Revisiting r- and K-Selection:
Why this classic theory no longer fits modern ecology

-Shivam Shrotriya

Few would dispute the influence Eric R. Pianka (1939-2022) left on evolutionary and theoretical ecology. He was a renowned American biologist known for his seminal work on lizards. His most significant works include niche measurement, niche overlap and competition, and r- and K-selection in life-history evolution. On Pianka's death (12th September 2022), we held a Friday Forum discussion at the Wildlife Institute of India hostel, commemorating his great work developing these now-ubiquitous ecological concepts. The r- and K-selection model (Pianka 1970) was one of the topics discussed, and it was astonishing to see how most of the participants knew the theory and understood its core ideas well but didn't quite grasp why the theory is considered an outdated concept in modern literature on life-history research.

I reckon that most of us do not delve into literature beyond our core research field and accept the concepts learnt in our ecology classes as foundational without raising questions. Pianka himself introduced the concept of r- and K-selection in the ecology curriculum through his book Evolutionary Ecology, first published in 1974, which is considered a classic. Many of the ecology textbooks to date not only include a section on the r- and K-selection but also give a sense that it is a time-tested and well-accepted theoretical concept. Years back, during my general readings, I read an excellent blog post by Dr Jeremy Fox on how r- and K-selection is a zombie idea in ecology (Fox, 2011), which sparked more reading into this topic. In this article, I'm giving a short overview of what the r/K selection theory entails and why it makes little sense to interpret life histories in light of the modern understanding of evolutionary ecology.

The r- and K-selection explains why some animals have lots of babies while others have only a few.

The basic idea revolves around the selection of life histories as strategies towards either maximising breeding productivity or maximising breeding efficiency by increasing the survival potential of the offspring. The species that are thought to follow r-selection, or maximise reproduction, produce a large number of offspring during breeding. Most of these offspring die young, but the breeding numbers ensure that enough individuals survive to keep the species going and transfer the parental genes to the next generation. The young ones grow fast and start reproducing early in life. Such species are supposed to have evolved in unpredictable climates or where environmental conditions fluctuate a lot, and population size is far from reaching the carrying capacity of their environment. Examples of r-selected species could be insects, frogs, fishes and invasive plants. On the other hand, the species that are thought to follow K-selection reproduce less frequently, have fewer babies, and invest their time and energy in raising and protecting their young ones. The individuals in these species grow slowly and take longer to mature and reproduce. These species are supposed to have evolved in stable environments where food and space limited the population size, or in other words, the population dynamics is operating at the carrying capacity.
Although there is a higher competition for resources in these populations, the individual survival probability is higher, particularly at a young age. Some of the examples of K-selected species could be elephants, wolves, whales and us, the humans.

On the surface, the theory of r- and K-selection appears to make perfect sense, classifying all the species into r- or K-selected based on their reproduction strategy. It even logically follows further, seemingly predicting the population growth stage and physiology of the species based on the reproduction rates

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Why it is then that the r- and K-selection is considered an outdated and zombie idea? Reznick *et al*., (2002), reviewing r- and K-selection theory, quoted Stearns (1992) in the opening: *"This explanation was suggestive and influential but incorrect."*

The purpose of a scientific theory is not only to explain the existing patterns but also to predict about the subject based on knowledge of connected information. As the interest in life history research gained momentum following Pianka's work, researchers soon realised that the theory was failing to meet its predictions. Empirical and experimental studies repeatedly found that the populations of the same species evolving under different densities still showed selection for similar life history. On the other hand, at times, populations of different species with similar densities and resource availability grew apart in their life history strategies (see examples in Reznick *et al.,* 2002; Mallet 2012).

What were the main reasons behind this monumental failure? To start with, the model offers an overly simplistic model of life history evolution as the outcome of a single selective pressure- density dependence. But the world is not so simple. For example, the model does not involve predation, a real parameter that can affect the life histories. In addition to density-dependent selection, populations may face other types of selection pressures, such as frequency-dependent selection.

A frequency-dependent selection is when the success of a life history trait, as being a prolific breeder or having a few young ones, depends on how common or rare it is in the population. For example, in a fish species where most individuals spawn many eggs, predators might be feasting on these eggs, leaving only a few survivors. A few individuals in this population may increase their reproductive fitness by investing in spawning fewer eggs and hiding them better.

Simplicity and failure to account for additional parameters are not the only reasons. There lies a conceptual flaw in the model itself. To understand this, we need to learn a bit of history of how Pianka came up with the r- and K-selection ideas. Everyone who studies basic population ecology knows the logistic growth model of population.

The original logistic model was developed by Verhulst (1938) as a contrast to exponential growth, explaining self-limiting growth in biological populations. And almost all the textbooks represent this model mathematically as:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

Where, r represents the intrinsic rate of population increase when the population density is very low, N is the initial population size, and K is the population size at equilibrium where addition and subtraction rates in the population are equal. The model is a mathematical statement saying that the population growth at an early stage, when density is low and resources are practically unlimited, would be as close to the intrinsic growth rate. As individuals start adding, the competition for resources rises and begins to play its role in limiting population growth, and the graph of growth takes an S-shape.Later works by Pearl, attempting to estimate the cap on the human population (Pearl 1930), Gause, conducting experimental studies on the growth of microorganism populations (Gause 1934), and Odum's 1953 book Fundamentals of Ecology steered to the K - the upper asymptote of S-shape curve - being generally perceived as carrying capacity or saturation level of the population growth (in Mallet 2012).

The concept of r and K selection has its origin in the famous island biogeography theory (MacArthur and Wilson 1967). In their envisioned island under the first colonisation and having unlimited resources, MacArthur and Wilson thought that in the absence of competition during early colonisation, the selection would favour the individuals that could breed more and utilise the resources. When the population grows close to the carrying capacity and intensifies competition, selection would favour the individuals that remain in the population for longer over multiple reproductive cycles. MacArthur and Wilson termed these density-dependent pressures and r- and K-selection processes, standing for higher reproduction and carrying capacity. Pianka extended this concept to the evolution of life histories, stating that species evolving under r-selection end up having r-selected strategy and vice versa. The life history evolution was seen as a trade-off between r and K (Figure 1); as the population grows larger and closes on K, growth can no longer be sustained. A major problem piece here is K, a parameter that looks real but is near to impossible to measure for real-world populations. The resources fluctuate, the environments change, and the populations could evolve more complex mechanisms to deal with the rising densities. For example, the carrying capacity of a lake with a fish species could come down immediately if waters are exposed to toxins. Such a stochastic event might also reduce r along with K, making predictions even more complicated. This linear relationship between r and K hides another parameter in plain sight, the slope of line-α, measuring per-capita strength of intraspecific competition, or density-dependence. It is a parameter often ignored in the classes on r- and K-selection. The line in Figure 1 can be drawn if we know any two parameters, r and K or α. Suppose we happen to pick the second way of representation, are species no longer K-selected and instead become α-selected where selection for steeper slope would mean a higher density dependence

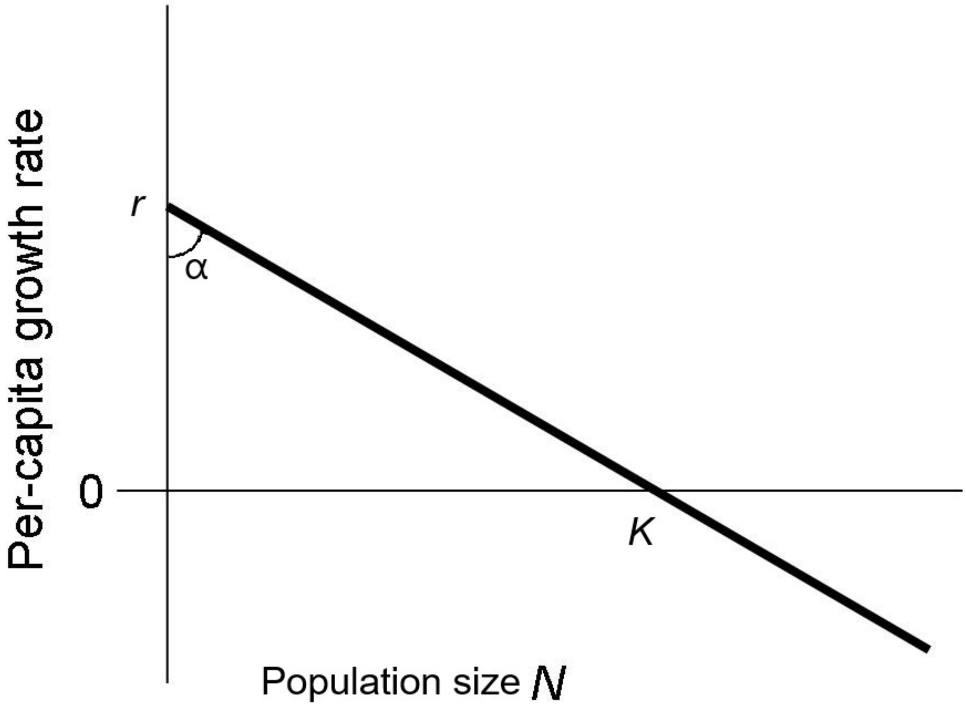

Figure 1.
The density-dependent population growth can be represented as a linear relationship between r — the growth rate — and K — the carrying capacity *(Modified from Fox, 2011).*

(or higher intra-specific competition effect) and would bring down the population equilibrium at lower density? Experimental studies show that populations evolving under low and high densities show differences in competitive ability but not in life-history strategies (see Reznick *et al*., 2002). Measuring α in empirical studies is more accessible than K, and it makes better predictions about the resource limitations remaining within the density-dependent growth model and density-dependent regulations on growth via intra-specific competition. You may also notice that in the r and α model, no trade-off is required between r and K.

The use of the logistic model with r and K as estimation parameters also falls prey to interesting mathematical paradoxes, for example, Levin's paradox (Kuno 1991; see more in Mallot 2012). It is quite possible in real world scenario where the initial population size N is higher than the carrying capacity K. Let's take example where a deer population now has to live within only half of the area previously available to them due to submergence of part of the landscape, making N at this stage already crossing new K. The intrinsic growth rate may also turn negative; reproductive capacity could decline following a change in favourable climatic conditions. An intuitive prediction would be that this population is depleting and heading towards a possible extinction. But if you put a negative r and an N larger than the K into the logistic growth equation, what you get is population growing to infinity. Try it out yourself!

A model of r- and α-selection might overcome many of the problems caused by r- and K-selection for population growth studies. However, it is still insufficient when studying the evolution of life history strategies. The r- and α-selection model remains a different version of the logistic equation:

$$\frac{dN}{dt} = rN - \alpha N^2$$

where, α is connected with K via $\alpha = r/K$. The logistic equation might hold better for some populations near equilibrium, but it is unrealistic for most cases beyond lab-grown populations of microorganisms. It ignores the effects of separate sexes having different life histories, populations with discrete generations, or time delays in the response to density, effects of dominance and heterosis on mating systems, or group-living advantages. In rare instances, density-dependence could take a counter-intuitive shape; for example, populations at very low densities tend to decline further due to a failure in enough mating opportunities, also known as the Allee effect (Asmussen 1979).

Reznick *et al*.,(2002) concluded that "by focusing on a continuum of density dependence and dichotomizing suites of life-history traits, the r—K paradigm brought a lot of excitement to the empirical study of life histories. As empirical studies progressed, it became clear that the predictions of r- and K-selection were not always upheld and that the underlying assumptions (density regulation) were not easily evaluated. This dose of reality helped the field develop a more rigorous theory." The main alternative to study life histories is demographic theory or age-structured mortality models (Stearns 1992). Different age groups in a population may express mortality under density-dependent or independent selection pressures. Resource limitation might affect juvenile survival more, and predation might be pressuring the adult population. The increased adult mortality would favour early maturing and higher reproductive effort, while increased juvenile mortality would favour delayed maturity and decreased reproductive effort.

The purpose of this article is to educate the students and draw the attention of educators that r- and K-selection theory, as developed by MacArthur and Wilson and later expanded by Pianka, was a wonderful theory with no real application in actual populations. The textbooks and classes still keep teaching it as one of the core ideas in ecology, and that must be changed. The r- and K-selection could be taught for its historical relevance, yet the students must learn the current and more appropriate theories.

Key references:

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