in optimum media, can occur in the VNS (a marker of *L*-strategy), and presumably accomplish *K*-strategy when grown in the phyllo- and rhizoplane, are a good example of bacteria with a mixed-type ecological strategy.

Therefore, the ecological strategy of the *L*-type may be one of the important mechanisms responsible for the regulation of the population of many (or even most) bacteria in nature. The formation of spores and the existence of VNS are unambiguous markers of the *L*-strategy. However, the bacteria that do not form spores and cannot transit to the VNS can also be *L*-strategists. It is unclear whether or not the last variant of the *L*-strategy includes some elements of the other strategic types, as in bacilli and pseudomonads. Rhodococci and, to a lesser degree, arthrobacters are slow-growing bacteria [26]. Under conditions close to natural (a flow-through system with pond water high in nitrogen and phosphorus and low in carbon), *Rhodococcus erythropolis* and *Arthrobacter globiformis* were found to grow at a rate of 0.008–0.016 h⁻¹. Such a slow growth rate can explain the relatively small increase in the population of these bacteria in ponds in June as compared with their populations in March–April (a 3- to 4-fold increase in the case of rhodococci and a 5- to 7-fold increase in the case of arthrobacters). These data suggest (but do not prove) that at least rhodococci may be pure *L*-strategists.

Thus, most of the bacteria discussed above probably accomplish the mixed-type ecological strategy. This fact, however, adds little to the understanding and classification of their life strategies in nature.

THE PARADOXES OF SPECIALIZED AND STRUCTURIZED COMMUNITIES

A search for *K*-strategists inevitably leads to the analysis of microbial communities, consortia, and structurized populations such as biofilms. Methanogenic and photosynthesizing consortia, cyanobacterial mats, and the dental plaque microflora exhibit a highly stable composition over long periods of time.

Of great interest is the dental plaque, since its habitat is characterized by very stable environmental conditions, its composition is fairly constant, and the process of plaque formation takes a long time. Investigations showed that the microbial compositions of the dental plaques of the mature inhabitants of New Guinea and New England (the United States) are almost the same (although diets in these countries greatly differ) and that the process of plaque formation takes 16–18 years [30].

It has been recognized that the high stability and integrity of the dental plaque microflora is due to the so-called intergeneric coaggregation, rather than due to nutritional relations between the component bacteria [31–34]. The coaggregation of the rod-shaped cells of

actinomycetes (*Actinomyces* or *Bacterionema*) with streptococci gives rise to specific structures reminiscent of corn cobs. Coaggregation was also observed between the morphologically similar cells of *Streptococcus sanguis* or *S. mitis* and *Haemophilus* sp., *Capnocytophaga* and actinomycetes, *Bacteroides* and other bacteria [31–33].

The bacterial diversity of the dental plaque, the stability of the microbial composition of its core, and the presence of endemic genera and species could be considered as an indication of the long-term *K*-selection. However, it should be taken into account that the stability of the dental plaque community is due to the coaggregation of cells and not to their competition for substrates. This contradicts the basic principles of *K*-strategy and suggests that the plaque-forming microflora accomplishes a new type of life strategy unknown for higher organisms. It is possible that the dental plaque resulted from the evolution of the entire heterogeneous dental microflora due to the action of a severe stabilizing selection. With such type of selection, any mutation leading to a deviation from the normal phenotype impairs the fitness of an organism to the environment [35]. In the case of the dental plaque, the stabilizing selection acts to conserve the composition of the plaque core. This is explained by the fact that, due to the coaggregation mechanism, any deviation from the normal phenotype or any change in the composition of the dental microflora results in a decrease in its fitness. Therefore, the stabilizing selection causes a coevolution of all species of the dental plaque. In this case, the component species may undergo *r*-, *K*-, and *L*-selections.

The dental plaque is by no means a unique microbial community. However, the communities that are dominated by metabiotic, rather than structural, relations may possess some of its specific properties. For instance, the bacterium *Acetohalobium arabaticum* of a methanogenic halophilic community acquired the ability to assimilate glycine betaine (an osmoprotectant synthesized by other bacteria of the community) in the process of the evolution of the entire community [36].

BACTERIAL ECOLOGY AND EVOLUTION ARE SEEKING THEIR SELF-IDENTITY

It is evident that bacteria evolve under the action of more numerous factors than higher organisms do. Caldwell *et al.*, who published a paper under the intriguing title “Do Bacterial Communities Transcend Darwinism?” [37], were perhaps correct when they formulated the hypothesis of proliferation as a propellant of bacterial evolution, instead of the theory of natural selection. Like this theory, the hypothesis implies that an organism may reproduce faster and more efficiently as a result of a mutation and/or a genetic recombination. However, as Caldwell *et al.* write, “... autoreplicating macromolecules may proliferate more efficiently if they are associated and reproduce in a prokaryotic cell (for instance, by means of membrane formation);

prokaryotic cells sometimes proliferate more efficiently if they are associated and reproduce in an eukaryotic organism (by means of symbiosis or simple attachment); both prokaryotic and eukaryotic organisms sometimes proliferate more efficiently if they are associated and reproduce as communities (by means of behavioral adaptation) ...” [37].

In my opinion, the foregoing proves that the conception of ecological strategy proposed for higher organisms is inapplicable to bacteria. Certainly, different bacteria may respond in different ways to the same changes in the environment and, hence, a particular bacterium may adhere to a particular ecological (or life) strategy. However, the life strategy of bacteria is almost always the sum of diverse elementary behavioral reactions, some of which may coincide with the canonical life strategies described above. For instance, pseudomonads may exhibit not only the behaviors described as *L*-strategy (transition to the VNS), *r*-strategy (rapid growth under optimum conditions), and *K*-strategy (high *a* in the rhizo- and phylloplane) but also the behaviors that have not yet been classified (such as the formation of biofilms and the alternation of the life phases of the free-living state, biofilm, and VNS). Sometimes, these elemental life strategies are difficult to differentiate. For instance, the growing vegetative *Escherichia coli* cells may follow either *r*- or *K*-strategy, depending on the cultivation conditions [11, 38].

Various bacterial responses and behavioral reactions can and should be classified not in terms of ecological strategies but in terms of ecological tactics [26]. The ecological strategy of a particular bacterium is a combination of various ecological tactics. The number of such combinations may be so great that the classification of bacterial life strategies will be difficult.

Thus, the application of the ecological paradigms formulated for higher organisms to bacterial ecology and evolution may lead to misinterpretations and fallacies. Bacterial ecology and evolution are currently at the very beginning of their way to self-identity.

ACKNOWLEDGMENTS

This work was supported by the Russian Foundation for Basic Research (project no. 98-04-49393) and by the AC2-2000-10006 grant.

REFERENCES

1. Ramenskii, L.G., Introduction to the Complex Pedological and Geobotanical Analysis of Soils, *Izbrannye trudy* (Selected Works), Leningrad: Nauka, 1938, 1971, pp. 231–232.
2. Grime, J.P., *Plant Strategies and Vegetation Processes*, Chichester: Wiley and Sons, 1979.
3. MacArthur, R.H. and Wilson, E.O., *The Theory of Island Biogeography*, Princeton (New Jersey): Princeton Univ. Press, 1967.
4. Pianka, E.R., On *r*- and *K*-Selection, *Am. Nat.*, 1970, vol. 104, pp. 593–597.

5. Whittaker, R.H., *Communities and Ecosystems*. Translated under the title *Soobshchestva i ekosistemy*, Moscow: Progress, 1980.
6. Pianka, E.R., *Evolutionary Ecology*, New York: Harper and Row, 1978. Translated under the title *Evolutsionnaya ekologiya*, Moscow: Mir, 1981.
7. Mirkin, B.M., *Chto takoe rastitel'noe soobshchestvo* (What Is the Plant Community), Moscow: Nauka, 1986.
8. Dobzhansky, T., Evolution in the Tropics, *Am. Sci.*, 1950, vol. 38, pp. 209–221.
9. Southwood, T.R.E., The Relevance of Population Dynamic Theory to Pest Status, *Origins of Pest, Parasite, Disease, and Weed Problems*, Cherret, J.M. and Sagar, G.R., Eds., Oxford: Blackwell Sci. Publ., 1975, pp. 35–54.
10. Koch, A.L., The Adaptive Responses of *Escherichia coli* to a Feast and Famine Existence, *Adv. Microbiol. Physiol.*, 1971, vol. 6, pp. 147–217.
11. Koch, A.L., How Bacteria Face Depression, Recession, and Derepression, *Persp. Biol. Med.*, 1976, vol. 20, pp. 44–63.
12. Kogut, M., Are There Strategies of Microbial Adaptation to Extreme Environment?, *Trends Biochem. Sci.*, 1980, vol. 5, pp. 15–18.
13. Kogut, M., Microbial Strategies of Adaptability, *Trends Biochem. Sci.*, 1980, vol. 5, pp. 47–50.
14. Dykhuizen, D. and Davies, M., An Experimental Model: Bacterial Specialists and Generalists Competing in Chemostat, *Ecology*, 1980, vol. 61, pp. 1213–1227.
15. Gerson, U. and Chet, J., Are Allochthonous and Autochthonous Soil Microorganisms *r*- and *K*-Selected?, *Rev. Ecol. Biol. Soil*, 1981, vol. 18, pp. 285–289.
16. Velikanov, L.L. and Sidorova, I.I., Some Biochemical Aspects of Fungal Ecology, *Usp. Mikrobiol.*, 1983, vol. 18, pp. 112–132.
17. Andrews, J.H., Relevance of *r*- and *K*-Theory to the Ecology of Plant Pathogens, *Current Perspective in Microbial Ecology*, Klug, M.J. and Reddy, C.A., Eds., Washington: Am. Soc. Microbiol., 1984, pp. 1–7.
18. Andrews, J.H., Life History Strategies of Plant Parasites, *Adv. Plant Pathol.*, 1984, vol. 2, pp. 106–130.
19. Andrews, J.H. and Harris, R.F., *r*- and *K*-Selection and Microbial Ecology, *Adv. Microb. Ecol.*, 1986, vol. 9, pp. 99–146.
20. Kozhevnikov, P.A. *Mikrobnnye populyatsii v prirode* (Microbial Populations in Nature), Moscow: Mosk. Gos. Univ., 1989.
21. Panchishkina, M.B., Kozhevnikov, P.A., and Zvyagintsev, D.G., The Types of Bacterial Population Dynamics in Soils, *Mikrobiologiya*, 1988, vol. 57, pp. 476–480.
22. Zvyagintsev, D.G., Kozhevnikov, P.A., Kochkina, G.A., and Polyanskaya, L.M., Microbial Succession in Soil and Determination of the Ecological Strategies of Particular Populations, *Mikrobiologiya*, 1981, vol. 50, pp. 353–359.
23. Gorbenko, A.Yu. and Panikov, N.S., Quantitative Description of the Growth Dynamics of Heterotrophic Microorganisms in Soil with Reference to Production Processes in Biogeocenoses, *Zh. Obshch. Biol.*, 1989, vol. 50, pp. 38–59.
24. Dorofeev, A.G., Bondarenko, T.F., Zvyagintsev, D.G., and Panikov, N.S., Growth Kinetics of Microorganisms with Different Ecological Strategies in a Dialysis Culture at Low Specific Growth Rates, *Mikrobiologiya*, 1984, vol. 53, pp. 271–274.
25. Dorofeev, A.G. and Panikov, N.S., Growth Efficiencies of Microorganisms with Different Ecological Strategies in Continuous Cultures, *Mikrobiologiya*, 1988, vol. 57, pp. 606–614.
26. Golovlev, E.L., *Biology of Saprotrophic Bacteria, Doctoral (Biol.) Dissertation*, Pushchino, 1983.
27. Golovlev, E.L., An Alternative State of Asporogeneous Bacteria, *Mikrobiologiya*, 1998, vol. 67, pp. 725–735.
28. *Microbial Ecology of Leaves*, Andrews, J.H. and Hirano, S.S., Eds., New York: Springer, 1991.
29. Chiarini, L. and Tabacchioni, S., and Bevirino, A., Interactions between Rhizosphere Microorganisms under Iron Limitation, *Arch. Microbiol.*, 1993, vol. 160, pp. 68–73.
30. Bowden, G.H.W., Ellwood, D.C., and Hamilton, I.R., Microbial Ecology of the Oral Cavity, *Adv. Microb. Ecol.*, 1979, vol. 3, pp. 135–217.
31. Kollenbrander, P.E. and Andersen, R.N., Multigeneric Aggregation among Oral Bacteria: A Network of Independent Cell-to-Cell Interactions, *J. Bacteriol.*, 1986, vol. 168, pp. 851–859.
32. Kollenbrander, P.E., Intergeneric Coaggregation among Human Oral Bacteria and Ecology of Dental Plaque, *Annu. Rev. Microbiol.*, 1988, vol. 42, pp. 627–656.
33. Kollenbrander, P.E. and London, J., Ecological Significance of Coaggregation among Oral Bacteria, *Adv. Microb. Ecol.*, 1992, vol. 12, pp. 183–218.
34. Gibbons, R.J. and Nygaard, M., Synthesis of Insoluble Dextran and Its Significance in the Formation of Gelatinous Deposits by Plaque-forming Streptococci, *Arch. Oral Biol.*, 1986, vol. 13, pp. 1249–1262.
35. Schmalhausen, I.I., *Faktory evolyutsii* (Factors of Evolution), Moscow: Nauka, 1986.
36. Zhilina, T.N., Halophilic Methanogenic Microbial Community, *Doctoral (Biol.) Dissertation*, Moscow, 1992.
37. Caldwell, D.E., Wolfaardt, G.M., Korber, D.R., and Lawrence, J.R., Do Bacterial Communities Transcend Darwinism?, *Adv. Microb. Ecol.*, 1997, vol. 15, pp. 105–191.
38. Luckinbill, L.S., *r*- and *K*-Selection in Experimental Population of *Escherichia coli*, *Science*, 1978, vol. 202, pp. 1201–1203.