

Pianka E R. On *r* and *K* selection. *Amer. Naturalist* 104:592-7, 1970.
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Natural selection in saturated environments (where demand for resources approximates supply) is density dependent, favoring competitive ability at the expense of slow growth and delayed reproduction. In contrast, in competitive vacuums (resource supplies greatly exceed demand), selection is independent of population density and favors rapid growth, early reproduction, and short life spans. Concepts of *r* and *K* selection are clarified and their correlates listed. [The *SCIS* indicates that this paper has been cited over 170 times since 1970.]

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"Although the terms *r* and *K* selection were coined in 1967,¹ the concepts date back considerably farther. The idea is simply that natural selection favors a different suite of adaptations when there is a surfeit of resources than when resources are in short supply. The former circumstance usually occurs in changing environments where selection favors rapid growth and early reproduction at the expense of competitive ability. Whereas in the latter sort of saturated environment, competitive ability is at a premium even if the trade-off of slower growth and delayed reproduction is necessitated. Because populations subjected to the first set of forces boom and bust, they are called 'opportunistic' populations in contrast to the more stable 'equilibrium' populations that occur in more constant environments.

"During 1968-69, I found these simplifying concepts to be most useful in teaching elementary population biology at Texas—as I gradually interwove them into my course I developed

the table of correlates eventually published in my 1970 letter to the editor. But when bright students like Ann Langley asked me for references for further reading on the subject, I found myself at an impasse—virtually nothing existed. This prompted me to write the note, after trying out my ideas on graduate students and in seminars.

"In the note I briefly reviewed the history of use of the concepts, and attempted to clarify them, recognizing that they did not constitute a true dichotomy but rather merely represented endpoints of a spectrum (for this I coined the term the '*r*-*K* selection continuum'). In addition to listing the correlates of *r* and *K* selection, I extended the notions to comparisons between populations and emphasized that an individual or a population's position on the *r*-*K* continuum was always changing. I argued that terrestrial organisms are somewhat polarized in their positions along this continuum noting that most insects and annual plants are relatively *r*-selected whereas the majority of vertebrates and perennials are comparatively more *K*-selected. I speculated on the possible importance of the threshold of annuality in generating this apparent natural dichotomy. The table of correlates and one figure have been incorporated into several textbooks and the entire paper has recently been reprinted in a collection of readings.²

"As the jargon caught on, other workers used the terms and applied them to numerous specific circumstances and organisms, citing my note for documentation. More recently, the paper has begun to be cited as often as not by adversaries who consider the concepts dangerously oversimplified (also, the terms have been taken too literally and the concepts have sometimes been misunderstood and misused). It is surprising to me how many people think of *r* and *K* selection as 'new' concepts!"

1. MacArthur R H & Wilson E O. *The theory of island biogeography*. Princeton, NJ: Princeton Univ. Press, 1967. 203 p.

2. Pianka E R. On *r* and *K* selection. *Readings in sociobiology*. (Clutton-Brock T H & Harvey P H, eds.). San Francisco, CA: Freeman, 1978. p. 45-51.